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Travel at low energetic cost by swimming and wave-riding bottlenose dolphins

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OVER the past 50 years there has been much speculation about the energetic cost of swimming and wave-riding by dolphins[1–11]. When aligned properly in front of the bow of moving ships[1–3], in the stern wake of small boats[4,5], on wind waves[6], and even in the wake of larger cetaceans[7–9], the animals appear to move effortlessly through the water without the benefit of propulsive strokes by the flukes. Theoretically, body streamlining as well as other anatomical and behavioural adaptations contribute to low transport costs in these animals. The economy of movement permitted by wave-riding has been perceived as an energetic advantage for the swimming dolphin[2,3,10], but has been hard to prove in the absence of physiological data for exercising cetaceans. Here we determine the aerobic and anaerobic costs of swimming and wave-riding in bottlenose dolphins and find that the minimum cost of transport for swimming dolphins is 1.29 ± 0.05 J kg^{-1} m^{-1} at a cruising speed of 2.1 m s^{-1}. Aerobic costs are nearly twice as high for swimming seals and sea lions, and 8–12 times higher for human swimmers[12]. Wave-riding by dolphins provides additional benefits in terms of speed. The results indicate that behavioural, physiological and morphological factors make swimming an economical form of high-speed travel for dolphins.

To determine whether there is an energetic saving associated with wave-riding, we trained bottlenose dolphins to follow a moving boat (Fig. 1). Freely swimming dolphins remained at least 1 m below the water surface and were positioned outside the boat's wake. Wave-riding dolphins preferred positions within the stern wake at a depth of ~0.5 m. Heart rate, respiratory rate and post-exercise blood lactate concentration were measured for both positions.

The results show that the physiological responses of swimming dolphins differed from those of wave-riding animals. At swimming speeds up to 2.9 m s^{-1}, the physiological responses of dolphins followed patterns similar to those of other marine mammals[12,13]: there was a graded, but not necessarily linear, increase in average heart rate, respiration rate and metabolic rate with increased swimming speed (Fig. 2; Table 1). Dolphins swimming at 2.1 m s^{-1} had respiratory rates, heart rates and blood lactate concentrations not significantly different from resting values (two-sample *t*-test[14] at $P < 0.05$). We attribute these results to the relatively low energetic demands of swimming at this speed[15] and to a pre-exercise, anticipatory response that occurred during the resting measurements. All three physiological parameters were raised when swimming speed was increased to 2.9 m s^{-1}. For example, at 2.9 m s^{-1}, respiratory rate was 70% higher than resting values, blood lactate was 30% higher, and average heart rate was 62% higher. As the boat speed was increased to 3.8 m s^{-1}, the dolphins preferentially rode the stern wave. During wave-riding at this speed the average heart rate decreased, and respiratory rate and blood lactate concentration were similar to values obtained during swimming at 2.9 m s^{-1}.

TABLE 1 Predicted metabolic rate and aerobic transport costs for swimming and wave-riding bottlenose dolphins

Speed (m s^{-1})	Average heart rate (beat min^{-1})	Metabolic rate (ml O_2 kg^{-1} min^{-1})	Transport cost (J kg^{-1} m^{-1})
2.1	76.0 ± 1.0	8.07 ± 0.33	1.29 ± 0.05
2.9	126.3 ± 7.3	24.67 ± 2.41	2.85 ± 0.28
3.8 (wave-ride)	101.7 ± 6.6	16.55 ± 2.18	1.46 ± 0.19

Only the highest speed was used for wave-riding. Metabolic rates were calculated from average heart rate using equation (1). Transport costs were calculated by dividing metabolic rate by swimming or wave-riding speed[18]. For these calculations, metabolic rate (ml O_2 kg^{-1} min^{-1}) was converted to metabolic energy (J)[23] assuming a caloric equivalent of 4.8 kcal per l O_2 and a conversion factor of 4.187×10^3 J kcal^{-1}. Results are presented as the mean value ±1 s.d.; $n = 4$ for each speed.

By comparing the physiological responses of swimming and wave-riding dolphins travelling at the same speed, we can evaluate the relative effort associated with each mode of travel. At 3.8 m s^{-1} the respiratory rate of wave-riding dolphins was 5.5(±0.5 s.d.) breaths per min ($n = 3$); this compares with 8.8(±1.6 s.d.) breaths per min ($n = 5$) for freely swimming dolphins moving at the same speed. Lactate concentration for a swimming dolphin wearing the heart-rate harness was three times higher (103.6 mg dl^{-1}; 11.6 mM) than the value for wave-riding dolphins moving at a similar speed. Although limitations in the instrumentation prevented the measurement of heart rate during high speed swimming, the results for respiratory rate and blood lactate concentration suggest that the energetic demands of wave-riding are considerably less than those of swimming at comparable speeds.

