

*Magellanic Penguins *Spheniscus magellanicus* commuting through San Julian Bay; do current trends induce tidal tactics?*

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The behaviour of Magellanic Penguins *Spheniscus magellanicus* commuting between their foraging areas and breeding areas in San Julian Bay, Argentina was studied to examine whether tidal rip currents affected travelling patterns. Although there was no apparent relationship between departure and arrival patterns and the state of the tidal cycle, birds travelling against the current dived for longer periods and had shorter rests on the surface than birds travelling with the current. In addition, birds swimming against the current hugged the banks of tidal rivers much more closely than did birds swimming with the current, thus reducing the magnitude of the current against which they had to swim. In cases of extremely high current speeds, birds travelling upstream walked. Models regarding the energetics of movement indicate that the strategies adopted by Magellanic Penguins can result in substantial energy savings.

tidal currents and examine the potential benefits that any modified behaviour might have.

Materials and methods

Most field work was carried out between 6 and 15 December 1999 on Magellanic Penguins breeding on Isla Cormoran (67°43'W, 49°17'S) (Fig. 1) and foraging for chicks. In addition, however, some work conducted on birds foraging for chicks at Puerto Deseado (65°53'W, 47°45'S) and at Isla Cormoran during December 1997, conducted for another purpose, has also been briefly included here for purposes of comparison.

There is extensive documentation to demonstrate that volant birds should alter many aspects of their flight patterns according to a number of intrinsic and extrinsic factors (see e.g. Hedenström and Ålerstam 1995, Pennycuik 1997) such as wind direction and strength (e.g. Ålerstam and Hedenström 1998, Liechti et al. 2000). Not all birds fly as their main mode of travel, however, and penguins presumably have to deal with analogous conditions when swimming underwater. In this respect, birds living in areas with rip currents derived from enclosed bays in areas with a substantial tidal range are most likely to be affected and therefore most likely to show deviations in standard behaviour patterns related to movement.

We investigated the commuting behaviour of Magellanic Penguins *Spheniscus magellanicus* breeding on islands within San Julian Bay, Argentina. These birds generally forage outside the bay although their colonies are located between 4 and 6 km from the open sea (Fig. 1). We aimed to determine the extent to which commuting behaviour might be modified by

Timing of foraging according to tidal cycles

In order to determine whether penguins might modify the timing of their foraging trips according to tide, patterns of departure and arrival at the colonies, the number of birds moving past two fixed points on the beach separated from each by a distance of ca. 50 m, was counted over set intervals. The total number of birds moving towards and away from the sea was nominally noted for 10 min every hour between 05:30 and 21:30 hours between 9 and 14 December, complete 24 h watches being precluded by darkness. However, these counts were also stopped for short periods where man-induced disturbance (such as visitors to the island) occurred. In addition, on a number of days, the total number of birds arriving or departing was noted continuously at 10 min intervals for periods of up to several hours around the time of low tide. Although at absolute low tide there is a brief period of slack water, the shape of the sandbanks within the San Julian Bay leads to particularly strong currents around the time of

low tide where current changes in direction are also most extreme.

Patterns of movement according to current

We observed the manner in which commuting birds travelled according to the current conditions to which they were exposed. We noted conditions under which birds actually walked rather than swam. In addition, we noted the dive and surface durations of penguins swimming with and against the current, separating birds further into those leaving and returning to the colony since it is known that diving patterns in some penguins are dependent on this (e.g. Siegfried et al. 1975). In order to assess better details of diving behaviour in commuting birds, six adult penguins brooding chicks were equipped with Lotek time depth recorder tags

(DST 100, Lotek Marine Technologies, St John's, Newfoundland, Canada) to determine patterns of dive duration in relation to surface duration. The units, which measured 18 mm in diameter \times 56 mm long, were set to record depth (resolution better than 0.3 m) continuously at 1 s intervals in a 1.5 Mb memory. Information was downloaded via interface directly onto a computer on site. Devices were taped to feathers on the birds' lower backs (see Wilson et al. 1997).

