Der Energiebedarf der Pygoscelis-Pinguine: eine Synopse

Energy requirements of Pygoscelid penguins: a synopsis

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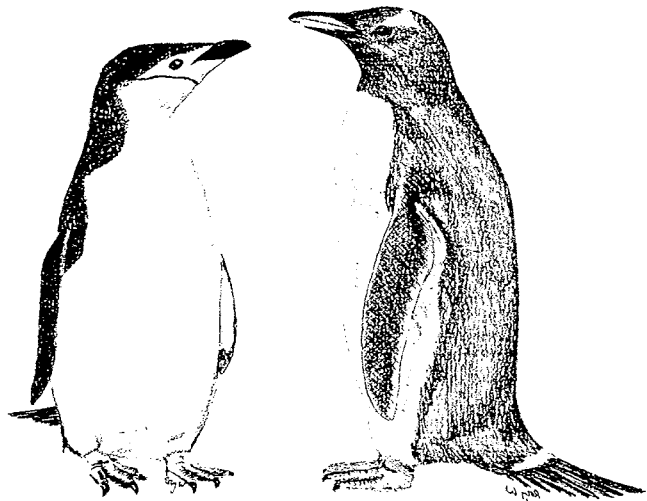
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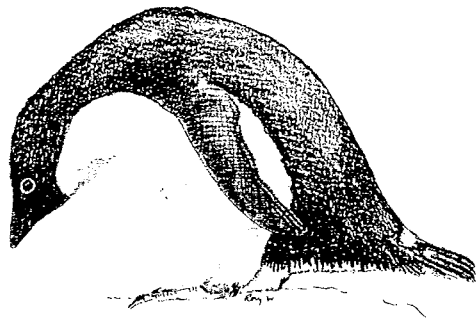Institut für Meereskunde an der Universität Kiel, Abteilung Meereszoologie
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Chinstrap   Gentoo

Adélie

...penguins are never quite as elegant,
awkward or comical as one expects them to be.
They do not stand about holding drinks or
colloquies. Rather, they stand around mating,
pecking, and batting each other with their
flippers like agitated toddlers. They clamber
over rocks covered in their own guano, fall
down in the stuff, regurgitate food for their
young, and croak, bray, trumpet and squawk as
if they had no notion at all that we like to think
of them as silly little people... Most of all, they
spend their greater part not standing at all, nor
doing their trademark silly walk, but
swimmming, diving, and porpoising in the
world's southern ocean waters as the marine
creatures they really are.

James Gorman

for Barbara, Laura, Nicolai and Charlotte

CONTENTS

ZUSAMMENFASSUNG

Die vorliegende Synopse basiert auf den Ergebnissen dreier Antarktisexpeditionen. Die dabei gewonnenen Daten wurden seit 1989 in 31 Manuskripten publiziert bzw. zur Publikation eingereicht. In der nachfolgenden Synopse sowie in den bisher noch nicht erschienenen Arbeiten wurde erstmals anhand neuer und bereits veröffentlichter Daten der Energie- und Nahrungsbedarf der 3 Pygoscelispinguinarten, Adélie- (*Pygoscelis adeliae*), Zügel- (*P. antarctica*) und Eselspinguin (*P. papua*) für die Brutsaison berechnet. Zu diesem Zweck wurden Daten über Mikroklima, Aktivität der Tiere an Land, Umsatz der Fettreserven, sowie Daten über den Energiebedarf bei Ruhe und während des Schwimmens in kaltem Wasser (4°C) zu einem Modell zusammengefaßt. Die verschiedenen Daten sowie die Ergebnisse des Modells wurden mit publizierten und mit eigenen Ergebnissen anderer Untersuchungen verglichen, so z.B. mit hydrodynamischen Untersuchungen an Pinguinmodellen im Strömungskanal der Versuchsanstalt für Wasserbau und Schiffbau, Berlin, sowie mit Ergebnissen aus Untersuchungen mit doppelt-markiertem schweren Wasser an Pinguinen im Freiland.

Der gemessene Ruheumsatz der Adéliepinguine an Land bestätigte bereits in der Literatur veröffentlichte Werte. Doch obwohl die gemessenen Werte für den Ruheumsatz in kaltem Wasser erheblich niedriger lagen als bisher angenommen, stimmte der daraus berechnete Wärmeverlust mit von Kooyman (1976) an Adéliepinguinbälgen gemessenen Werten überein. Die von mir an schwimmenden Pinguinen gemessenen Transportkosten waren ebenfalls erheblich geringer als bisher, allerdings an anderen Arten, gemessene Werte. Meine Ergebnisse stimmen aber sehr gut mit Untersuchungen der hydrodynamischen Eigenschaften an Pinguinmodellen im Wasserkanal überein. Schließlich wich der für Adéliepinguine anhand von Zeit-Aktivitätsbudgets und Respirationsmessungen berechnete Tagesenergiebedarf nur zu 3-15 % vom Tagesenergiebedarf ab, der mit Hilfe von doppelt-markiertem schweren Wasser an Tieren im Freiland gemessen worden war.

Schlüsselparameter in dem für Adéliepinguine erstellten Energiemodell waren Dauer und Energiebedarf während a) Ruhe und Laufen (Adulte und Küken) und b) während des Schwimmens und Ruhe im Wasser (Adulte) sowie c)

Verbrauch der Fettreserven der Adulten und d) Energiebedarf der wachsenden Küken. Die Berechnungen ergaben, daß Adéliepinguine während des Brütens 680 g Krill pro Tag benötigen, um ihren Energiebedarf zu decken. Diese Menge steigt auf 820 g pro Tag an, nachdem die Küken geschlüpft sind und erreicht 1010 g pro Tag, wenn die Küken Kindergärten gebildet haben. Insgesamt verbraucht ein Adéliepinguinbrutpaar zusammen mit den Küken pro Brutsaison 174 kg Krill. Unter Annahme gleicher Modellparameter ergibt sich für Zügel- und Eselspinguine ein Nahrungsbedarf von 160 kg bzw. 286 kg pro Brutpaar und Saison.

Die Einflüsse der Instrumentierung sowie die Auswirkungen menschlichen Handelns auf Zeit-Aktivitätsbudgets, Energiebedarf und Wohlbefinden der Pinguine wurden ebenfalls untersucht. Hierbei stand die Optimierung der Arbeitsmethoden, bzw. die Reduzierung des Stress' bei den untersuchten Pinguinen im Vordergrund. Generell zeigte sich, daß extern angebrachte Ringe oder Meßgeräte den Reibungswiederstand der Pinguine im Wasser stark erhöhen und daher zu einer Verminderung der Leistungsfähigkeit der Tiere auf See führen. Untersuchungen, bei denen doppelt-markiertes schweres Wasser eingesetzt wird, führen aufgrund der notwendigen Injektionen ebenfalls zu einer Beeinträchtigung der Tiere. Ölverschmutzung zerstört die Isolations-eigenschaften des Gefieders und führt zu stark erhöhtem Energieverbrauch der Pinguine im Wasser. Weitere Faktoren wie Fluggeräte und menschliche Annäherung setzen die Tiere einem "psychischem Stress" aus, wodurch ebenfalls Zeit-Aktivitätsbudgets und Energiebedarf negativ beeinflußt werden. Die Ergebnisse dieser Untersuchungen wurden in der jeweils darauffolgenden Expedition berücksichtigt. In dieser Synopse werden zusätzlich Vorschläge zur Reduzierung dieser Einflüsse gemacht.

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ABSTRACT

Based on the results obtained during 3 Antarctic expeditions, which have been published or submitted in 31 manuscripts since 1989, I compiled in this synopsis the energy and food requirements of Adélie (*Pygoscelis adeliae*), Chinstrap (*P. antarctica*) and Gentoo (*P. papua*) penguins during the breeding season. For that purpose, I used data on microclimate, bird activity on land, the usage of fat reserves, and data on the energetic costs associated with swimming and resting in cold water (4°C). The different data as well as the results of the model were cross-checked with published data or results obtained through other experimental methods, i.e. hydrodynamic investigations on plastic-cast models in a circulating water tank or studies on live penguins using doubly-labelled water.

Resting metabolic rate (RMR) of Adélie penguins on land concurred with data published in the literature. Although RMR of penguins in cold water was significantly lower than published values, calculation of penguin heat loss using these figures was matched by the results of Kooyman et al. (1976) who determined heat conductivity in penguin pelts. Similarly, cost of transport in penguins swimming under-water was significantly lower than published values for other penguin species. However, my results were matched by those of a study on hydrodynamic properties of plastic-cast penguin models. Finally, calculations of the field metabolic rates of Adélie penguins using respirometry data and time-activity budgets were matched to within 3-15 % by the results of a doubly-labelled water study.

Key parameters in the model for Pygoscelid penguin energetics were duration and energy expenditure a) during resting and walking (adults and chicks) and b) during swimming and resting at sea (adults), as well as c) fat loss in adults and d) energy requirements of the growing chicks. It was found that Adélie penguins require 680 g krill per day during incubation, 820 g d⁻¹ during the brood and 1010 g d⁻¹ during the crèche phase, respectively, for themselves and their brood, amounting to a total of 174 kg per breeding pair during the breeding season. Assuming similar values for key parameters in the model, food requirements of Chinstrap and Gentoo penguins were 160 and 286 kg of krill per breeding season.

The effects of instrumentation and human interference on the activity budgets, energy requirements and well-being of Pygoscelid penguins were also investigated. These investigations were aimed at improving experimental methods and reducing stress for the study animals. Generally, it was found that externally-attached devices increase hydrodynamic drag and therefore lead to a reduction in the performance of penguins at sea. Studies using doubly-labelled water also affected the animals as a result of the injections and blood sampling. Pollution with oil destroys the insulative properties of penguin feathers and leads to highly increased metabolic rates during swimming and resting in the water. Other factors such as airplanes and helicopters as well as approach by humans cause "psychological stress" and also influence penguin activities and energetics. The results of these investigations were applied during each subsequent expedition. Further suggestions on how to minimize these effects are given in this synopsis.

INTRODUCTION

Three species are contained within the Pygoscelid genus: the Adélie (*Pygoscelis adeliae*), the Chinstrap (*P. antarctica*) and the Gentoo (*P. papua*) penguin. They are the most abundant of the Antarctic penguins, with population estimates of 2, 1.3 and 0.3 million pairs, respectively (Wilson 1983). Like many other sea birds, penguins often breed in very large colonies. At Esperanza (Hope) Bay, Antarctic Peninsula, (56°59'W, 63°24'S), where most of the work presented here was conducted, approximately 230 000 adult Adélie penguins breed each year (Wilson 1983). They forage within 90 km of the bay (Wilson et al 1991b) for themselves and their ca. 150 000 chicks (Davis and McCaffrey 1986). During the breeding season, Pygoscelid penguins of the Antarctic Peninsula rely almost exclusively (87-99%; Trivelpiece et al. 1987) on krill (*Euphausia superba*). Analysis of bone fluoride content shows that krill, a fluoride-rich crustacean, is also very likely to comprise the main diet of Pygoscelid penguins throughout the year (Culik 1987). In areas of sympatry, this may lead to competition for krill with other penguin species, marine mammals and, as suggested recently, even man (Croll, *pers. comm.*).

The amount of krill needed by Pygoscelid penguins in their energetically highly demanding environment has been the subject of some speculation. Although food requirements have been deduced from stomach contents, digestion by the birds while at sea makes estimates based on such data likely to be too low (Croxall and Prince 1987; Trivelpiece et al. 1987). The use of doubly-labelled water to determine energy expenditure has proved more useful in this respect, but results should be interpreted carefully since penguins significantly alter their behaviour when experimentally manipulated (Nagy et al.1984; Costa et al. 1986; Gales et al. 1990; Wilson and Culik 1993 and unpublished data). The same is true for birds fitted with external or implanted devices, which can be used to obtain information about behaviour at sea and physiological responses to varying environmental conditions (Culik and Wilson 1991b; Culik et al. 1993; 1994a). The results of laboratory studies, using respiration chambers in conjunction with treadmills and water tanks or tunnels to measure oxygen consumption and deduce food requirements, may also be subject to bias, since under such restrained conditions penguins are unlikely to behave as they would in

the wild. Data obtained in such experiments must therefore be interpreted with care (e.g. Pinshow et al. 1977; Culik et al. 1990a; Culik and Wilson 1991c).