The aerobic transport costs of swimming and wave-riding dolphins also indicate an energetic advantage associated with wave-riding (Table 1). At 2.1 m s^{-1}, a routine cruising speed for wild bottlenose dolphins[7], the cost of transport for swimming was 1.29 ± 0.05 J kg^{-1} m^{-1}. Transport costs doubled as swimming speed was increased to 2.9 m s^{-1}. With an increase in boat speed to 3.8 m s^{-1}, the dolphins switched to wave-riding. The resulting transport costs were lower than anticipated, and only 13% higher than for swimming at 2.1 m s^{-1}. Thus, the wave-riding dolphin obtains a significant advantage in speed for little energetic investment.

The hydromechanics that allow this energy savings during wave-riding are difficult to discern. Scholander[1] suggested that propulsion could be gained by simply 'leaning' a streamlined fluke into the forward slope of the bow wave. Others have detailed the theoretical balance between drag and buoyancy of the wave-riding dolphin, and lift forces created by the pressure field in front of a moving ship's bow[6,9,10]. With sufficient assistance from the wave, propulsive stroking by the dolphin is reduced to the effort required to position the animal. Indeed, the wave-riding dolphin appears motionless once in position, with fluke movements limited to low-amplitude corrective strokes for repositioning. Only brief bursts of inhalation and exhalation at the water surface will interrupt the ride. Such mechanical advantages in the form of assisted propulsion by

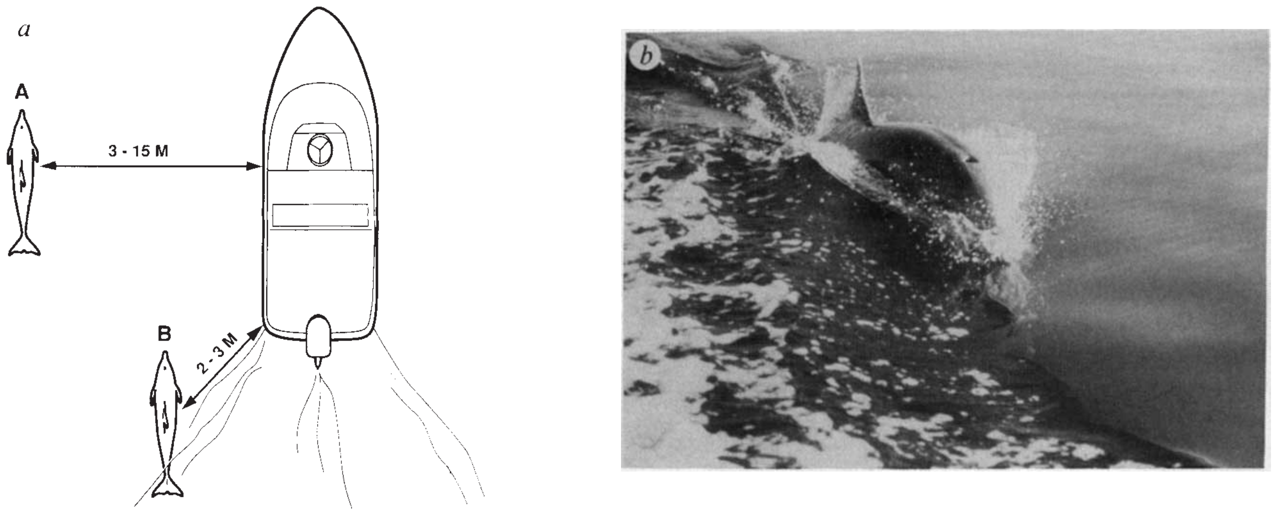

FIG. 1 *a*, Swimming position of bottlenose dolphins relative to the motorboat. Swimming animals (*a*) were positioned abeam outside the boat wake. The position for wave-riding (*b*) was approximated by the trainer and refined by the dolphins. *b*, Position of a bottlenose dolphin riding the stern wake of a boat. Wave-riding dolphins remained ~0.5 m below the water surface except for brief respiratory events (pictured). (NOSC photo.)