When the tide was almost low, the outgoing water took the form of a river, with clearly defined banks made of mud and clay. We noted the position the birds adopted in the body of moving water with respect to the banks and as a function of whether birds were swimming against or with the current. Specifically, we recorded whether the penguins swam within 2 m of the bank or further out in the body of water where the current was stronger. We made these observations both

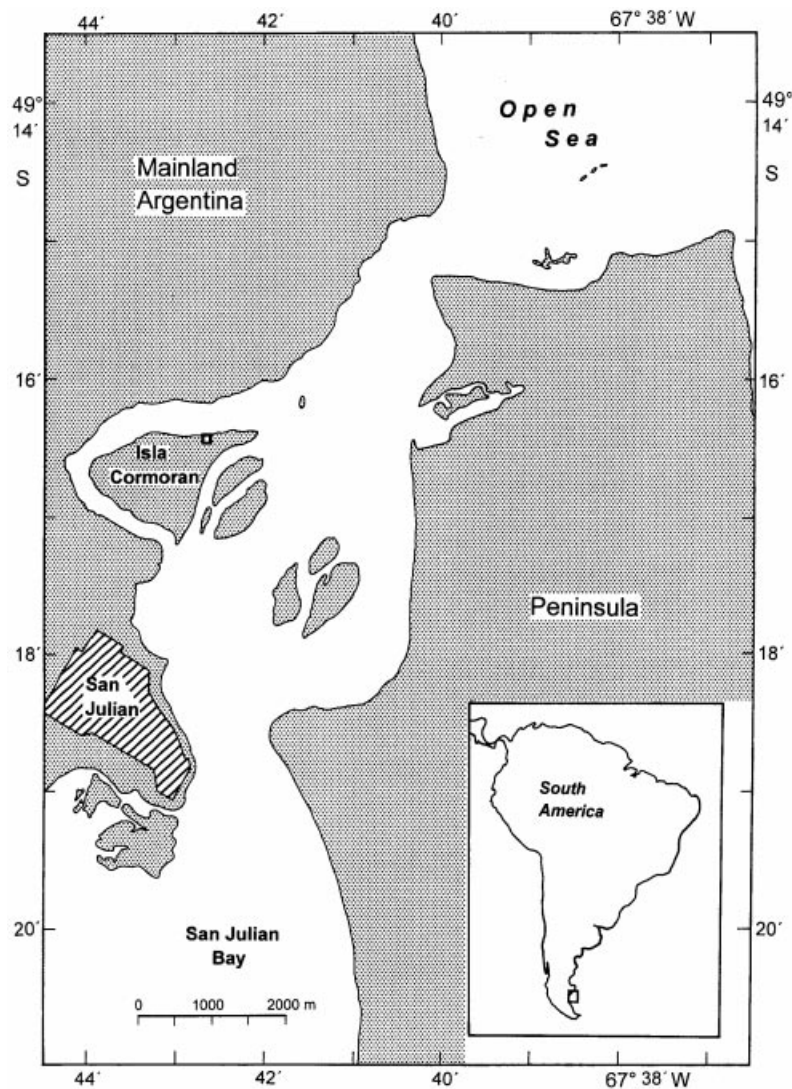


Fig. 1. Map of the study area showing the penguin breeding islands and their relation to the San Julian Bay.

for stretches where the water ran in a straight line and where it meandered. In the latter case, we also noted whether birds within 2 m of the bank were on the inside or outside edge of the curve making up the meander.

Current strength

It was clear during the study that current strength was highly variable according to tidal cycle. In order to get some estimation of the strength of the current we manufactured a primitive current gauge by sticking one end of a plastic strip to a wire support, itself stuck perpendicular to a wooden slat. Immersion of the wooden slat in the water to a certain depth, with the smallest surface area of the slat facing current flow caused the plastic strip to bend back. The degree to which the plastic strip bent was read off on the wood as an angle, the scale having been previously drawn on the wood. The unit was calibrated for current strength by pulling the measuring system across a pool at defined speeds and noting the bend angle of the plastic strip as a function of each speed.