Unfortunately, handling and consequent disturbance to the birds cannot be prevented if we wish to understand their physiological adaptations, activity budgets and the resulting energetic requirements. However, the error caused by experimentation itself can be assessed and even eliminated if a variety of different methods is used, their deleterious effects on the study animals are quantified and minimized, and the results are cross-checked. Using the results from our field work in Antarctica, I attempt in this synopsis to calculate the food requirements of Pygoscelid penguins throughout the breeding season, checking individual data against those obtained with a different method or those published in the litterature.

The energy requirements of penguins on land (*Chapter 1*) were determined in Antarctica using respirometry and implantable heart rate transmitters on adults and chicks in conjunction with bird observation, either directly or by a remote-controlled video camera, and records of the microclimate in the colony. Energy expenditure of penguins in the water (*Chapter 2*) were measured by employing, in Antarctica, respirometry to determine the oxygen consumption of penguins while swimming in a 21m long, sea-water filled canal. Additionally, some of the birds were carrying implanted heart-rate transmitters. Data on swimming metabolism were analysed with respect to swimming speed and used to determine the cost of swimming at sea, aerobic dive limits as well as hydrodynamic drag coefficients. A doubly-labelled water study was aimed at obtaining metabolic rates of penguins in the field (*Chapter 3*) and provided independent data to assess the validity of assumptions made in the calculations of field metabolic rates derived from activity budgets and respiratory studies.

Using the apparatus for the investigation of penguin energetics, it was possible to measure (and reduce) the effects of our methods on the well-being of the birds. The results of these investigations are summarized under "Effects of experimental methods on penguin activity and swimming costs" (*Chapter 4*). Finally, helicopter and airplane traffic during provisioning of the station, bird handling by scientists, visits by tourists and oil pollution led to the study of the "Effects of human interference on penguins" (*Chapter 5*). For the sake of clarity, most statistical details were omitted from this synopsis.

1. ENERGY EXPENDITURE OF PENGUINS ON LAND

During the breeding season, the food requirements of penguins on land are essentially determined by a) the microclimate, b) bird activities and c) the amount of energy contributed by body reserves. Furthermore, energy is also required by the growing chicks. Although fine resolution of day-to-day energy requirements throughout the breeding season would be ideal, this could not be achieved. I suggest, therefore, separating the reproductive period into three main sections: 1) incubation, 2) adults with small chicks (brooding) and 3) chicks in crèches. Energy requirements of Pygoscelid penguins for the remainder of the year, i.e. pre-or post breeding and during moult were not determined in this study.

1.1 Microclimate

The microclimate in the Adélie penguin colony at Seal Point, Hope Bay, was recorded (Culik 1995) during the breeding season of 1989-90 and is summarized in Table 1.

Weather conditions were most favourable in the second half of December, when adults were brooding small chicks. Four birds in the same colony had been equipped with heart rate (HR) transmitters (provided by A.J. Woakes, Birmingham; Culik 1995), an indirect method for determining energy expenditure (Woakes and Butler 1983), and were observed every 3 hours for 20 Min. between Dec 14 and Jan 7. Multi-factorial analysis of HR with respect to meteorological variables (n= 1661), however, showed no significant relationship (r^2= 0.05). Presumably, during the study period, factors other than the weather had a stronger influence on HR.

In an earlier study (Culik et al. 1989), HR of incubating Adélie penguins was recorded at the same locality during a storm (Nov 27 to Dec 16, 1987). HR (in beats per Min. or bpm) was found to correlate with wind speed (V_w in m s^{-1}), as HR= 85.8 + 1.35 V_w (r^2= 0.44, n= 51). Furthermore, bird activity was found to be affected by the weather: the number of times penguins stood per hour decreased with wind speed. This led to the conclusion that the lower critical tem-

perature (-10 °C in still air) in Adélie penguins was dependent on both ambient temperature and wind speed, and that these birds, although seemingly well insulated, had to thermoregulate on land even at temperatures above -10°C.

Table 1: Meteorological conditions in the Adèlie Penguin colony at Seal Point, Hope Bay, Antarctica, during the study period in the austral summer of 1989-90.

		Temperature		Insolation	Relative	Wind
		Soil	Air		Humidity	Speed
		(°C)	(°C)	(W m^{-1})	(%)	(m s^{-1})
Dec.	Mean	1.8	-0.8	207	80	4.6
08-18	Minimum	-1.4	-4.1	0	61	0.1
	Maximum	9.2	3.7	909	94	13.7
Dec.	Mean	4.2	1.1	231	84	3.5
19-31	Minimum	-0.1	-2.7	0	45	0.1
	Maximum	0.2	5.9	1091	98	11.1
Jan.	Mean	3.9	0.4	145	88	3.7
1-18	Minimum	0	-2.4	0	54	0.1
	Maximum	11.9	8.1	908	99	15.7

1.2 Activity

According to reports in the literature (Culik et al. 1989) Adélie penguins show some degree of circadian rhythmicity during the breeding season. Using hourly determinations of HR and activity of 5 incubating Adélie penguins, an attempt was made to quantify these rhythms. However, mean HR and activity showed no diurnal periodicity in early Dec (Culik et al. 1989). The general activity pattern of 4 adult Adélie penguins and one chick was subsequently determined on a 3-hourly basis via direct observation (Culik 1995) from a hide (Table 2). During the entire breeding season, resting accounted for more than 55% of all observations made on adults on land, with a maximum of 66.5% during incubation. The chick also rested most of the time (72%).

Table 2: Activities (% of all observations) of four adult Adélie Penguins on land (top) during the austral summer of 1989-90. Periods correspond to incubation, brooding and chicks in crèches (December 14-18, n = 598, December 19-31, n = 588, January 1-7, n = 341, respectively). The lower section indicates the activities (%) of one Adélie Penguin chick during January 12-18, 1988 (n = 745).

		ACTIVITY				
Period	Position	Rest	Motion	Preen	Feed	Walk
Adults						
Dec.	Lie	53.8	8.0	1.2	0	0
14-18	Stand	12.7	11.6	9.2	0.8	2.7
Dec.	Lie	37.7	3.1	0.2	0	0
19-31	Stand	17.7	12.2	16.5	6.5	6.1
Jan.	Lie	13.1	1.1	0	0	0
1-7	Stand	48.1	14.2	16.0	2.8	4.6
Chick						
Jan.	Lie	48.3	1.7	0	0	0
12-18	Stand	24.0	6.4	5.5	4.5	9.4

The energy requirements of resting Pygoscelid penguin chicks (n= 24) were determined in the laboratory via respirometry for the mass (Mb, kg) range of 0.11 - 2.95 kg (Culik 1994). Contrary to that suggested by the literature (Culik et al. 1990a), resting metabolic rates (RMR, in W) were remarkably similar in all 3 species, with RMR= 8.36 $Mb^{0.98}$ (r^2= 0.97). This is significantly higher than in Macaroni (*Eudyptes chrysolophus*) and Rockhopper (*E. crestatus*) penguin chicks, presumably due to the shorter growth period and consequently more rapid biosynthesis in Pygoscelid penguins (Culik et al 1990a).

Adults were less cooperative than chicks, and I was only able to determine resting metabolic rate (Wilson and Culik 1991) in Adélie penguins, where RMR= 4.8 W kg^{-1}. Comparison of this figure with data reported in the literature (see Culik and Wilson 1991c), however, showed that this might have been an overestimate, because the penguins used in this study were also subject to

another treatment (Wilson and Culik 1991) as well as having been implanted with HR transmitters. It seemed reasonable, therefore, to average all the reported findings, which yields a RMR= 3.75 W kg^{-1} (Culik and Wilson 1991c). This is also the value determined by Chappell and Souza (1988).

The energy requirements for walking (MR_w, in W kg^{-1}) were determined for 8 Adélie penguin chicks with respect to walking speed (v, m s^{-1}), and found to be MR_w= 8.9 + 41.3 v for speeds between 0 and 0.3 m s^{-1} (n= 310, r^2= 0.84; Culik et al. 1990a). Technical problems made it impossible to obtain similar data from adults. However, the relationship reported by Pinshow et al. (1977) gives significantly lower energy requirements for walking in adult Adélie penguins, with MR_w= 5.3 + 15.3 v. Penguins, however, do not always walk, but also toboggan over the snow. The incidence of tobogganing is highly correlated with "penetrability", i.e. softness of the snow (Wilson et al. 1991a). Judging from reduced frequency of leg movements with respect to walking, toboganning should be energetically cheaper for penguins travelling over snow or ice. However, no experimental apparatus could be designed to confirm this using respirometry.

Besides resting and walking, penguins also preen, deliver or receive food, or engage in a number of miscellaneous activities while standing or lying. These activities cannot easily be observed under laboratory conditions in a respiration chamber. I wished to measure energy expenditure in the free-living animal with a high degree of resolution (< 1 Min) and therefore sought for a method allowing to integrate all penguin activities on land, while at the same time incorporating the influence of micro-meteorological conditions. This was again best achieved by using implantable heart rate transmitters.

In adults, the lowest HR were observed when the birds were lying down, especially during resting periods (73 bpm in December and 70 bpm in January). HR rose to around 80 bpm when the penguins were standing quietly or preening while standing. Activity (other than preening) in standing penguins, as well as walking, resulted in a rise in HR to 83 bpm (incubation), 96 bpm (brooding) and 85 bpm (chicks in crèches). The highest HR were observed when the birds were feeding their chicks (111 bpm in late December). HR in one chick of crèche age (4 weeks old, mass 2.8 kg) were about 3 times higher than in adults, and the lowest values were recorded when the bird was lying

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quietly (225.3 bpm). Resting or slight activity led the HR to rise to 250 bpm, and the HR rose even higher during preening or walking. The highest values were recorded when the chick was feeding (281 bpm; Culik et al. 1990a, b; Culik 1994). Unfortunately, no data are available for HR and activity of small chicks.

Two adult Adélie Penguins were taken into the laboratory, and O_2-consumption ($l\ h^{-1}$) measured in an open flow respirometry system (Culik 1995) while simultaneously recording HR (Fig. 1). The birds were investigated in a series of experiments on land as well as in the water canal (see below). Activities in the respiration chambers included resting, activity that was not easily quantified such as escape behaviour and general agitation, walking and swimming. The results obtained are summarized by the regression $VO_2=$ -3.96 + 0.084 HR (n= 67, $r^2=$ 0.90, F= 560, p< 0.0001), where VO_2 is oxygen consumption ($l\ O_2\ h^{-1}$).
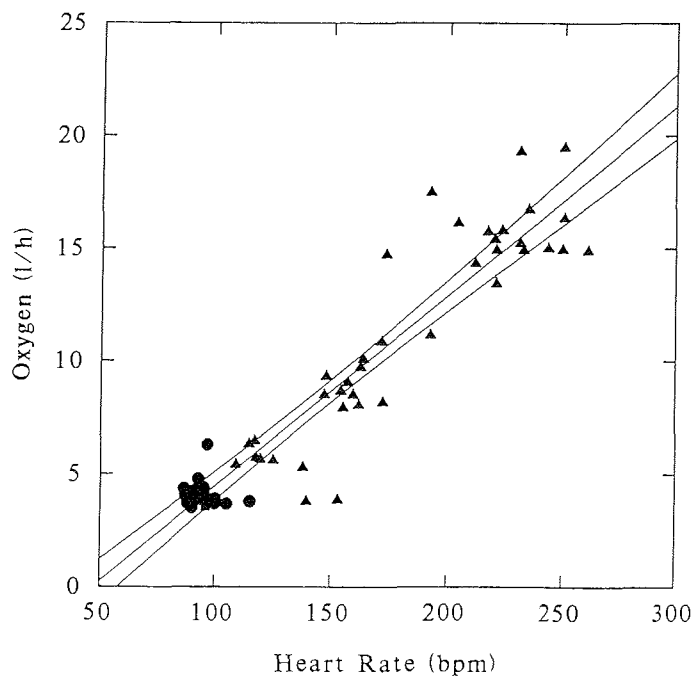
Fig 1: Heart rate (bpm) vs. oxygen consumption ($l\ h^{-1}$) during various activities in two adult Adélie Penguins. Circles: on land, triangles: in a water canal. The relationship obtained was $VO_2=$ -3.96 + 0.084 HR (n= 67, $r^2=$ 0.90, F= 560, p< 0.0001) and is shown with 95% confidence intervals.

