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Swim speed of free-ranging Adélie penguins Pygoscelis adeliae *and its relation to the maximum depth of dives*

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Swim speed and depth utilization were recorded at a sampling rate of 1 Hz in 14 free-ranging Adélie penguins in Adélie Land, Antarctica during the austral summers of 1996/1997 and 1998/1999. The average swim speeds during the descent, bottom and ascent phases of dives were independent of the maximum depth, while the variability in swim speed decreased with increasing maximum depth, reflecting the physiological constraints of diving. Descent speed, which varied less with maximum depth than speeds measured during other parts of dives, was significantly different among birds. In addition to the speed analysis, a new category of dive profiles with a flat bottom phase and an extremely reduced swim speed is reported. The probable benthic nature of such dives is discussed.

The accuracy of measurements of swim speed of free-ranging marine animals has been related to technological progress: swim speed has been estimated visually from cliffs or boats (Kooyman 1975, Kooyman et al. 1971) and has been assessed as a function of energy expenditure of animals in water channels (Hui 1988, Culik and Wilson 1991, Culik et al. 1994). However, because of the limited space available for the animals in such channels (Hui 1988) and the subjective component of visual estimations (Kooyman and Davis 1987), it is desirable that swim speed data be reliably obtained in free-ranging animals. The speeds of free-ranging animals were initially derived from telemetry studies by measuring the time elapsed between two localizations using either radiotracking (Trivelpiece et al. 1986) or satellite tracking (Davis and Miller 1992). However, both techniques are liable to underestimate instantaneous speed (Hull 1997, Wilson in press). The monitoring of the swim speed by recorders directly attached on the animals has resulted in substantial progress in our understanding of the travel capacities of marine animals (Wilson et al. 1989, Boyd et al. 1995, Otani et al. 2000). Recently, the swim speeds of free-ranging Adélie penguins have been obtained with a high temporal resolution and related to the birds' feeding behaviour (Ropert-Coudert et al. 2001) and to optimized energetics (Wilson et al. in press).

In this note, we consider the swim speed of free-ranging Adélie penguins in relation to the maximum depth of dives, and report on occasional benthic diving activity.

Methods

Loggers were deployed on 14 and 16 Adélie penguins breeding at Dumont d'Urville, Adélie Land (66.7° S, 140.0° E) during the austral summers of 1996/1997 and 1998/1999.

During 1996/1997, swim speed and depth were measured with 12-bit resolution, three-channel UWE-PDT loggers (102 mm long, 20 mm in diameter and weighing 50 g, Little Leonardo, Japan) with 16 Mb memory. During 1998/1999, swim speed and depth were measured with 12-bit resolution, five-channel UWE-PD2G loggers (110 mm long, 22 mm in diameter and weighing 80 g, Little Leonardo, Japan) with 16 Mb memory. Depth and temperature ranges were 0–200 m and -22 to 50°C for both loggers. In addition, both logger types had an absolute accuracy of 0.5 m and 0.05 m s^{-1} for depth and speed, respectively. Data were recorded at a frequency of 1 Hz. Speed was measured every second by counting the number of revolutions of an anteriorly-mounted propeller, which was converted into flow speed (m s^{-1}) using data obtained from calibration experiments in a pool as well as from data obtained from the animal (Blackwell et al. 1999, Ropert-Coudert et al. 2000). Loggers were attached on the birds' backs with glue (Araldite) and two cable-ties and mounted close to the tail so as to minimize drag (Bannasch et al. 1994). Besides drag reduction, calibration experiments on penguins' carcasses placed in a water flume indicated that this caudal position gave a good measure of real stream speed rather than perceived speed due to water flowing particularly fast over the point of the bird's maximum girth.

After one foraging trip that lasted on average 22.0 ± 9.1 h ($N = 13$ birds), birds were recaptured, the devices were removed and the data downloaded to a computer. Dives < 5 m were not analysed since they correspond mainly to porpoising (Yoda et al. 1999) or shallow sub-surface travelling with only a minor proportion of these dives corresponding to feeding activity (Ropert-Coudert et al. 2001). Deep dives were defined as dives with maximum depth > 40 m; this value represents a trough in the bimodal distribution of the maximum depth frequencies of birds (Fig. 1). Dives were further divided into commuting (descent and ascent) and bottom phases with two or more undulations > 2 m.