Swim speeds of Magellanic Penguins

During December 1997, four Magellanic Penguins at Puerto Deseado and 12 birds at Isla Cormoran were equipped with multiple channel loggers (Dklog 600, Driesen and Kern GmbH, Am Hasselt 25, Bad Bramstedt, Germany) by fixing the units with tape to the birds' lower backs as described in Wilson et al. (1997). The units had maximum dimensions of $122 \times 74 \times 24$ mm, weighed 120 g, and were equipped with a 2 Mb memory and 16 bit resolution. Among other things, these devices sensed swim speed with a differential pressure sensor accurate, after calibration on a life sized model of a Magellanic Penguin, to within 0.1 m/s. Units were left in place for the course of at least one foraging trip before they were removed and the data downloaded to computer.

Results

Timing of foraging according to tidal cycles

Magellanic Penguins breeding at Isla Cormoran tended to leave the island in the early morning, with most birds departing for the sea before mid-day, and returning to the island in the evening. Large numbers arrived right up to the time of our last possible watch at 21:30 hours (Fig. 2) although appreciable numbers of birds did return to the colony before mid-day. There was no evidence that the departures and influx of birds were influenced by the tides, either over a scale of hours or when counts were conducted continuously (Fig. 2).

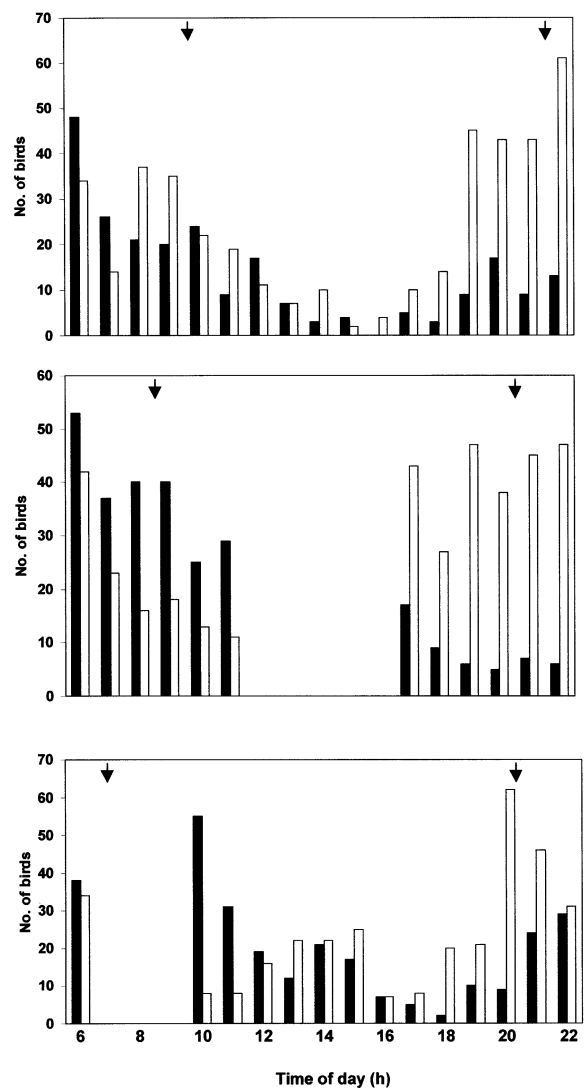


Fig. 2. Patterns of departure (black bars) and arrival (empty bars) of Magellanic Penguins breeding at Isla Cormoran, San Julian as a function of time of day for three typical days during the study period (top: 10 Dec; middle 11 Dec; and bottom: 12 Dec). Arrows show the time of low tide when tidal current conditions were most extreme. Absence of bars denotes time intervals during which no counts were made due to disturbance.