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In order to determine mean HR for each period in the brooding cycle, the value for the frequency of each activity (Table 2) and the corresponding HR (Culik 1994) were multiplied and added. The resulting mean HR for adults in the colony was 76.2, 82.6, 80.1 bpm while incubating, brooding small chicks or attending large chicks in crèches, respectively. These values were transformed using the regression above to yield oxygen consumption while at the nest of 2.44, 2.98 and 2.77 l h^{-1}, respectively (penguin mass 4.2 kg).

Time present in the colony was determined by regular nest checks (Wilson et al. 1989c, 1991b). Penguins equipped with depth gauges to determine activity at sea were alternately present at the nest or absent for, on average, 96 and 24.6 h during incubation and brooding, respectively. When the chicks were in crèches, parents remained art the nest for, on average 2.9 h and were absent for 21.1 h. During the incubation and brooding periods, adults had to take turns in leaving the colony, whereas when the chicks were in crèches, both parents could forage simultaneously. The duration of a foraging cycle diminished therefore from a mean of 192 h during incubation to 49.2 h during brooding and 24 h when the chicks were in crèches (Wilson et al. 1991b).

After observation of the chick's activities in the colony, the bird was taken into the laboratory and its oxygen consumption and HR were recorded in a respiration chamber. Three other chicks which had been kept in captivity (mass 2 - 3.4 kg) were used in similar experiments; the resulting regressions did not differ markedly from each other (ANCOVA, p>0.05). The birds were used in two sets of experiments: 1) in a respiration chamber with a treadmill, and 2) in a chamber without a treadmill. Accordingly, data were grouped to fit two regressions: 1) VO_2= -7.23 + 1.82 Mb + 0.03 HR (r^2= 0.59, n= 222) for all activities except for walking, and 2) VO_2= -11.89 + 1.17 Mb + 0.058 HR (r^2= 0.7, n= 98; Culik et al. 1990a).

As was done for the adults, mean HR of the chick while in the colony was calculated for resting and standing (237.5 bpm), and walking (257.7 bpm). Taking into account the relative proportions of the different behaviours (90.6% for rest and other activities and 9.4% for walking), this corresponds to a mean of 5.54 litres O_2 h^{-1} for a 3.04 kg chick (mean mass in crèches, Trivelpiece *et al.* 1987). In other words, metabolic rate of chicks in crèches is 1.43x RMR. No

HR data being available for brooded chicks, it was assumed that these consume, since they rarely walk, on average 1.2x RMR (Culik 1994).

1.3 Adult body reserves

The body mass of marked adult Adélie penguins was determined between Dec 22 and Jan 30 (n= 6) in 1989-90 and 1987-88 (Wilson et al. 1991b). Weighing took place ca. 20 hours after the birds were presumed to have last fed (Wilson et al. 1989c) in order to minimize the effects of variable stomach contents.
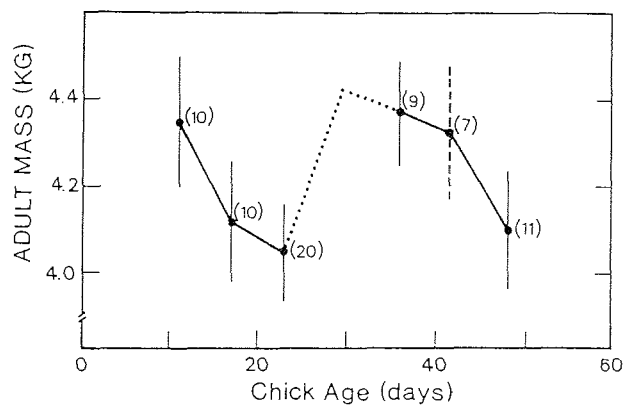
Fig 2: Changes in Adélie penguin body mass (kg) at Hope Bay, Antarctica, in relation to chick age. Data points represent means, vertical bars SE and values in brackets sample sizes. Solid SE bars: data from 1989-90 season, dashed SE: data from 1987-88 season. Mean chick hatching date (age= 0) was Dec 14.

Mean penguin mass dropped from 4.35 kg (SE= 0.16, n= 10) 11 days after the mean hatch date (chick age 0= Dec 14) to 4.05 kg (SE= 0.14, n= 20) just before the chicks began to join crèches. Subsequently, during the crèching period, mean adult mass rose again to 4.37 kg (SE= 0.12, n= 9) before decreasing to 4.19 kg (SE= 0.13, n= 11) at a mean chick age of ca. 50 d (Fig 2). Body mass decline was attributed to fat loss (Culik 1995), averaging 1 g h^{-1} before chicks joined crèches and 0.6 g h^{-1} thereafter, corresponding to 2 and 1.2 l O$_2$ h^{-1}, or 11.1 and 6.7 W, respectively. This entails that adults (RMR of 4.35 kg animal:

16.3 W) were only able to meet 32% and 59% of their energy requirements by digesting food during these two phases of the breeding season, respectively.

## 2. ENERGY EXPENDITURE OF PENGUINS IN THE WATER

Penguins, seals, dolphins and other sub-surface swimmers appear to move effortlessly through the water, gliding for long distances. Determination of the energetic costs of swimming, however, has proved difficult. In water flumes (Woakes and Butler 1983; Baudinette and Gill 1985; Ponganis et al. 1990) animals are forced to maintain a stationary position, cannot move freely nor swim at their preferred speeds, and incur turbulence and increased drag from the surrounding cage. Energy consumption of animals in the wild has been measured indirectly through heart rate (Woakes and Butler 1983; Williams et al. 1992) or using doubly-labelled water (Nagy et al. 1984; Culik and Wilson 1992; Chappell et al. 1993a), requiring a number of assumptions (Wilson and Culik 1993 and unpublished data), and careful interpretation of results.

In Antarctica, we used 1) externally-attached data-logging devices to determine swimming speeds and dive durations of penguins in the wild, and 2) a 21m long, still-water canal in conjunction with respirometry to determine the energy requirements of freely swimming Pygoscelid penguins directly. The results of these investigations on the living animal were 3) used to calculate aerobic dive limits, 4) compared to measurements made on plastic-cast, true-to-life penguin models and 5) compared to published transport costs of other, sub-surface swimming homeotherms. Finally, 6) the energetic requirements of heating cold food, incurred by penguins feeding on krill, were determined in the laboratory using respirometry.

2.1 Swimming speeds and dive durations of Pygoscelid penguins

Instruments measuring speed, depth and direction (Wilson et al 1993a) were shaped to minimize hydrodynamic drag (Culik et al. 1994a) and attached (Wilson and Wilson 1989a) to breeding Pygoscelid penguins at their nest site. Speed sensors were calibrated on a life-size cast model of a swimming Adélie penguin (Bannasch & Fiebig, 1992; experiments conducted in the circulating water tank of the Versuchsanstalt für Wasserbau und Schiffbau, Müller-Breslau Str. D- 10623 Berlin, Germany) as well as on living penguins in the swim canal in Antarctica. Adélie, Chinstrap and Gentoo penguins in the wild swam at mean

speeds of 2.2, 2.4 and 1.8 m s^{-1} (SD= 0.7, 0.7, 0.6, n= 1695, 2255 and 1653 from 17, 11 and 7 birds), respectively (Fig 3, Table 3; Culik et al. 1994b). Mean dive durations were 85, 78 and 86 s (SD= 28, 30, 35; n= 1613, 1636, 733, with 17, 11 and 7 birds used), respectively (Culik et al. 1994b).
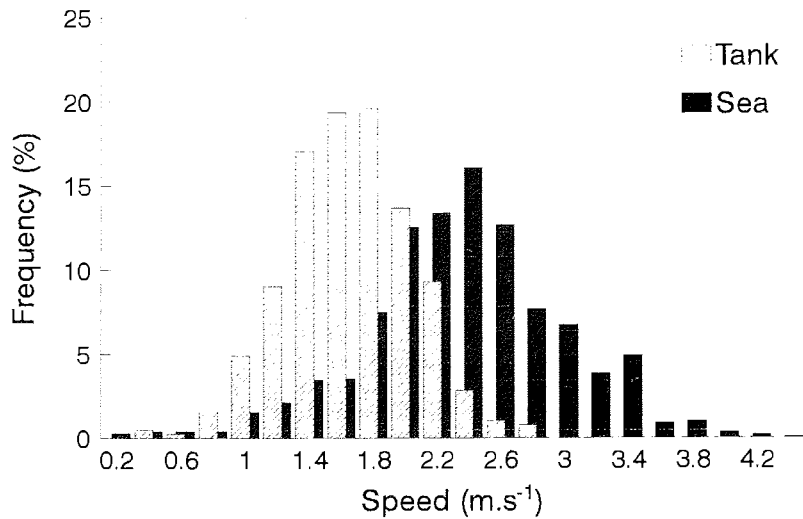

Fig 3: *Distribution of swimming speeds of Adélie penguins at sea, as determined with externally-attached instruments, and in the swim canal as determined via direct observation. The mean speed of Adélie penguins in nature (2.2 m s^{-1}) was also attained in the canal (mean speed 1.7 m s^{-1}) in 9% of all experiments.*

2.2 Experiments in the swim canal

The still-water canal as a technique for measuring energy requirements of swimming Pygoscelid penguins was first used at Esperanza station during the field season of 1987-88. The canal consisted of a 21 m long (plywood and steel frame) construction, 0.9 m wide and 0.7 m deep, sealed with a transparent polyethylene sheet and filled with sea-water (4°C). It was covered with transparent PVC sheets (10 cm beneath the water's surface) made conspicuous with netting to prevent the birds from surfacing while at the same

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Fig 4: (Top) The swim canal was 21m long and covered with transparent PVC-sheets to prevent the birds from surfacing. Penguins could only obtain air in respiration chambers placed at each end of the canal. Their behaviour, swimming speed and distance swum were observed from above using a head-set microphone and a tape recorder. The mirror on the left was used in a project aimed at studying swimming kinematics. (Bottom) While swimming in the canal, this Gentoo penguin is being coached by two conspecifics awaiting their turn. The birds learned within a few minutes where they could surface to breathe and were generally very cooperative.
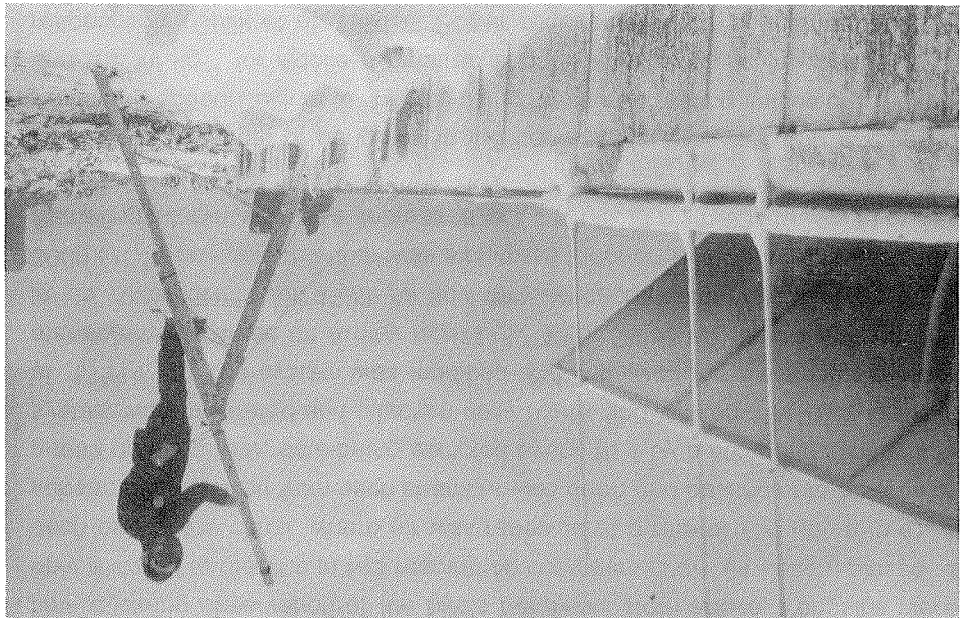
time allowing observation of the bird's behaviour from above. Penguins were only allowed to breathe in two respiration chambers (Vol= 94 l each) placed at each end of the canal, where air was renewed at a rate of 750 l h^{-1}(Fig 4). A subsample of the air from each chamber was dried and passed onto a paramagnetic gas analyser, data being sampled every 10 s by a computer. The whole system was calibrated and checked daily (Culik and Wilson 1991b, c; Culik et al. 1991a, b). The system was modified and improved for a second series of measurements made on Ardley Island (62°13'S, 58°55'W), South Shetland Islands, Antarctica in Jan 1992: Air flow through each chamber was increased to 3000 l h^{-1} and each chamber was monitored independently with one analyser. Sampling interval was also decreased to 2 s (Culik et al. 1993, 1994a, b).