Since the second mode of the maximum depth frequency distribution followed a normal distribution, regression statistics were used for all dives deeper than

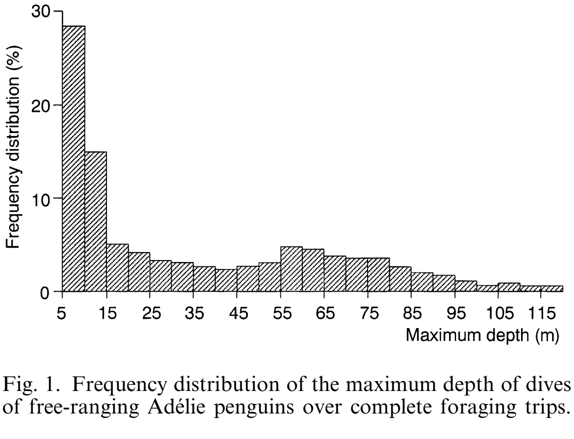

Fig. 1. Frequency distribution of the maximum depth of dives of free-ranging Adélie penguins over complete foraging trips.

40 m. All statistical tests were performed according to Sokal and Rohlf (1969) using Statview (version 4.57, Abacus Concepts Inc., Washington, U.S.A.) software. For all statistical tests, the significance level was set at 5%.

Results

Reliable depth and speed data were obtained for 5909 dives deeper than 5 m from 13 birds (7 during summer 1996/1997 and 6 during summer 1998/1999). Overall, during the dives the 13 penguins swam at 1.95 ± 0.30 m s^{-1} but swim speed profiles of dives varied greatly within foraging trips (Fig. 2). High speed profiles at the beginning and end of trips were similar to the profiles described by Yoda et al. (1999) that corresponded mainly to porpoising and sub-surface travelling (Fig. 2a). As our sampling interval (1 s) was slightly shorter than the time birds are airborne during the porpoising leap, there was no apparent turnoff of the propeller on our speed profiles. Similarly, the maintenance of a constant speed during non-feeding dives (Fig. 2b) and the speed reduction during the undulatory phase of feeding dives (Fig. 2c) have been documented elsewhere (cf. Ropert-Coudert et al. 2001). On the other hand, an unusual dive type with different dive and swim speed profiles was observed in our data: the depth at the bottom phase of these dives was remarkably constant (depth variation between the beginning and the end of the bottom phase < 1 m), while the speed dropped substantially, birds remaining almost motionless during the main duration of the bottom phase (Fig. 2d). Thirteen of these square-wave profile dives were identified in seven birds, while a further six dives conformed closely, but not absolutely, to this dive type. The maximum depth of these dives, ranging from 16 to 48 m (N = 7 birds) differed between birds but tended to be similar within any individual, especially if dives were adjacent in time.

Overall, the average swim speed during a dive (S_{dive}) decreased ($F_{1,5994} = 262.8$, $P < 0.0001$) with increasing maximum dive depth M_d (Fig. 3a, $S_{dive} = 0.002M_d + 2.01$). However, when analysed separately, speeds used during commuting (descent speed: $F_1 = 0.9$, $P = 0.34$; ascent speed: $F_1 = 0.13$, $P = 0.72$) and hunting phases (undulatory speed: $F_1 = 0.19$, $P = 0.66$) were independent of the maximum depth of dives (Fig. 3b). For both shallow and deep dives, the average descent and ascent speeds remained constant at 2.03 ± 0.28 m s^{-1} (N = 5909 dives) and 1.95 ± 0.31 m s^{-1} (N = 5909 dives), respectively. Although also constant, the undulatory speed during deep dives was slower at 1.67 ± 0.31 m s^{-1} (N = 2245 dives) than the commuting speed used