Patterns of movement according to current

Penguins changed movement patterns according to the strength of the current. Penguins commuting between the island and their foraging areas did so by swimming stretches just underwater inter-spaced with periods where they rested at the surface (Fig. 3). However, birds spent longer underwater and relatively less time at the surface with increasingly unfavourable current conditions (Figs 3 and 4). This general observation was modified according to whether the birds were returning to the colony or departing to sea to forage so that, for example, birds

leaving and swimming with the current were underwater between pauses for significantly longer than those returning with the current ($\bar{x} = 22.4$ s, SD 7.5, $N = 20$ and $\bar{x} = 15.7$ s, SD 9.2, $N = 43$, respectively; $t = 2.84$, $P < 0.05$) although the surface pauses were not significantly different ($\bar{x} = 7.8$ s, SD 4.0, $N = 19$ and $\bar{x} = 5.9$ s, SD 4.4, $N = 37$, respectively; $t = 1.83$, $P > 0.05$). Similarly, birds returning against the current were underwater for significantly longer than birds leaving against the current ($\bar{x} = 26.2$ s, SD 8.3, $N = 33$ and $\bar{x} = 19.4$ s, SD 9.5, $N = 31$, respectively, $t = 3.05$, $P < 0.05$) although in this case surface pauses were also significantly different ($\bar{x} = 3.5$ s, SD 3.0, $N = 57$ and $\bar{x} = 2.4$ s, SD 1.6, $N = 39$, respectively, $t = 2.09$, $P < 0.05$). In one particular stretch, where the current was particularly strong, the observed patterns were even more apparent, with birds leaving with the current remaining submerged for a mean of only 6.8 s (SD 4.0, $N = 26$) and resting on the surface, drifting with the current for a mean of 27.1 s (SD 13.4, $N = 10$). All birds returning against this particular stretch of water walked.

When the tidal movements had reduced the water to the form of a river, penguins appeared able to

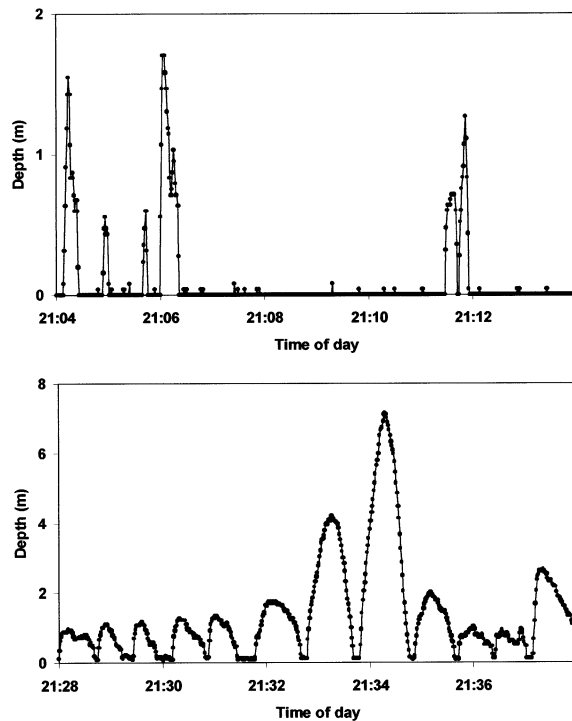


Fig. 3. Examples of dive profiles during the first 10 min for Magellanic Penguins leaving the colony travelling with the current (top trace) and leaving the colony travelling against the current (bottom trace) for birds breeding at Isla Cormoran within the San Julian Bay. Both individuals were travelling within an hour of low tide when current conditions were most extreme.