Power requirements of penguins in the canal were analysed with respect to swimming speed(Culik et al. 1994b) using measured resting values of 8.4, 8.75 and 8.2 W kg^{-1} for Adélie, Chinstrap and Gentoo penguins in water at 4°C, respectively (Culik et al. 1991a). Power requirements for penguins resting in the canal were lower than reported in the literature. For instance, Kooyman et al. (1976) found that Adélie penguins "resting" in water at 4°C required 11 W kg^{-1} or 30% more than in my experiments. However, in the study of Kooyman et al. (1976) the birds were strapped to a board and forcibly immersed into the water.

Power requirements of Pygoscelid penguins resting in cold water were remarkably similar, and did not reflect the differences in mean sea water temperatures experienced by the three species (0, +3 and +10°C in Adélie, Chinstrap and Gentoo penguins, respectively, Culik et al. 1991a). The values were used to calculate thermal conductance of the birds, which was found to be 3.2, 3.3 and 3.3 W °C^{-1} m^{-2}. These values coincide well with the thermal conductance determined for Adélie penguin pelts (3.25 W °C^{-1} m^{-2}; Kooyman et al. 1976). Interestingly, thermal conductance in Humboldt penguins (*Spheniscus humboldti*) as calculated from the data in Butler and Woakes (1984) was also similar at 2.86 W °C^{-1} m^{-2}, although these birds live in Peru and Chile where sea water temperatures average 14°C. Correspondingly, (assuming a linear relationship) metabolic rate of penguins resting in water (P_r in W kg^{-1}) is related to temperature by P_r= -0.3 T_a + 9.61, where T_a is ambient temperature in °C (Culik et al. 1991a).

The measured power requirements while swimming (P_s, in W kg^{-1}) were best matched (Fig 5a) by a cubic function of the type $P_s= av + bv^2 + cv^3 + P_r$, where v is swimming speed(m s^{-1}). Transport costs (COT, the cost of transporting 1 kg of mass over 1 m, in J kg^{-1} m^{-1}) are obtained using the function COT= P_s / v (Table 3). The resulting curve fit for Adélie penguins (COT vs. swimming speed) is shown in Fig 5b (Culik et al. 1994b). Power requirements while swimming, as well as transport costs were analysed similarly in Chinstrap and Gentoo penguins.

Table 3: Transport costs (COT in J kg^{-1} m^{-1}) of Pygoscelid penguins swimming under-water are best described by COT= $(av + bv^2 + cv^3 + P_r) / v$, where v is swimming speed(m.s^{-1}). Power required for resting in water is given by P_r (W kg^{-1}). n refers to the number of measurements made, animal n indicates the number of birds used, mass is their mean mass and SD the standard deviation of the mass.

|	Adélie	Chinstrap	Gentoo
a	9.84	14.29	18.28
b	-6.75	-8.84	-14.72
c	1.7	1.66	3.89
P_r (W kg^{-1})	8.4	8.75	8.2
r^2	0.98	0.75	0.82
animal n	12	7	10
mass (kg)	4	3.8	5.5
SD	0.4	0.3	0.6
Speed			
range (m s^{-1})	0.8-2.8	1-2.4	0.4-2.4
mean (m s^{-1})	1.67	1.77	1.49
SD	0.4	0.3	0.4
n	387	228	139

In the swim canal, penguins determined their own swimming speed, which averaged 1.7 m s^{-1} (SE= 0.03, n=148) for all three species (Fig 3; Culik et al.

1991a, 1994b). A detailed analysis showed that Adélie penguins accelerated from 0 to 2.4 m s^{-1} within the first 3 m of the canal, maintaining a speed > 2 m s^{-1} for more than half the distance (Culik and Wilson 1991c). These speeds are significantly higher than the speeds at which Hui (1988) and Baudinette and Gill (1985) conducted their experiments on Humboldt and Little (*Eudyptula minor*) penguins. Furthermore, these authors had used turbulent water flow through a cage, in which the penguin was supposed to swim. As a result, the transport costs determined in these studies are significantly higher than those determined for Pygoscelid penguins using the still-water canal (Table 4). Nagy et al. (1984) determined swimming energetics in free-living African penguins (*Spheniscus demersus*) using doubly-labelled water and speed meters attached to the birds. Problems associated with their interpretations, such as deriving transport costs from RMR on land, FMR and time/activity budgets are discussed in Culik and Wilson (1991c) and Wilson and Culik (1993).

Table 4: *Cost of transport (COT, in J kg^{-1} m^{-1}) in penguins with respect to swimming speed(m s^{-1}) during the experiment and natural speed at sea (top: literature, middle: Esperanza, bottom: Ardley). [a]Hui (1988); [b]Baudinette and Gill (1985); [c]Nagy et al. (1984); [d]Culik and Wilson (1991c); [e]Culik et al. (1991a); [f]Culik et al. (1994b); [g]Wilson et al. (1989a); [h]Stahel and Gales (1987)*

Species	COT	Swimming Speed	
		experiment	nature
Humboldt[a]	13.4	0.5-1.25	1.9[g]
Little[b]	12.1	0.6-0.9	1.5[h]
African[c]	15.5	1.7-2.3	2.2[g]
Adélie[d]	7.5	2.1	2.2[f]
Chinstrap[e]	4	2.5	2.4[f]
Gentoo[e]	7	2.3	1.8[f]
Adélie[f]	7.1	2.2	2.2[f]
Chinstrap[f]	6.3	2.4	2.4[f]
Gentoo[f]	8.9	1.8	1.8[f]

The two data sets on Adélie penguins (Table 4) differ by only 6% from each other, although the equipment had been modified. The discrepancies between the two sets of measurements are larger for Chinstrap and Gentoo penguins (57% and 27%, respectively). However, these birds were not as cooperative as Adélie penguins and often could not be induced to swim or engaged in escape behaviour while in the canal. The general trend, i.e. low transportation costs in Pygoscelid penguins for free sub-surface swimming at preferred speed, however, is not affected by this.
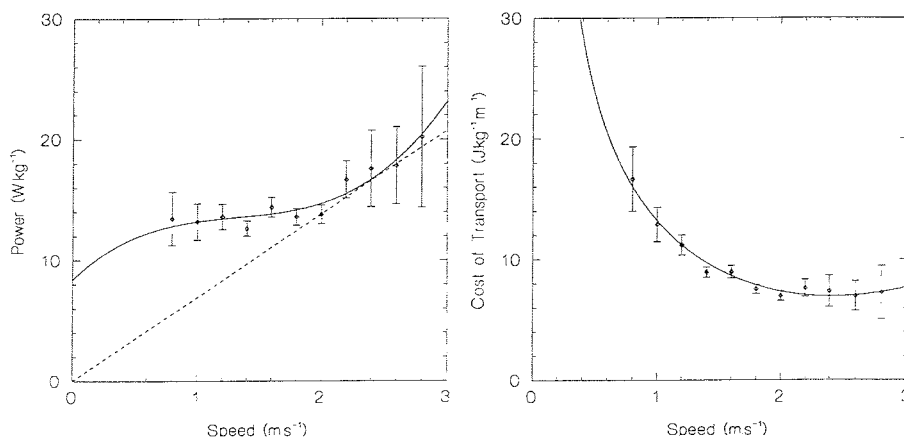
Fig.5: (left) Power input (W kg⁻¹) in Adélie penguins (n= 12) swimming at will in a 21m long, sea-water filled canal in Antarctica (r²= 0.91). The stippled line touches the power curve where transport costs are lowest. (right) Transport costs (COT) in Adélie penguins as calculated from power input (COT= Power / speed; r²= 0.98). Bars show standard error of the means.

Transport costs of Adélie penguins in the canal are lowest at 2.4 m s⁻¹ (Fig 5a). This is somewhat surprising, since the birds prefer to swim at 2.2 m s⁻¹ in the wild (Table 4). However, experiments with Adélie penguins carrying externally attached data-loggers in the swim canal (such as those employed here to measure swimming speed in the wild) showed that swimming speed was reduced by 7.7% (see chapter 4 and Culik et al. 1994a). Thus, without instrumentation, Adélie penguins in the wild possibly have a higher mean speed of 2.4 m s⁻¹.

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2.3 Aerobic dive limits

Prior to a dive, penguins store oxygen in arterial and venous blood, muscle tissue and air sacs (Kooyman 1989). The total amount of oxygen available to the birds while swimming under-water can be calculated if parameters such as the oxygen binding capacity of blood and muscle and the saturation prior to the dive are known. In the case of the Adélie penguin, these parameters are available from the literature. They are summarized in Table 5.

Similar calculations for Chinstrap and Gentoo penguins yield oxygen stores of 57 and 63 ml O_2 kg^{-1}, respectively, prior to a dive. It is surprising that Pygoscelid penguins should store more than 30% of the oxygen required during the dive in their air sacs and use this, presumably by ventilating their lungs, without suffering from aeroembolism, i.e. the bends. It is unlikely, however, that the oxygen in the respiratory tract is available to the exercising muscles during the dive. As in most other air breathing aquatic animals (Kooyman 1989) penguins engage in diving bradycardia after submersion, reducing HR from pre-dive rates as high as 250 beats per minute (bpm) to 107 bpm during the dive (Culik 1992). Muscle perfusion is presumably mainly restricted to the interdive interval (i.e. when the bird is at the surface) with an associated tachycardia of HR= 258 $T_s^{-0.2}$ (found in one Adélie penguin where HR is in bpm, and T_s is the duration of surface time in s; r^2= 0.43, n= 40 measurements, Culik 1992), which diminishes with surface time. However, it is now widely assumed that penguins and other birds dive after inspiration and use the oxygen in their respiratory system while diving (Croll et al. 1992, Kooyman 1989, Stephenson et al. 1989), although the mechanisms for this are still poorly understood.