METHODS. We trained two adult Atlantic bottlenose dolphins (*Tursiops truncatus*; mean body weight, 145 kg) to match their swimming speed with that of a motorboat (Boston Whaler, Model 21 ft). Position of the animals relative to the boat was determined by a trainer and maintained with signals presented through a submerged hydrophone. The swimming dolphin was maintained in positions that avoided turbulent areas around the boat. Both dolphins preferentially swam about 1 m (>2.5 × body diameter) below the water surface during the swimming tests. At this depth the augmentation in drag from surface waves is reduced[10]. Surface intervals were limited to respiratory periods and accounted for <10% of the experimental period. During wave-riding each dolphin was allowed to refine its position within the stern wake. As a result, the distance between the boat and the dolphin varied with both position and speed. A 14-m-deep ship channel in Kaneohe Bay, Oahu, Hawaii was used for the experiments. Water currents are generally less than 0.3 m s^{-1} in this area and were considered negligible during the tests. Each session consisted of a 5-min pre-exercise rest period, and a 5–6-min warm-up swim, followed by a 10–25-min experimental swim at a single speed. Depending on the boat speed, most sessions covered ~1–2 nautical miles (1.8–3.7 km) in a straight-line course. Speed of the boat was monitored with a Speed Log recorder calibrated before and after the experiments by timed trials over a measured course. Mean surface water temperture was 24.6 ± 1.2 °C.

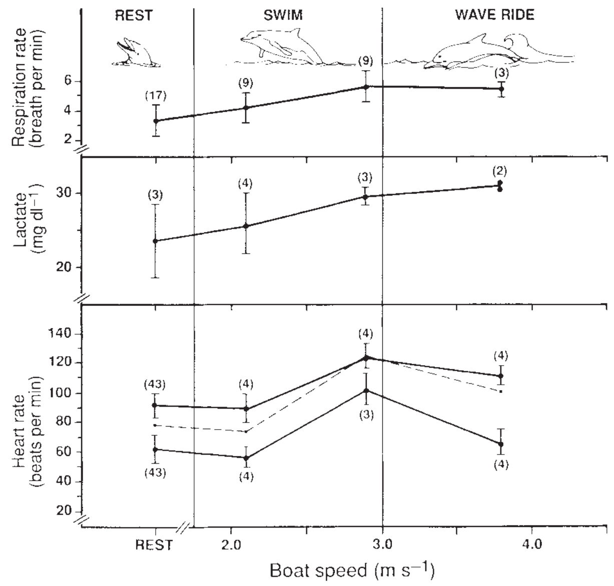

FIG. 2 Heart rate, blood lactate and respiration rate for resting and active dolphins. Mean values ±1 s.d. are presented for each parameter. Numbers in parentheses denote the number of experimental sessions. Heart rate of the dolphins cycled between periods of tachycardia following a breath and bradycardia during submergence. Upper and lower solid lines for heart rate show levels of bradycardia and tachycardia, respectively. The dashed line is the average heart rate at each speed.

METHODS. Electrocardiograph signals were continuously recorded (Birtcher, Model 365) from two 8.5-cm suction cup electrodes on the skin; a nylon harness kept the cups in place during swimming. The harness was small (<5% of the frontal area of the dolphin) and positioned close to the theoretical transition point for boundary layer flow[24]. In view of this, its effect on energetic cost at cruising speeds was considered insignificant. Note that the effect of the harness will increase with speed; actual maximum speeds of the unencumbered dolphin may be higher than determined here. A plate electrode (3.0-cm diameter) beneath each suction cup was positioned on the sternum between the pectoral fins and mid-lateral in the axillary area of the right pectoral fin. Wires from the electrodes were braided and trailed to the side of the swimming animal. Respiratory rate was measured for 1 min at 5-min intervals by observers with stopwatches. Metabolic rate (V_{MR}) was calculated from average heart rate ($\bar{V}_{HR}$) using the equation

$$V_{MR}(\text{ml O}_2\ \text{kg}^{-1}\ \text{min}^{-1}) = 0.33\bar{V}_{HR}\ (\text{beats per min}) - 17.01 \qquad (1)$$

(correlation coefficient, $r = 0.98$) determined for the two dolphins pushing against a load cell[25,26]. During the load cell tests heart rate was measured with two cross-chest electrodes; metabolic rate was determined simultaneously by open flow respirometry. The equation is based on $n = 106$ steady-state sessions spanning loads of 0–185 kg, and average heart rates from rest (78.6 ± 7.2 beats per min) to maximum levels (139.4 ± 4.1 beats per min). Likewise, metabolic rates spanned resting to maximum values (T.M.W. *et al.*, manuscript in preparation). Average heart rate of the swimming dolphins used for metabolic calculations fell within this range of values. Samples for lactate analyses were obtained from blood vessels located in the dolphin's fluke. Collection was facilitated by training the dolphins to present their flukes voluntarily for sampling. Using this technique, we obtained all samples within 2 min of completion of exercise. Chilled samples were centrifuged and the serum analysed for lactate concentration (YSI Industrial Analyzer, Model 27). The analyser was calibrated daily with standards spanning the experimental range of values.