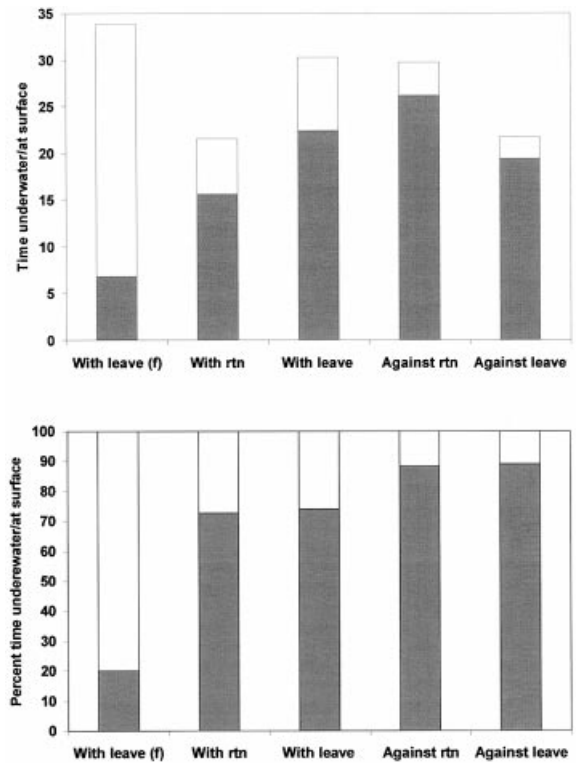


Fig. 4. Mean durations spent underwater (shaded bars) and at the surface (empty bars) for Magellanic Penguins commuting in San Julian Bay according to whether the birds were swimming with, or against, the current and whether they were leaving from, or returning to (rtn), the colony. The upper figure shows absolute values (s) and the lower the percentage times. The left hand bar marked 'with leave (f)' shows the case of birds leaving the colony swimming with the current in a particularly narrow stretch of water where current speeds were exceptionally high.

select the specific part of the river in which they swam so as to minimize costs. Thus, birds in straight sections of the river swimming with the current (either departing or returning) swam more often in the middle where the current was strongest (see below) than expected by chance ($\chi^2 = 57.3$, $P < 0.05$) while birds swimming against the current swam more often within 2 m of the bank than expected by chance ($\chi^2 = 12.5$, $P < 0.05$) (Table 1). This behaviour was also reflected in penguins swimming against the current through meandering sections. Here, the number of birds swimming on the inside edge of a curve (60 (72%)) was significantly higher than the number of birds swimming on the outside edge (18 (22%)) ($\chi^2 = 55.9$, $P < 0.05$) and very few birds actually swam in the middle except to change from one side to another (Fig. 5a). Birds swimming with the current in meandering sections either swam in the middle (77%) or on the inside edge (23%) and were never observed to swim on the outside edge (Table 1).

One particular stretch of the tidal river created an extensive loop of ca. 650 m, deviating substantially from the straight line distance (ca. 175 m) taking the penguins to and from the colony (Fig. 5b). We noted that while the current was against the direction of travel 56 bird groups (group size 1–6 birds) swam round the loop (24%) while 174 groups (group size 1–29 birds) (76%) walked the shorter distance over-land ($\chi^2 = 60.5$, $P < 0.05$).

Current strength

Measurements made with the current metre showed that current strength was highly variable, but typically increased with increasing distance from the bank (Fig. 6). Our measures are only crude estimates, however, since current strength was also likely to be a function of water depth, which also tended to increase with increasing distance from the bank.

Penguin swim speeds

All penguins equipped with loggers normally swam at speeds between 1 and 3 m/s. However, in all birds, abrupt and short peaks were apparent at various times during the foraging trip which are likely due to prey capture. In addition to this, and excluding these peaks, some birds travelled at rather specific speeds for most, or all, of the foraging trip (Fig. 7a) while others used a variety of different speeds, with a tendency to adhere to a specific speed for a particular length of time before changing to another (Fig. 7b).