The aerobic dive limits of Pygoscelid penguins can be calculated using the function and parameters determined for under-water swimming in the canal (Table 3). Using transport costs as determined in the swim canal, I calculated that the birds are able to dive aerobically for 76, 76 and 79 s, respectively (Table 6), significantly longer than previously suggested (e.g. Chappell *et al* 1993b). However, penguins in the canal had to accelerate and decelerate once every 21m (the length of the canal), something which they would not normally do in nature. Trivelpiece et al. (1986) using radio transmitters on Adélie penguins determined that the birds would swim for ca. 1 Min below the water

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surface before stopping in order to breathe. At their normal cruising speed of 2.2 m s^{-1} this amounts to a distance of 132 m. In order to compensate for this, the physical power required to accelerate and decelerate (P_a, in W kg^{-1}) was subtracted from the power requirements of penguins swimming in the canal (see Table 3). This correction term was (after the appropriate transformations) $P_a = -v^3 / (m.f.l)$, where m is muscle efficiency (0.25, Schmidt-Nielsen 1983), f is flipper efficiency (0.4, Oehme and Bannasch 1989) and l is the length of the canal (21m). The corrected power requirements are those for sustained swimming at constant speed.

Table 5: *Total oxygen stores in Adélie penguins amount to 58.6 ml kg^{-1} prior to a dive. 12.7% of this is stored in arterial blood, 27% in venous blood, 28.8% in the muscles and 31.5% in the air sacs.*

|	Blood				
	Arterial	Venous	Muscle	Air sacs	Source
Proportion of body mass (%)	3.4	8.9	35		Chappell et al. (1993b)
Amount of resp. pigment (g l⁻¹)	175	193	36		Chappell et al. (1993b) Mill and Baldwin (1983)
Oxygen binding capacity (ml g⁻¹)	1.37	1.37	1.34		Lenfant et al. (1969) Kooyman (1989)
Saturation prior to dive (%)	95	70	100	17.6	Stephenson et al. (989) Croll et al. (1992)
Oxygen available during dive (%)	96	96	100	75	Stephenson et al. (1989) Croll et al. (1992)
Volume of air in resp.tract (ml kg⁻¹)				140	Chappell et al. (1993b)
Oxygen (ml kg⁻¹)	7.43	15.81	16.88	18.48	

Aerobic dive time for sustained swimming in Adélie penguins (ADT_c, s) was calculated using $ADT_c = 20.1\ OXY\ /\ (P_s - P_a)$, and corresponding dive distance (ADD_c, m) using $ADD_c = 20.1\ v\ OXY\ /\ (P_s - P_a)$. The conversion factor is 20.1 J ml^{-1} O_2, OXY are O_2 stores (ml) available prior to a dive, P_s (W) is the power required for swimming in the canal, P_a (W) is the energy required for both acceleration and deceleration and v is swimming speed($m\ s^{-1}$). Aerobic dive limits not corrected for acceleration and deceleration have $P_a = 0$ in the above equations.

Maximum under-water time (Fig 6, stippled line) is obtained if the penguin stops swimming, since energy requirements in the water are lowest during rest. However, aerobic under-water time (in the canal, lower stippled line) of ca. 90 s can be maintained over a wide speed range, although it decreases sharply at speeds >2m s^{-1}. When swimming at constant speed (i.e. after subtracting the energetic cost associated with acceleration and deceleration), the maximum dive time still occurs at v=0, i.e. when birds rest under-water. A second peak (upper stippled line), however, is found at 2.6 m s^{-1}, with an aerobic dive time of 120 s. Since penguins do have to accelerate in the wild, at least once every time they dive, their aerobic dive times will lie somewhere in between the two stippled curves shown in Fig 6.

In a similar manner to aerobic dive time, aerobic dive distance during sustained swimming increases at higher speeds (no acceleration or deceleration: upper solid line), so that for example birds swimming at 3 m s^{-1} can travel 350 m before oxygen stores are depleted. The probability of prey encounter is dependent on distance travelled (Wilson 1991), and therefore the overall rate of prey encounter depends on swimming speed. However, since penguins are visual hunters (Wilson et al. 1989c, 1993b), the number of prey perceived per unit time is likely to decrease if penguins swim too fast (Wilson 1991). Thus, appropriate optimization for penguins swimming under-water may be time, distance or speed dependent. The choice to optimize for any of these parameters is itself dependent on activity, e.g. travelling to foraging areas, searching or feeding.

Aerobic dive limits were calculated (Table 6, Culik et al. 1994b) using mean speeds determined by data loggers (see above) and deriving the power requirements and transport costs for those speeds. Using data on penguin dive

durations in the wild, also determined by data-loggers (Culik et al. 1994b), I calculated the percentage of these dives exceeding the estimated aerobic dive limits. Thus, in the wild, 54% of all Adélie penguin dives exceed 76s, the aerobic dive time for birds swimming in the canal. However, when swimming at constant speed (i.e. without acceleration and deceleration, assuming transport costs of 4.8 J kg^{-1} m^{-1}) only 14% of all dives in the wild exceed 113 s. Using the same procedure, only 4% of all dives made by Chinstrap penguins exceed the aerobic dive time and 96% of all dives are calculated to be aerobic, if the birds use sustained swimming for under-water locomotion.
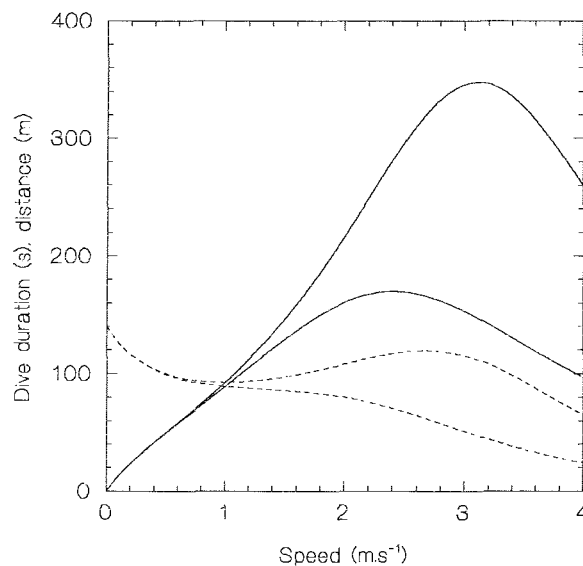
Fig 6: Dive distance (m; solid lines) and dive duration (s; stippled lines) for Adelie penguins, calculated using the data from the swim canal experiments (lower lines) and after correction for acceleration and deceleration (sustained swimming: upper lines). While accelerating and decelerating every 21 m, an Adélie penguin can cover for example 175 m at 2.4 m s-1 within its aerobic dive limits. If the animal swims without interuption (sustained swimming) and does not accelerate or decelerate, that distance increases to 350 m at 3 m s-1.

Contrary to the results of Chappell et al. (1993a) it would thus appear that in Adélie penguins, power required for swimming is not 8.2x BMR or 29.7 W kg^{-1}, which would allow aerobic dive times of only 39 s (interestingly, Chappell et al. 1993b, using time depth recorders measured mean dive times of 73s). There also seems to be no need to search for anaerobic biochemical pathways in order to explain the long duration of penguin dives. In fact, investigation of the

muscle fibers of Little penguin (*Eudyptula minor*) pectoralis and supracoracoideus, the muscles employed in swimming, showed that they were basically aerobic with little capacity for producing ATP during muscle anoxia (Mill and Baldwin 1983). These findings were mirrored for the Adélie penguin by Bannasch (1986). Thus, it seems that, rather than diving anaerobically, penguins simply consume very little energy (2.9 - 4.3 xBMR) while swimming under-water, and perhaps even less than calculated here. In this regard it is important to note that the swim canal was only 0.9 m wide, leaving about 0.15 m on either side of the penguin flippers, thereby increasing hydrodynamic drag on the swimming birds through wall effects.

Table 6: *Aerobic dive limits calculated for swimming Pygoscelid penguins. (For calculation of power requirements for swimming and oxygen stores see Tables 3 and 5, respectively). Swimming speeds and dive durations of penguins in nature were obtained using externally-attached data-loggers (Culik et al. 1994b) A) Data obtained in the swim canal and B) calculated by subtracting power required for acceleration and deceleration in the canal from A). "Dives exceeding ADT" (aerobic dive time) is the proportion of dives made by Pygoscelid penguins in the wild lasting longer than the ADT.*

	Adélie	Chinstrap	Gentoo
Oxygen stores (ml kg^{-1})	58.6	57	63
Swimming speed(m s^{-1})	2.2	2.4	1.8
A: In the canal			
Power (W kg^{-1})	15.5	15.1	16.1
COT (J kg^{-1} m^{-1})	7.1	6.3	8.9
Aerobic dive distance (m)	167	182	142
Aerobic dive time, ADT (s)	76	76	79
Dives exceeding ADT (%)	54	37	62
B: Sustained swimming at sea			
Power (W kg^{-1})	10.5	8.5	13.3
COT (J kg^{-1} m^{-1})	4.8	3.6	7.4
Aerobic dive distance (m)	248	322	171
Aerobic dive time, ADT (s)	113	134	95
Dives exceeding ADT (%)	14	4	44

Assuming the energy content of fresh krill to be on average 3.7 kJ g^{-1}(Davis et al. 1989), an Adélie penguin of mass 4 kg swimming in the canal requires 7.6 g krill per km. With the energy liberated from 1 g of krill, the bird could swim 0.13 km. Assuming the stomach capacity of the Adélie penguin in this example to be 1000 g, the bird would have a range of 130 km with the energy liberated from a full stomach. While swimming continuously, without surface pauses every 21 m, krill requirements per km are reduced to 2/3, so that a full stomach would allow a penguin in the wild to cover nearly 200 km. This is considerably more than the distance a penguin could cover by foot, since during walking, krill is consumed at a rate of 31 g km^{-1}, which gives a maximum range of only 32 km (calculated from Pinshow et al. 1977).

2.4 Hydrodynamic drag

The low values reported for penguin swimming energetics (Culik and Wilson 1991b, c; Culik et al. 1991b, 1993, 1994a, b) using the swim canal could recently be supported by independent measurements made on a plastic-cast true-to-life model of a swimming Adélie penguin (Bannasch & Fiebig 1992). The hydrodynamic characteristics of the model were tested in a large circulating water tank at the Institut für Waserbau und Schiffbau, Berlin (Bannasch et al. 1994). The model was wingless, which meant that the drag coefficient of the body only was assessed.

While maintaining a sustained swimming speed of v= 2.2 m s^{-1}, live Adélie penguins have a power consumption of 10.5 W kg^{-1}(Table 6) or 42 W for a 4 kg bird. Assuming muscle and flipper efficiencies to be 0.25 (Schmidt-Nielsen 1983) and 0.4 (Oehme and Bannasch 1989, Culik and Wilson 1991c), respectively, the mechanical power (Pm) generated by the swimming penguin is only 10% or 4.2 W. Since the drag coefficient C$_d$= 2F / dv^{2}A, where F is the drag force F= Pm / v, d is the density of the medium (1028 kg m^{-3} for sea water at 4°C), v is the swimming velocity and A is the frontal area of the bird (0.02083 m^2, Oehme and Bannasch 1989) a drag coefficient of 0.0368 was calculated for Adélie penguins at that speed. This value is expectedly lower than the drag coefficient of C$_d$= 0.0496, measured on the inflexible Adélie penguin model in Berlin at 2.2 m s^{-1} (sea-water, 4°C, 3.5% salinity; Bannasch et al. 1994; Culik et al. 1994b), and is better than the drag coefficient of an ideal spindle (Cd =

0.04, Nachtigall and Bilo 1980). The model, however, did not have the feathered surface structure and the compliant body of the living animal, characteristics which can reduce hydrodynamic drag by a large fraction (Bannasch, pers. comm.). The similarity of these results, however, independently supports the validity of the findings on living penguins.

In a personal communication, Bannasch suggested subtracting basal metabolic rate (3.7 W kg^1) from the power required for maintained swimming. This net power input of 6.8 W kg^{-1} (P_m= 2.7 W) would yield a C_d= 0.0238, all other things being equal. The question arising from this is whether the C_d could really be that low in the swimming penguin, or whether other parameters, such as muscle and flipper efficiency would have to be adjusted to more realistic values. The efficiency of a ship's propeller, e.g. is 0.8 or twice that assumed here for a penguin's flipper (Bannasch, pers. comm). This field is now open for further investigation and modelling.