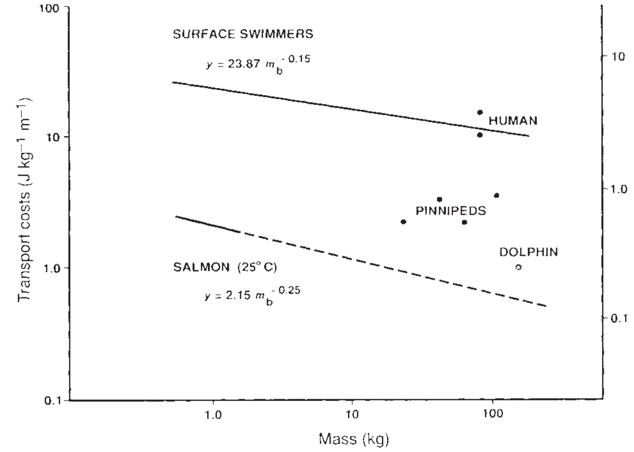

FIG. 3 Cost of transport for swimmers. The results for humans[20], pinnipeds[12,19] and dolphins (this study) are shown. The upper solid line denotes the best-fit regression for surface swimmers and includes data for ducks, penguins, mink, muskrat, sea otters and humans[27]; the lower line represents the best fit regression (solid) and extrapolation (dashed) for swimming salmon[17]. The extrapolation is based on that in ref. 18; y represents transport costs in J kg^{-1} min^{-1}; m_b is body mass in kg.

wave-riding may explain the phenomenal sustained swimming speeds of more than 8 m s^{-1} originally reported for dolphins at sea[16].

Whether freely swimming or wave-riding, dolphins have low minimum transport costs compared with many swimmers (Fig. 3). The minimum cost of transport for swimming bottlenose dolphins was only 2.1 times the predicted value for a hypothetical dolphin-sized fish[17]. During wave-riding the costs increased slightly to 2.4 times predicted levels. It is remarkable that the difference in swimming costs between fishes and dolphins is not larger, especially if the energetic demands of endothermy and the additional drag associated with the heart-rate harness used here are considered. The hydrodynamic shape of the dolphin may play a part; transport costs determined in this study are between theoretical values based on laminar and turbulent water flow around the body[18].

Comparisons with other mammalian swimmers also demonstrate the energetic advantages of dolphin swimming. Transport costs for swimming pinnipeds (seals, sea lions) are 2.5–5.7 times the predicted values for comparably sized fish[12,19]. Humans are exceptionally inefficient surface-swimming mammals; regardless of the stroke used we maintain transport costs that are 8–12 times the value for dolphins and 21 times the predicted values for fish[20].

Dolphins and porpoises may use several behavioural strategies to reduce energetic costs during high-speed swimming[21,22]. They preferentially seek out bow and stern wakes (this work, and refs 4, 5), and will match the speed of moving ships for minutes to hours[10]. We have found that what appears to be playful behaviour to the casual observer on ship also provides an economical (albeit not free) ride for the dolphin. ☐

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Overcompensation and population cycles in an ungulate

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ALTHOUGH theoretical studies show that overcompensatory density-dependent mechanisms can potentially generate regular or chaotic fluctuations in animal numbers, the majority of realistic single-species models of invertebrate populations are not overcompensatory enough to cause sustained population cycles[1–3]. The possibility that overcompensation may generate cycles or chaos in vertebrate populations has seldom been considered. Here we show that highly overcompensating density-dependent mortality can generate recurrent population crashes consistent with those observed in a naturally limited population of Soay sheep. The observed interval of three or more years between crashes points to sharp 'focusing' of mortality over a narrow range of population density.

Although comparative analyses of density dependence in large mammal populations has yielded important general insights about the significance of population limitation sharply concentrated at high population levels[4–6], more refined analyses of particular systems have been hampered by a lack of detailed long-term demographic data, particularly concerning adult survival[6–8].

The Soay sheep population on St Kilda has been monitored in detail between 1959 and 1968 (ref. 9), and from 1985 to the

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