Table 1. Proportions of Magellanic Penguin groups swimming in tidal currents, reducing the sea to the form of a river, in the middle of the body of water (>2 m from the bank) and at the edge of the body of water (<2 m from the bank and inside or outside edge where relevant) as a function of whether the birds were travelling with or against the current and whether birds were swimming in S-bends or in straight sections. Since there are no inside or outside edges on straight sections, the 'outside edge' refers to all birds travelling close to the edge.

	Outside edge % (N)	Inside edge % (N)	Middle % (N)
Against the current			
S-bends	6 (5)	72 (60)	22 (18)
With the current			
S-bends	0 (0)	23 (12)	77 (41)
Against the current			
Straight section	26 (81)	–	6 (9)
With the current			
Straight section	0 (0)	–	100 (54)

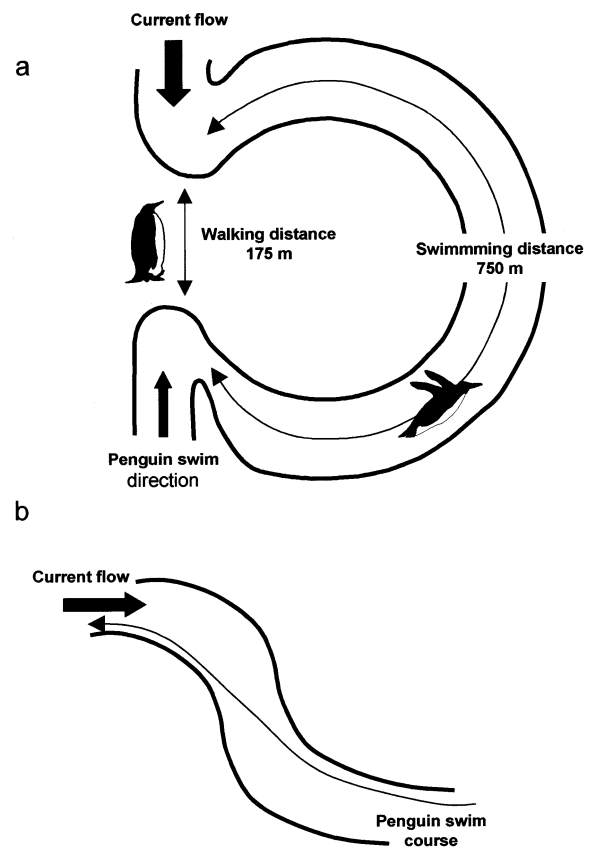


Fig. 5. Schematic diagram of the routes taken by Magellanic Penguins commuting within San Julian Bay (a) in a situation where the birds could either swim a loop against the current or walk directly across it (see text). (b) shows the path typically taken by penguins swimming against the current in a meandering section of the river. Fat arrows indicate current flow.

Discussion

Our observations indicate that Magellanic Penguins breeding within San Julian Bay modify their commuting behaviour substantially according to immediate perceived current conditions by minimizing the time

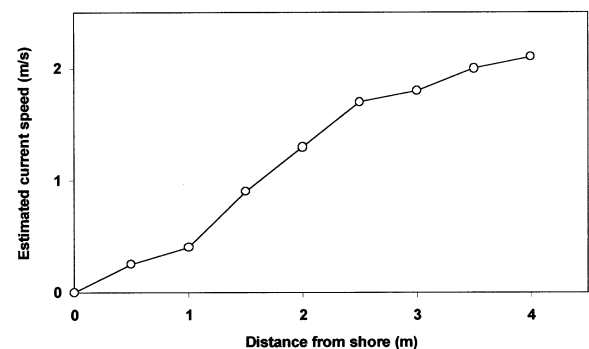


Fig. 6. Current strength in a typical stretch of the tidal river at San Julian Bay as a function of distance from the bank.