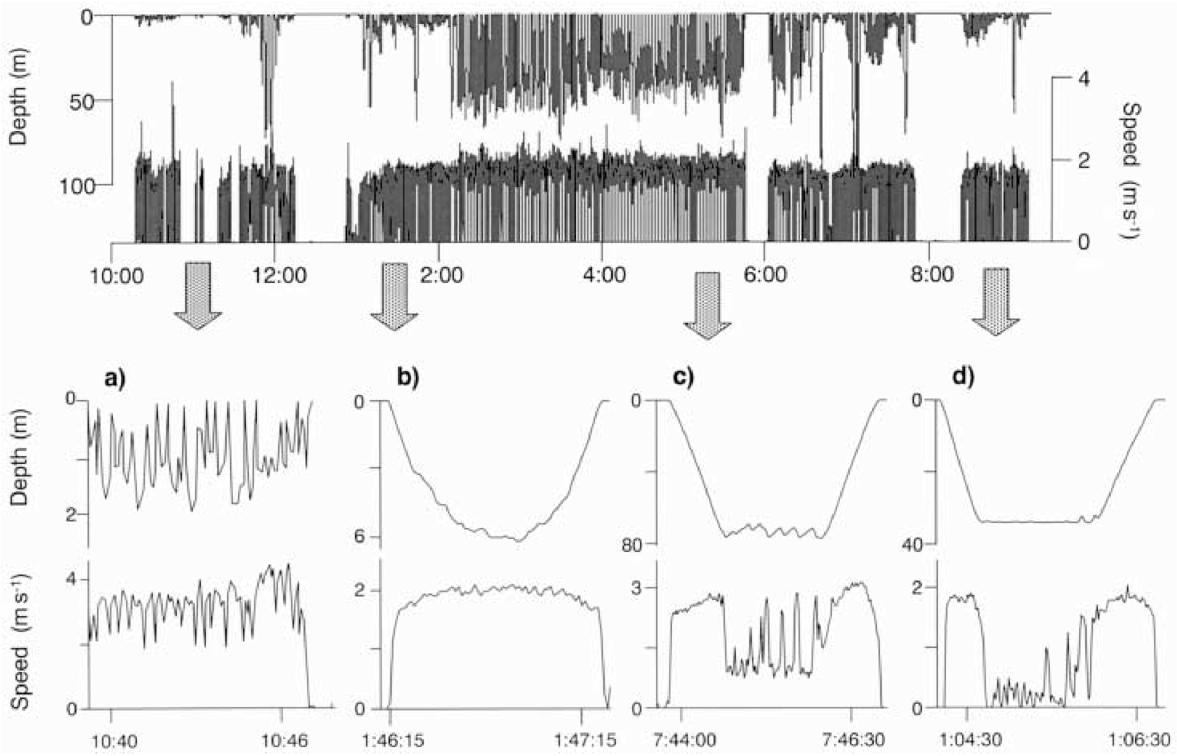

Fig. 2. Depth and speed profiles for a full foraging trip (top graph) and (a) porpoising, (b) non-feeding dives, (c) feeding dives and (d) flat-bottom dives of a free-ranging Adélie penguin.