2.5 Transport costs in sub-surface swimmers

Combining the values for sustained swimming in Pygoscelid penguins with transport costs (measured in experiments considered 'realistic', see p. 22) from other homeothermic sub-surface swimmers such as seals (*Phoca vitulina*; Davis et al. 1985), sea lions (*Zalophus californianus*; Costello and Whittow 1975, Feldkamp 1987) and dolphins (*Tursiops truncatus*; Williams et al. 1992), where body mass (Mb) ranged between 3.8 and 145 kg, transport costs were found to be COT= 7.01 $Mb^{-0.205}$ (r^2= 0.43, n= 9; Fig. 7, Culik et al. 1994b). Transport costs of Chinstrap penguins are lower than predicted by this curve, those of Gentoo penguins are higher, and those of Adélie penguins are almost the same as predicted.

Unfortunately, data available on sub-surface swimmers are still sparse or not comparable due the differences in the methods employed. Swimming costs in dolphins (Fig 7, square) for instance, stem from indirect measurements of energy consumption in open water using heart rate. HR had been calibrated in the laboratory via respirometry, the animals swimming against the drag of a load cell, and the problems associated with diving bradycardia could not be eliminated from the tests conducted in open water (see Williams, Friedl et al.

1992). Although the relationship shown (Culik et al. 1994b) is therefore only a first approximation, transport costs in sub-surface swimming homeotherms are approximately 3.3 x higher than extrapolated for swimming salmon (Brett 1964) and only one third of the transport costs of surface swimming homeotherms (Williams 1989).
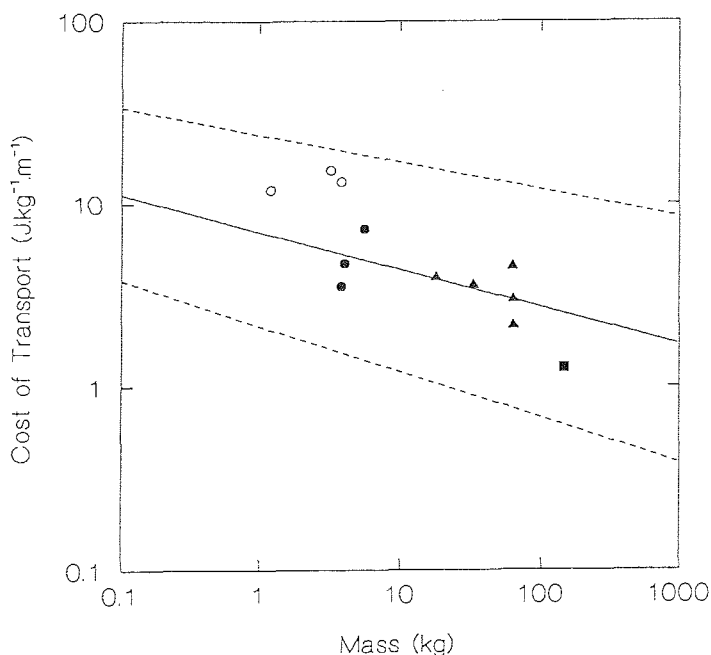
Fig. 7: Transport costs (COT) in sub-surface swimming homeotherms (continuous line) were calculated from data presented here (filled circles) and published results on pinnipeds (Davis et al. 1985, Costello and Whittow 1975, Feldkamp 1987, triangles) and bottlenose dolphins (Williams, Friedl et al. 1992, square). The resulting regression is $COT= 7.011 \, Mb^{-0.205}$ ($r^2= 0.43$, $n= 9$). For comparison, previously published results on penguins (Baudinette and Gill 1985, Nagy et al. 1984, Hui 1988, open circles), derived from experients at slow speeds in turbulent water flumes or using doubly-labelled water are also shown. The upper dotted line shows COT in surface-swimming homeotherms (Williams 1989), where $COT= 23.9 \, Mb^{-0.15}$, and the lower dotted line is COT in fish extrapolated from swimming salmon (Brett 1964), where $COT= 2.15 \, Mb^{-0.25}$.

2.6 The cost of heating cold food

Besides transport costs, swimming Pygoscelid penguins foraging for them-selves and for their brood incur metabolic costs because they feed on marine ectotherms. Sea water as well as krill (*Euphausia superba*) temperatures in Antarctic waters average 0°C, whereas the body temperature of e.g. Adélie penguins is 38.8°C (Wilson and Culik 1991). In order to test the amount of energy required to heat cold stomach contents, post-absorptive (i.e. the birds had not fed for > 6h) Adélie penguins (n= 5) carrying temperature transmitters implanted into the body cavity were fed either cold krill or cold water at 0°C or hot krill or hot water at 37°C and then immediatly placed into a respiration chamber to determine oxygen consumption and HR for periods of 100 Min. The experiments were repeated (after appropriate delays) until every bird had been fed all of the substances above (Wilson and Culik 1991).

The results showed that in all birds fed cold krill or cold water, metabolic rates (MR) rose to a maximum of 4x pre-ingestion levels, before decreasing after 20 Mins to become constant. Cold-fed penguins had 20% higher MR for as long as 45 Min after ingestion and 12% lower core temperatures than before (pre-ingestion levels: 3.7 W kg^{-1} and 38.8 °C, respectively). Core temperature (measured on the stomach wall, within the peritoneal cavity) decreased to 32.9 °C in birds fed cold water, but only to 37.1 °C in birds fed cold krill.

By integrating oxygen consumption during these experiments to the point where MR were again as low as during resting, it was found that Adélie penguins need to invest 110 kJ in order to heat 1000 g (average daily catch, Trivelpiece et al. 1987) of cold krill from 0 to 39 °C (Wilson and Culik 1991). This is somewhat less than the result obtained by calculating the amount of energy physically required (167 kJ) to heat this mass (specific heat capacity of krill of 4.17 J g^{-1} °C^{-1}).

Penguins could either be reducing the immediate energetic cost of heating cold food by extending the heating process, or/and by using muscle-generated, ex-cess heat while foraging. The extent of such an energy-saving strategy, which would depend largely on ingestion rates, is still unknown. For the purpose of calculation of overall energetic requirements (Chapter 3), the (comparatively small) costs of heating cold food will therefore be included.

3. METABOLIC RATES OF PENGUINS IN THE FIELD

The results presented in Chapters 1 and 2 are necessary prerequisites for the calculation of overall energy -, and derived from this, food consumption of Pygoscelid penguins in the wild. Using energy consumption as determined for the major activities together with activity budgets, I was able to calculate a) the amount of food required during the breeding season by chicks and b) the amount of food required by the adults for their own needs and those of their brood. The results of these model calculations were checked against c) field metabolic rates determined on Adélie penguins during the breeding season using doubly-labelled water.

3.1 Food requirements of Pygoscelid penguin chicks

The duration of the growth period of the three species (Trivelpiece et al. 1987) differs. On the Antarctic Peninsula, Adélie and Chinstrap penguin chicks fledge 50 - 55 days after hatching, while Gentoo penguin chicks require 71 days (Trivelpiece et al. 1987, 1990). Growth constants of Pygoscelid penguins reflect this, Adélie and Chinstrap penguins having higher growth constants than Gentoo penguins (Volkman and Trivelpiece 1980). As derived from adult stomach contents, the amount of food delivered to Gentoo penguin chicks until fledging is more than twice the amount delivered to the chicks of the two other species (Trivelpiece et al. 1987).

Since chick energy demands influence the foraging behaviour of Pygoscelid penguin parents (Wilson and Culik 1992), these demands could be a key parameter in reducing competition and thereby segregating the ecological niches of Adélie, Chinstrap and Gentoo penguins in areas where the 3 species are sympatric (c.f. Trivelpiece et al. 1987).

Using the data presented in Trivelpiece et al. (1987, 1990) on duration of parental care and chick mass, as well as the data on chick body composition derived by Myrcha and Kaminski (1980) together with metabolic rates determined here, I calculated the amount of krill required by Pygoscelid penguin chicks (Fig 8; Culik 1994). The following assumptions were made: a) Brooded

chicks spend 60% of their time resting and 40% active. The latter includes thermoregulatory costs (Culik 1995). Therefore MMR= 1.2 RMR (MMR= mean metabolic rate, RMR= resting metabolic rate). b) Chicks enter crèches at age 21 d (Trivelpiece et al. 1987). c) In crèches, activity (and thermoregulatory) costs are increased with respect to brooded chicks, and MMR= 1.43 RMR (Culik 1995). d) Penguins feed to 100% on krill. This is a slight over-estimation, as Adélie and Chinstrap penguins feed to 99% on krill and Gentoo penguins only to 86.5% (Trivelpiece et al. 1987). e) Metabolisable energy content of krill = 3.7 kJ g^{-1} (Davis et al. 1989). f) Metabolic rates of chicks decrease to 1.3 times adult levels within 9 d after peak mass is reached (Brown 1987). Adult penguins have a RMR= 0.027 $Mb^{0.74}$ (Brown 1987) and MMR= 1.43 RMR in large chicks (Culik et al. 1990a did not present results for fledging chicks). g) while chicks grow, RMR as measured by respirometry accounts for synthesis costs, to which tissue energy content (Myrcha and Kaminski 1980) has to be added (Brown 1987).

In order to feed one Adélie penguin chick from hatching to fledging (Culik 1994; Fig 8), parents need to provide 29.8 kg of krill over a period of 54 days (5.2 kg from hatching to the crèche phase and 24.6 kg from then until fledging). In Chinstrap penguins this value is very similar, at 31.7 kg per chick over 54 days. Gentoo penguin parents, however, have fed a single chick 46 kg within the first 54 d. Parental effort of Gentoo penguins in mid-February is expected to be higher than in other Pygoscelid penguins at the end of the breeding season, because their large chick requires more food than those of the other two species at that age. According to Trivelpiece et al. (1987) Gentoo penguins have 3.84 nest reliefs per day at that time (as opposed to 2.88 and 1.98 in Chinstrap and Adélie penguins). Unfortunately, there are no data available for at-sea behaviour of Gentoo penguins during that period.

Since Gentoo penguin chicks only fledge at an age of approx. 71 d (Volkman and Trivelpiece 1980), an average of 56.4 kg of krill is eaten per chick during this time, about twice the amount given to Adélie and Chinstrap penguin chicks. Why there should be such a pronounced difference between the reproductive strategies of Gentoo penguins and their relatives is unclear. It would be expected that Gentoo penguin parents abandon their chicks 17 d after peak mass is reached, similar to the two other Pygoscelids, rather than feeding them twice as long. Volkman and Trivelpiece (1980) suggest, however, that fledging in

Gentoo penguins may occur as early as at 62 days (this would correspond to only 50 kg of krill fed).
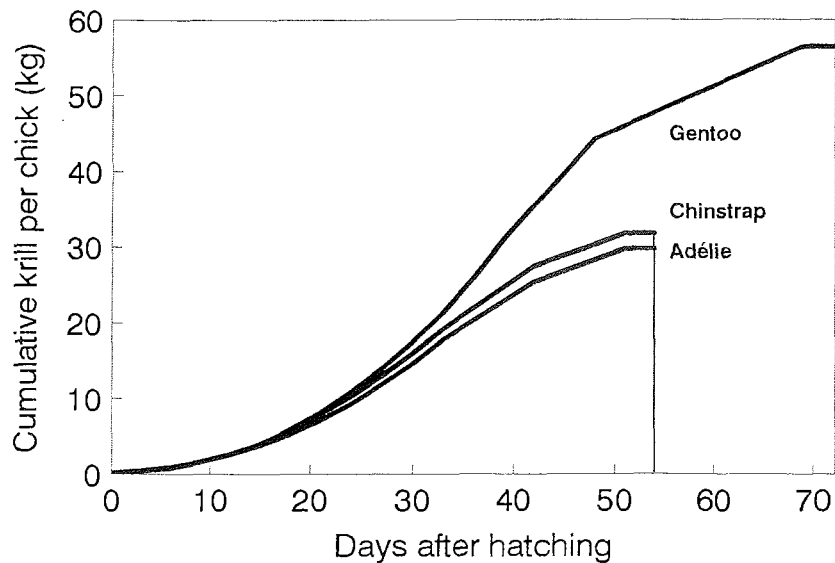

Fig 8: Cumulative krill consumption (kg) per chick for Pygoscelid penguins from hatching to fledging. Adélie and Chinstrap penguins fledge aged 53 d, whereas Gentoo penguins fledge aged 71 d. For model and assumptions see text.