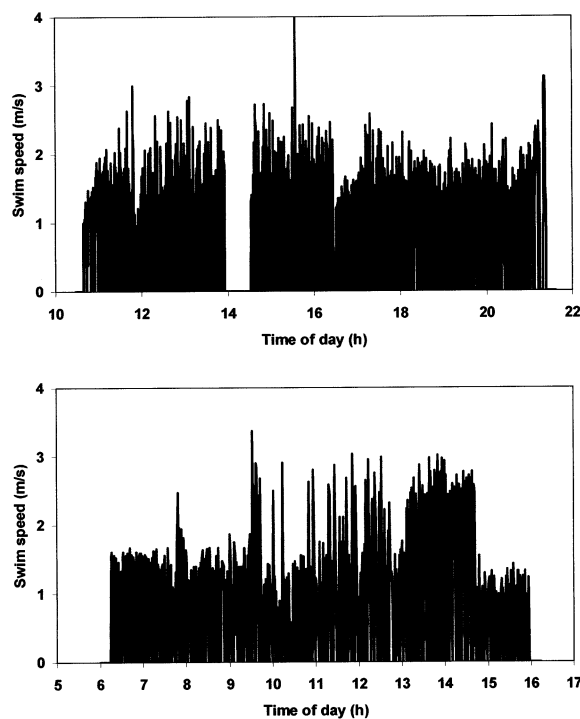


Fig. 7. Swim speeds of Magellanic Penguins over the course of single foraging trips showing (upper trace) fairly constant swim speeds over the whole trip (apart from occasional peaks assumed to be due to prey pursuit) and (lower trace) different speed ranges adhered to at different times during the foraging trip. The data in the upper trace come from a bird equipped at Puerto Deseado, an area without the extensive tidal rips found in the San Julian Bay region, while the data in the lower trace come from a bird equipped at Isla Cormoran.

spent swimming against the strongest currents and maximizing the time spent swimming with currents flowing in their preferred direction of travel by swimming in the centre or at the edge of tidal rivers accordingly. Furthermore, birds swimming against the current in meandering tidal rivers tend to minimize both the distance travelled and the time spent swimming in stronger currents by swimming near to the bank on the inner corners. Many individuals apparently saved time and/or energy by walking under certain conditions. The advantages of walking a short cut rather than swimming may be quantified for the situation depicted in Fig. 5 by comparing the effective energetic cost of swimming 650 m against the current with that of walking 175 m.

If we assume that Magellanic Penguins at San Julian walk at 0.73 m/s (Wilson et al. 1999) and that this corresponds to an energy expenditure of 16 J/s/kg (data derived from Pinshow et al. (1977) for Adélie Penguins *Pygoscelis adeliae* (mass 3.8–6.0 kg (Williams 1995) walking at this speed), then a Magellanic Penguin with a mean mass of 4.1 kg (Scolaro et al. 1983, Gandini et al. 1992, unpubl. data) expends $16 \times 4.1 = 65.6$ J/s to

walk at this speed. Birds walking 175 m will therefore take $175/0.73 = 240$ s and expend $240 \times 65.6 \approx 15750$ J.

Estimating swimming cost is more complex. Although costs are likely to be dependent to some extent on swim depth because costs of swimming near the surface are usually greater due to surface gravitational waves (Stephenson et al. 1989), we consider here simplistically that Magellanic Penguins have the same energy expenditure when swimming (both paddling at the surface and swimming underwater) as congeneric Humboldt Penguins *Spheniscus humboldti*. Thus, birds expend 11.1 J/s/kg at normal travelling speeds (Luna Jorquera 1996) or $11.1 \times 4.1 = 44.5$ J/s/bird. Normal speeds for Magellanic Penguins underwater are of the order of 2.1 m/s and are considered to be fairly invariant (Wilson et al. 1995). We assume this to be the case here, irrespective of current conditions. We also assume that the travelling speed of birds paddling at the surface is similar to that of African Penguins *Spheniscus demersus* at ca. 0.3 m/s (Wilson 1985, unpubl. data). Thus, the ground speeds of birds swimming underwater and at the surface against the current are $(2.1 - \phi)$ and $(0.3 - \phi)$, respectively, where ϕ is the current speed (m/s). The overall speed, however, is given by the amount of time that birds spend underwater compared to that at the surface. In the case of birds returning to the colony against the current, the dive pause ratio is 26.2 to 3.5 s (Fig. 4) so that the overall speed (m/s) is

$$S = (26.2/(26.2 + 3.5))(2.1 - \phi) + (3.5/(26.2 + 3.5))(0.3 - \phi) \quad (1)$$