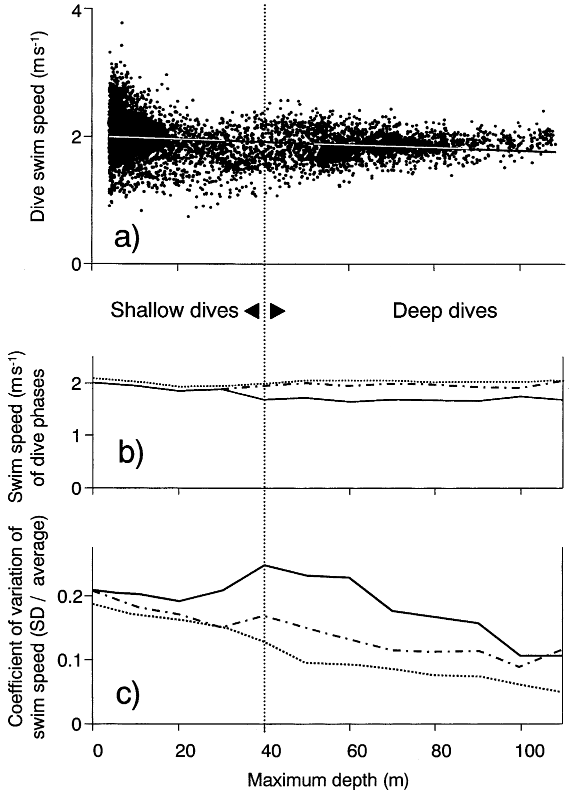

Fig. 3. Swim speed of free-ranging Adélie penguins as a function of the maximum depth of dive averaged during (a) the whole dive; (b) each dive phase, i.e. descent (dotted line), ascent (hatched line) and undulatory phase (solid line); (c) coefficient of variation of the swim speed for each dive phase. In (b) swim speed has been averaged over 10-m intervals to aid visualization.

for deep dives (2.03 ± 0.03, $N = 2244$, Student's t-test, $t_{4486} = 47.05$, $P < 0.0001$). In addition, the coefficient of variation decreased progressively in the case of the commuting speeds, although more erratically for the undulatory speeds, with increasing maximum depth (Fig. 3c).

Discussion

Swim speed recordings of harbour porpoise *Phocoena phocoena* (Otani et al. 2000) and Antarctic fur seals *Arctocephalus gazella* (Boyd et al. 1995) have revealed that these animals change their speed according to the maximum depth of the dive, with increasing maximum depths corresponding to increased swim speed. However, Adélie penguins seem to adopt a different strategy. In the present study, the apparent decrease in swim speed with increasing depth for all data considered together is at odds with the lack of correlation between swim speed and depth for all phases of dive (descent, bottom phase, ascent) considered separately. This spurious correlation arises as a result of two factors: (i) that the proportion of time spent in the bottom phase increases with increasing depth and (ii) the swim speed of birds during the bottom phase is markedly lower than that during either descent or ascent. Thus, undifferentiated speed values taken from deeper regions comprised a higher percentage of bottom phase speeds than a similar sample taken in shallower waters. Consequently, the swim speed of Adélie penguins during each phase of the dive can be taken as remaining approximately constant with increasing diving depth. This finding is important since drag increases exponentially with swim speed (Williams et al. 1993) and power requirements, calculated for penguins swimming in a water channel, increase as a cubed function of swimming speed (Culik et al. 1996). Although the results of Culik et al. (1996) may not be applicable to diving penguins for which burst and gliding swimming, as well as changes in the buoyancy, may modify the power requirements for swimming (see Skrovan et al. 1999), the maintenance of a constant speed at different depths tends to indicate that birds do not increase the rate of energy expenditure related to swimming activity when diving deeper. However, the range of speeds decreased with the maximum depth perhaps because during shallow dives oxygen consumption is less critical (see Williams et al. 1999). However, such a narrower speed range is surprising. The buoyancy of birds is expected to decrease with increasing depth (Wilson et al. 1992) and this should contribute to minimize the hydrodynamic constraints on swimming. Thus, it can be speculated that the narrower speed ranges rather result from selective constraints on the time-budget: at greater depths, birds will tend to travel at similar speeds because the time-window in which they could operate is limited and the probability of encountering favourable prey over a particular dive may fluctuate.

If birds are to optimize the hunting component of their feeding dives, i.e. the time spent during the undulatory bottom phase, they are expected to use speeds that correspond to the minimum cost of transport (Boyd et al. 1995), which has been estimated at around 2.0 m s^{-1} in Adélie penguins swimming in a water channel (Culik and Wilson 1991, Culik et al. 1994). This value is similar to that of the commuting phases of the free-ranging birds in our study. The greater variability of the ascent speeds in deep dives compared to descent speeds is probably regulated by both biomechanic and behavioural factors. Biomechanical studies on underwater swimming in bottlenose dolphins *Tursiops truncatus* show that the ascent phase of dives is characterized by burst and glide (Skrovan et al. 1999) and this alone may contribute to the variability of the speed. On the other hand, studies on the feeding behaviour of free-ranging Adélie penguins have revealed that an appreciable percentage of prey is caught during the early part of the ascent (Ropert-Coudert et al. 2001) and such prey pursuit and capture may necessitate sudden bursts of speed. Similarly, the feeding activity of Adélie penguins during the bottom phase of dives is accompanied by an overall reduction of the speed with occasional brief accelerations (Wilson et al. in press). This probably accounts for the large variability observed during the undulatory phases of dives.