Whereas Adélie and Chinstrap penguins fledge on average 0.97 to 0.99 chicks per breeding pair, and therefore have similar energetic costs per brood and per chick, Gentoo penguins fledge 1.08 chicks per pair. The total amount of food they need to provide for their offspring is therefore increased to 61.1 kg per breeding season. The results of these calculations are slightly different from those presented by Trivelpiece et al. (1987) based on adult stomach contents and chick feeding rates. They found values of 25, 34 and 70 kg krill per breeding pair of Adélie, Chinstrap and Gentoo penguins.

In their calculations, Trivelpiece et al. (1987) assumed that all adult stomach contents were delivered to the chicks. Using nest relief frequencies (N in d^{-1}) and adult stomach contents (A in kg) given in Trivelpiece et al. (1987), chick food requirements determined as above (C, in kg krill d^{-1} per chick; Tab 2) and

data on number of chicks per nest (S, calculated from Trivelpiece et al. 1987), the mean amount of food daily remaining in the stomach of each adult after feeding the brood (Fig 9) was calculated as F = NA - CS (Culik 1994). It shows that parents keep only a minimum of food for themselves just prior to the time when chicks begin forming crèches. Thereafter, nest relief intervals are increased, and the percentage of food parents can keep for themselves rises. This model coincides well with previous calculations (Culik and Wilson 1991c) and with parent body mass, which also reaches a minimum prior to crèche formation (Fig 2; Wilson et al. 1991b). Due to to the assumption of fewer nest relief intervals in the model, Adélie penguins seem to retain less food for themselves than Gentoo and Chinstrap penguins. Since body mass of Adélie penguin adults decreased before chicks joined crèches (Culik and Wilson 1991c), it seems unlikely that the birds were able to meet their energy requirements by digesting enough food while foraging at sea.
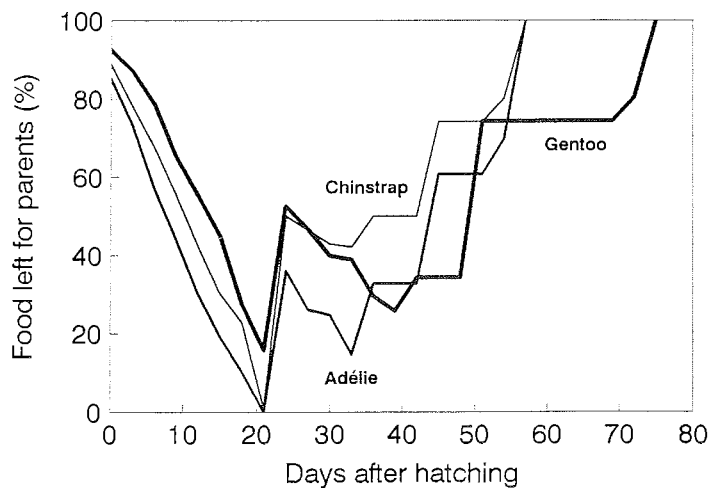

Fig 9: Percentage of food remaining in parent stomachs after feeding the brood. Chicks join crèches at age 21d, thus allowing parents to increase the number of nest reliefs per day. For assumptions see text.

Data obtained from loggers (recording speed, direction and depth, Wilson et al. 1993) deployed on adults during the same expedition show, that all three

species used the same area for feeding (Fig 10; Wilson 1994). This does not support the theory of Trivelpiece et al. (1987) that Adélie penguins have twice the foraging range of Gentoo penguins. Segregation of the three species, and reduction of interspecific competition may be achieved solely by the different chronology of chick hatching dates: Adélie penguin chicks hatch 2 weeks before Gentoos and 4 weeks before Chinstraps (Trivelpiece et al. 1987).
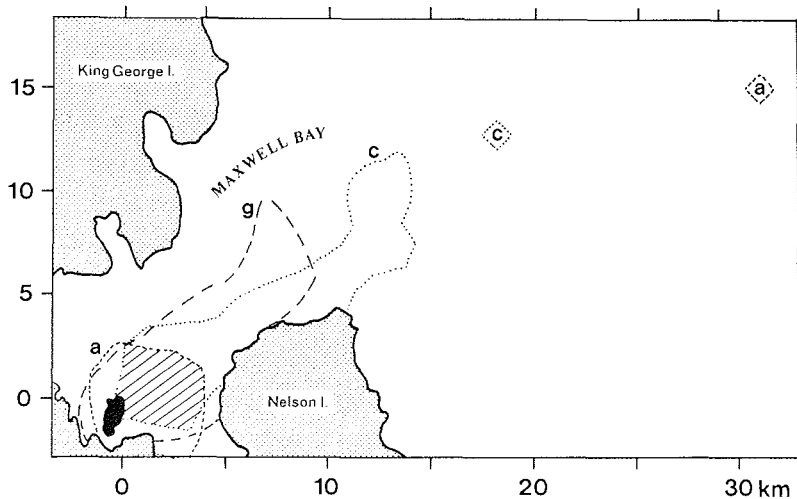
Fig 10: Foraging ranges (99.5% of time at sea limits) of Adélie (a), Chinstrap (c) and Gentoo (g) penguins from the colonies on Ardley Island. Although there are differences in the maximum distance reached by each species, foraging ranges overlap to a large extent (hatched area).

3.2 Food requirements of Pygoscelid penguin adults

For a model of cumulative krill consumption in Adélie penguins foraging in the Hope Bay area (where most of the above data were derived) during the breeding season, the following assumptions were made (Culik 1995): the birds arrive at the colonies around Nov. 1 (day 0), spend on average 10 days prior to egg laying (courtship) and incubate their eggs for a period of ca. 35 d (days 10-45; Davis and McCaffrey 1986). Chicks hatch around Dec. 16 (day 46) and

join crèches 21 d later, around Jan. 6 (day 67). After spending on average 35 d in crèches, chicks fledge (aged ca. 55d) around Feb. 9 (day 102) and leave the colony.

The model presented in Table 7 assumes that:

a) the swimming distances determined by Sadleir and Lay (1990) for foraging Adélie Penguins at Cape Bird (92, 18, and 18 km during incubation, brooding and crèche stages, respectively) also apply to the situation at Esperanza, Hope Bay. Unfortunately, no data are presently available for penguins foraging in the Hope Bay area, but data from other areas confirm these results (Fig 10).

b) the percentage time that breeding Adélie Penguins spend at sea is similar, irrespective of the stage during the breeding period (Wilson et al. 1989a),

c) the total time spent under-water by foraging Adélie Penguins consists of travelling at depths <5 m and foraging at depths >5 m (Wilson et al. 1991b),

d) of the 117 000 breeding pairs of Adélie penguins at Hope Bay, 87.6% lay 2 eggs and 11.3% lay 1 egg (Davis and McCaffrey 1986),

e) 68% of the eggs hatch and 80% of the hatchlings survive to crèche age (Trivelpiece et al. 1987). There are thus 218 000 eggs, 148 000 hatchlings and 117 000 chicks joining crèches at Esperanza Bay (i.e. mean clutch or brood sizes are 1.86, 1.11 and 1 (Table 7) during incubation, brooding and crèching, respectively.

f) the Esperanza colony size of 117 000 breeding pairs of Adélie Penguins does not vary throughout the breeding season.

g) adults walk on average 1 h per foraging trip between their colony and the sea (at 2 km h^{-1}; Pinshow et al. 1977). This time is subtracted equally from "rest at sea" and "rest away" data given in Wilson et al. (1991b).

h) the conversion factor of oxygen to kJ is 20.1 kJ l O_2^{-1}(Schmidt-Nielsen 1983), and the digestible energy content of fresh krill caught by penguins at Esperanza Bay is 3.7 kJ g^{-1} (Davis et al. 1989)

i) the energetic cost associated with heating cold (0°C) krill to body temperature (39°C) is 0.11 kJ g^{-1} (Wilson and Culik 1991).

In Table 7, values of oxygen consumption for different activities (see above) were summed to yield overall oxygen consumption per foraging cycle. This consumption estimate was then converted into the mass of krill (g) that would be required to produce this, to which the energy required for heating this amount was added (also expressed in g krill). Per foraging cycle, Adélie

Table 7: Duration of parental activities and related energetic costs to Adélie penguins. In addition to indicated sources, the model is based on data of Sadleir and Lay (1990) for foraging ranges, and on data from Davis and McCaffrey (1986) for the number of eggs per breeding pair. Mean mass of adults = 4.2 kg

	Period in reproductive cycle			
	Incubation	Brooding	Crèching	Source
Total cycle time(h)	192.0	49.2	24.0	Wilson et al. 1991b
ADULTS				
On nest (h)	96.0	24.6	2.9	Wilson et al. 1991b
Oxygen (l h⁻¹)	2.4	3.0	2.8	Culik (1995)
Total oxygen (l)	**234.4**	**73.2**	**8.0**	
Rest away (h)	32.9	3.3	12.9	Wilson et al. 1991b
Oxygen (l h⁻¹)	3.6	3.6	3.6	Culik & Wilson 1991c
Total oxygen (l)	**118.8**	**11.9**	**46.6**	
Rest at sea (h)	21.4	6.8	2.2	Wilson et al. 1991b
Oxygen (l h⁻¹)	6.3	6.3	6.3	Culik & Wilson 1991c
Total oxygen (l)	**134.8**	**42.8**	**13.9**	
Swimming (h)	40.7	13.5	5.0	Wilson et al. 1991b
Oxygen (l h⁻¹)	11.7	11.7	11.7	table 6
Total oxygen (l)	**475.2**	**157.6**	**58.4**	
Walking (h)	1.0	1.0	1.0	
Total oxygen (l)	**11.3**	**11.3**	**11.3**	Pinshow et al. 1977
Fat loss (g h⁻¹)		1.0	0.6	Wilson et al. 1991b
Oxygen (l h⁻¹)		2.0	1.2	Petrusewicz & Mac-
Total oxygen (l)		**-49.0**	**-28.7**	fayden 1970
CHICKS				
Chick feeding interval (h)		24.6	12.0	Wilson et al. 1991b
Brood size (chicks)	1.9	1.1	1.0	Trivelpiece et al. 1987
Mean chick mass (kg)		0.7	3.0	Trivelpiece et al. 1987
Rest & other (O₂, l h⁻¹)		0.61	4.50	Culik (1995)
Walking (O₂, l h⁻¹)		0.59	0.62	Culik (1995)
Mean tissue deposition (O₂, l h⁻¹)		0.78	0.78	Myrcha &
Chick total oxygen (l)		**54.1**	**70.8**	Kaminski 1980
Krill/trip (g)		*294*	*385*	
ADULT + CHICKS				
Grand Total (O₂, l)	**975**	**302**	**180**	all totals added
kJ	19590	6071	3624	20,1 kJ per l Oxygen
Krill per trip (g)	5295	1641	980	3,7kJ per g Krill
Heating cost (g krill)	157	49	29	Wilson & Culik 1991
Total per Cycle (g)	**5452**	**1690**	**1009**	
Krill per adult day (g)	**681**	**824**	**1009**	
Krill per colony day (t)	*159*	*193*	*236*	Hope Bay colony

penguins need to ingest 5450 g while breeding (96 h at sea), 1690 g during the brood phase (24.6 h at sea) and 1010 g during the crèche phase (21.1 h at sea). Calculated from this, brooded chicks receive on average 294 g krill per foraging trip, or 250 g d^{-1} per chick. Chicks in crèches receive on average more than twice this amount, i.e. 770 g krill d^{-1}.