This simplifies to

$$S = 0.88(2.1 - \phi) + 0.12(0.3 - \phi) \quad (2)$$

The time taken to complete the distance of 650 m = $650/S$ and the total energy expenditure for the distance is $44.5(650/S)$ J. Assuming that the birds swim generally at 1 m from the bank, where the current speed is ca. 0.3 m/s, then swimming birds expend approximately 18260 J which is some 16% more than those that walk, a good enough reason to explain why the majority of birds do not swim the stretch under consideration (cf. Hedenström 1993).

Cost of transport as a function of current speed

This situation can be extended to cover conditions where the tidal river does not meander so as to determine the current speed at which returning birds would gain energetically by walking alongside the river rather than swimming. The point at which the energy expended by walking birds exactly equals that expended by swimming birds is given by combining the energy

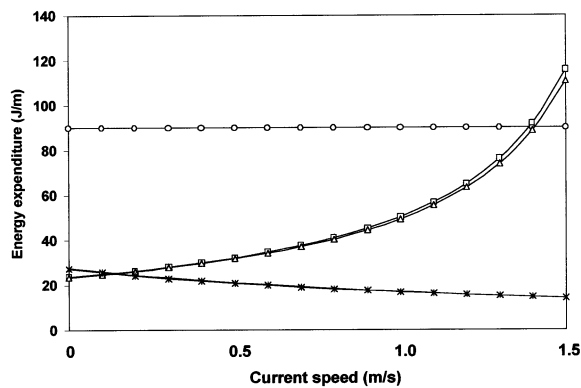


Fig. 8. Theoretical energy expenditure per metre travelled (cost of transport) in Magellanic Penguins returning to the breeding colony at San Julian and either walking (horizontal line with circles) and swimming against (ascending lines) or with (descending lines) a current of variable strength. The two almost identical ascending lines refer to birds arriving (squares) and leaving (triangles) swimming against the current, the two descending lines are so close as to be indistinguishable and refer to birds arriving and leaving swimming with the current. Similarity in values stems from the highly similar percentage times spent underwater for both leaving and arriving birds when faced with the same current conditions (see Fig. 4, lower graph).

expended by walking = $65.6/0.73$ J/m with equation (2) so that

$$89.9 = 44.5/(0.88(2.1 - \phi) + 0.12(0.3 - \phi)) \quad (3)$$

The solution for this for various values of ϕ is shown in Fig. 8 and takes into account the fact that penguins paddling on the surface against current speeds in excess of 0.3 m/s actually lose ground. In addition, there is a striking difference between birds swimming with, or against, the current with birds swimming against a current of 1 m/s expending more than twice as much energy per metre travelled as birds travelling with the current.

Overall, our study shows that although Magellanic Penguins do not apparently time their foraging trips so as to be commuting during periods of favourable current flow, they do modify their travelling behaviour substantially to minimize energetic costs according to current conditions. Further parameters, not examined by us, may also be varied by the penguins so as to minimize energy expenditure. An example of this could be travelling speed, which clearly shows considerable variation according to the current conditions (cf. Fig. 7), and which may lead to a shift in minimum costs of transport according to current strength. Appropriate treatment of this will require more data on selected speeds during known current conditions as well as knowledge of energy expenditure

of Magellanic Penguins swimming at different speeds (cf. Luna Jorquera 1996).

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