Finally, benthic diving activity is an important component of the foraging strategy of emperor *Aptenodytes forsteri* (Rodary et al. 2000) and rockhopper *Eudyptes chrysocome filholi* penguins (Tremblay and Cherel 2000) and is suspected, although its importance has not yet been established, for gentoo *Pygoscelis papua* and yellow-eyed *Megadyptes antipodes* penguins (see review in Tremblay and Cherel 2000). In this regard it is notable that benthic prey have been reported in the diet of Adélie penguins (Puddicombe and Johnstone 1988, Watanuki et al. 1994). Thus, the presence of typical benthic square-wave dive profiles in our data – associated with a remarkably constant depth for consecutive dives with reduced swim speed – supports the idea that Adélie penguins may occasionally execute benthic dives. In the light of a recent observation of benthic feeding by krill (Ligowski 2000), the main prey of Adélie penguins in Adélie Land (Ridoux and Offredo 1989), such behaviour appears tenable, although it appears unimportant compared to the same behaviour in emperor or rockhopper penguins. Further observations, in different seasons and perhaps areas, are needed in order to quantify the importance and exact function of these dives.

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Genetic monogamy in burrowing parrots Cyanoliseus patagonus*?*

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We report on a first DNA fingerprinting study of paternity in a Psittaciform bird, the burrowing parrot *Cyanoliseus patagonus*. In two consecutive breeding seasons, a total of 49 families was sampled, of which 11 breeding pairs were investigated each of two years. Extra-pair paternity was not encountered suggesting that burrowing parrots are socially as well as genetically monogamous. Strict genetic monogamy is comparatively rare in birds and occurs predominantly in some groups of non-passeriformes all of which exhibit long reproductive lifespans and essential paternal care. Psittaciformes fit this pattern. We conclude that paternal care plays a crucial role in the evolution and maintenance of genetic monogamy in the study species. Cases of intraspecific brood parasitism are rarely observed.

Extra-pair copulations (EPCs) are widespread among socially monogamous birds (e.g. Birkhead 1998), but a large interspecific variation in levels of extra-pair paternity (EPP) has been observed (Petrie and Kempenaers 1998). While in some species over half of the chicks are extra-pair young (EPY), e.g. in tree swallows *Tachycineta bicolor* (Kempenaers et al. 1999), there are some groups of birds where EPY are rarely found. Especially in Sphenisciformes (e.g. Moreno et al. 2000) and Procellariiformes among seabirds (summarised in Quillfeldt et al. 2001), as well as Strigiformes and Falconiformes among raptors (summarised in Müller et al. 2001), EPP seems to occur infrequently or may even be absent. The life histories of these non-passeriform groups of birds exhibit some striking similarities such as indispensable male parental care and long reproductive lifespans, which have been proposed as the causes for the low rates of EPP. If male care is essential, females should refrain from seeking EPCs if they risk losing their partner's investment in the brood. In particular, males of long-lived species should withdraw care to a brood if any doubt of parentage exists, as suggested by a model of male parental decisions (Mauck et al. 1999).

Psittaciformes (parrots and cockatoos) are another group of long-lived birds exhibiting very high levels of parental investment, but to our knowledge no analyses of EPP have been performed in this group of birds. Thus, the following study on paternity in the burrowing parrot *Cyanoliseus patagonus* represents the first DNA fingerprint study on paternity in a Psittaciform bird.

Methods

The burrowing parrot is one of the most southern Neotropical parrots. Burrowing parrots breed colonially excavating their own nest burrows by tunnelling into the faces of sandstone, limestone or earth cliffs. Nesting pairs use burrows dug in previous seasons but they enlarge the burrows every year (J. F. Masello and P. Quillfeldt unpubl. data). Each burrow is occupied by