Total krill requirements were divided by the duration of the foraging cycle and multiplied by 24 h to yield krill requirements per breeding adult and day. These are: 680 g during incubation, 820 g during the brood phase and 1010 g during the crèche phase. These figures, multiplied by the number of adult Adélie Penguins present at Hope Bay yielded the amount of krill consumed by the entire colony per day (159 t, 163 t and 236 t for the three phases, respectively). Daily krill requirements of the colony increase throughout the breeding season, mainly because of the food requirements of the brood.

3.3 Field metabolic rates of Adélie penguins.

Food requirements of Adélie Penguins as determined in Table 7 on the basis of activity budgets and energetic costs of these activities are matched to within 3-15 % by the results of a doubly-labelled water study on free-living birds (Culik and Wilson 1992). Since both methods are independent of each other, the accordance of the results (Table 8) indicates that although penguins engage in a variety of activities during the breeding season, the resulting energetic costs can be summarized by just a few parameters. These are the duration and energy expenditure of essentially four activities: a) in adults and chicks, rest on land (whether in the colony or outside, the difference is minimal) and walking, and b) in adults, swimming and resting at sea. Mass changes (i.e. fat loss) significantly influence the energetic balance, which necessitates regular weighing of the penguins. The period in the breeding season and the associated energy requirements of the growing chicks (and the brood size) are also important elements in this calculation. Other factors, however, such as the small variations in weather conditions encountered during our study and the various activities engaged in by penguins in the colony, might influence immediate energy requirements, but were of little overall significance. This is also shown by the results of a model presented earlier (Wilson et al. 1991b), where estimated food requirements per foraging trip (6060 g, 1620 g and 1070 g for

incubating and brooding adults and adults with chicks in crèches, respectively) are very similar to the values presented here (5450 g, 1690 g and 1010 g, respectively), although the meteorological conditions and activity within the colony were not taken into account.

Table 8: *Results of calculations based on a FMR study on breeding Adélie penguins at Esperanza. The birds were carrying externally attached devices and had 1.5 chicks as opposed to 1.1 and 1 in Table 7. The incremental energetic costs due to these differences were subtracted to enable comparison.*

| | Period during brood cycle | | |
	Incubation	Crèching	Source
Power (W kg^{-1})	10.1	14.1	Culik and Wilson 1992
Krill (g d^{-1})	990.6	1382.9	Culik and Wilson 1992
-Device costs (krill, g d^{-1})	-88.3	-32.7	Culik and Wilson 1991b
-Smaller brood (krill, g d^{-1})	-103.3	-192.4	Culik 1994
Krill per adult day (g)	**799**	**1158**	

Using the data for adults presented in Table 7, and the cumulative krill requirements of the average number of growing Adélie penguin chicks in Fig 8, I found (Culik 1995) that during the first phase of the breeding season, i.e. courtship, each Adélie penguin pair consumes 14 kg of krill (1600 tons for the whole Esperanza colony), or the equivalent energy stored as fat (Fig 11). When the eggs hatch, the krill requirements per breeding pair increase to 63 kg (7400 t). Between hatching and crèche formation, chicks consume 5.2 kg of krill each (1.1 chicks per breeding pair = 570 t for all chicks), while the cumulative krill requirements per breeding pair increase to 97 kg (11 350 tons). By the end of the breeding season, almost twice that amount of krill is consumed, i.e. 174 kg per breeding pair (20400 tons) of which each chick (by then only 1 chick per breeding pair left) consumes 29.8 kg (cumulative chick consumption: 3450 tons). Considering that Adélie penguins with small chicks and with chicks in crèches forage within <20 km of their colony, they can be seen as very important local krill consumers.

Contrary to Sadleir and Lay (1990; see above), Trivelpiece et al. (1987) speculated that Adélie Penguins forage within a radius of 43 km. Substitution of

their activity at sea data in the model yields krill requirements of brooding Adélie Penguins of 1080 g d^{-1} as opposed to the 800 g d^{-1} estimated here. According to Wilson (pers.comm.) foraging ranges of Adélie Penguins are highly variable from day to day, and perhaps between foraging areas, depending on food availability (Fig 12). The value presented by Trivelpiece et al. (1987) necessitates that Adélie Penguins swim for 22.3 h per day and must therefore be considered maximal, if nest relief intervals of around 24 h (Trivelpiece et al. 1987; Wilson et al. 1991b) are to be maintained during the brooding period.
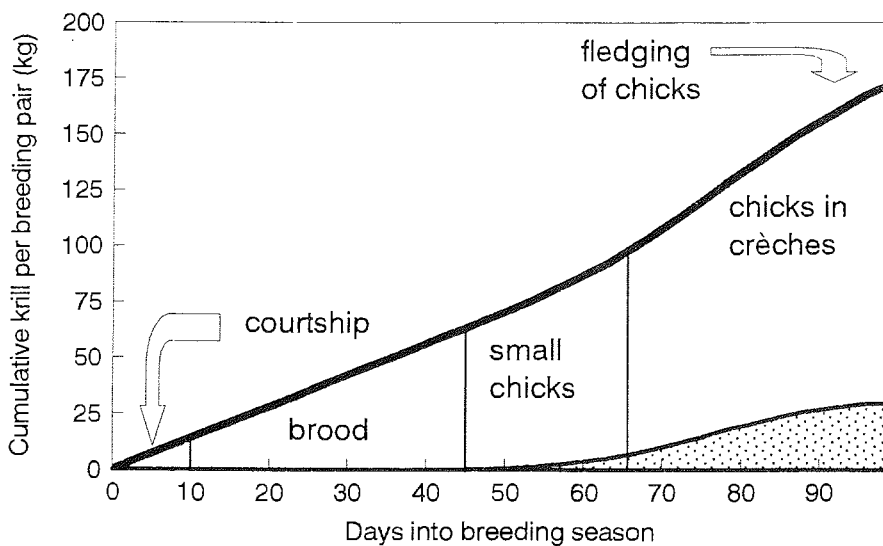
Fig 11: Cumulative krill requirements per breeding pair of Adélie Penguins (including chicks) throughout the reproductive season. The food requirements of one chick (dotted area) are included for comparison (c.f. Fig. 8).

Because no detailed data are available so far on foraging ranges and land based activities of Chinstrap and Gentoo penguins, similar calculations for these species are speculative. There is, however, evidence that interspecific differences are minimal (cf. Fig 10; Wilson, Reins, Matthias unpublished data). Substituting the energetic costs of swimming, the body mass and the food re-quirements of the chicks and assuming all other variables in Table 7 to be equal, each breeding Chinstrap penguin would have daily food requirements of 630, 720 and 1100 g of krill during incubation, brooding and crèche phases,

respectively. In Gentoo penguins, these values would be 940, 1040 and 1580 g d^{-1}. Due to the different durations of the reproductive phase, each pair of Chinstrap penguins would have consumed 160 kg of krill from the date of first arrival in the colony until chicks fledge. In Gentoo penguins, this value is calculated to be 286 kg (chicks stay in crèches for 50 d).
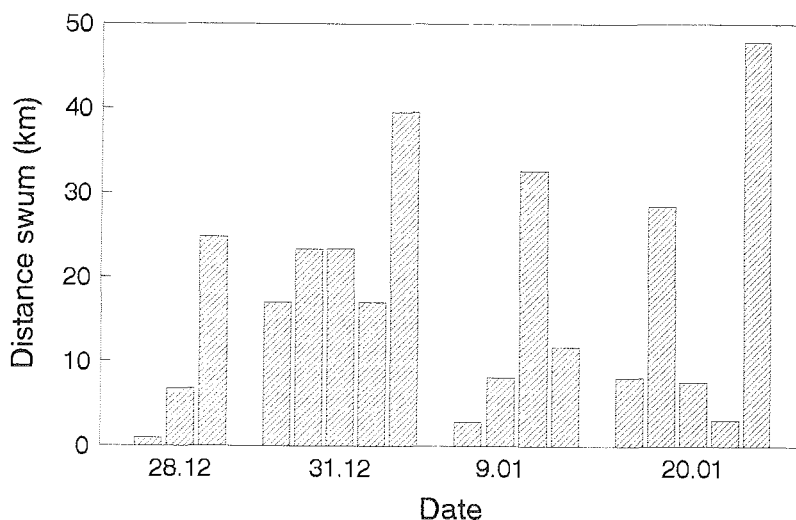
Fig 12: Foraging ranges of Adélie penguins at Ardley Island were highly variable during the breeding season of 1991-92 (Wilson, unpublished data). While searching for food, different penguins covered anywhere from 3 to 48 km on the same day (as on Jan 20).

The Pygoscelid penguin population on Ardley Island amounts to 1 056 Adélie, 244 Chinstrap and 3 809 Gentoo penguin breeding pairs (Trivelpiece et al. 1987). Food consumption by these birds around the island is therefore expected to be 1 300 tons per breeding season. The same calculation for the Pygoscelid population on King George and Nelson Island (65 300 Adélie, 625 800 Chinstrap and 12 600 Gentoo penguin breeding pairs, Trivelpiece et al. 1987) yields a consumption of 115 000 tons per breeding season, 22 600 tons of which would have been fed to the chicks (estimate of Trivelpiece et al. 1987: 24 000 tons). The entire Adélie, Chinstrap and Gentoo penguin population in the area of the Antarctic peninsula amounts to 0.466, 1.241, and 0.18 million

pairs (c.f. maps 9, 11 and 13 in Wilson 1983). During each breeding season, Pygoscelid penguins in that area are therefore expected to consume 332 000 tons of krill. These preliminary estimates may be further refined when more information on the activity budgets of Pygoscelid penguins becomes available (Wilson et al. in prep).

4. EFFECTS OF EXPERIMENTAL METHODS ON PENGUINS

The effects of instrumentation and manipulation on activity budgets and energy requirements of Pygoscelid penguins were investigated in order to quantify experimental error, improve methods prior to a new expedition and reduce stress for the study animals. In this chapter, the effects of a) flipper bands and b) instruments on Adélie penguins will be examined, and suggestions made to minimize these undesirable effects. Finally, c) the effects of injecting penguins with doubly-labelled water, a method used in the determination of energy expenditure in the field, will be discussed on the basis of direct observation of penguin activities in the colony and at-sea activities as determined with the use of externally attached data-loggers.

Swimming speed in penguins is affected by drag (Culik and Wilson 1991b), which itself is increased by the attachment of external devices to the birds (Bannasch et al. 1994). Since device-equipped penguins do not appear to alter the duration of their foraging trips nor increase their energy expenditure per unit time while at sea, several authors conclude that they swim at reduced speeds (Wilson et al. 1986, Gales et al. 1990, Culik and Wilson 1992). This ultimately results in a reduced foraging range and, since the probability of prey encounter is dependent on the distance travelled (Wilson 1991), presumably leads to reduced food intake and thus to reduced overall fitness (Wilson and Culik 1992).

4.1 Flipper bands

The individual marking of flying and flightless birds has a long history in ornithology. It is the only technique which is cheap, simple and effective, yielding results on bird migration, age-specific annual survival and recruitment. Consequently, hundreds of thousands of birds are annually ringed worldwide. Unfortunately, researchers all too often tend to neglect problems associated with rings and tags (but see Calvo and Furness 1992, for review). In Antarctic penguins, flipper bands have been used extensively by a variety of nations, and banding is an intricate part of the Council for the Conservation of Antarctic

Marine Living Resources' (CCAMLR) monitoring programme (Standard method A4).

Although some reservation about the technique has been expressed due to band loss (e.g. Weimerskirch et al. 1991), penguin mortality due to the band has hardly ever been considered. Sladen and Penney (1960) and Cooper and Morant (1981) report only slight feather wear, whereas Bannasch and Lundberg (1984) and Sallaberry and Valencia (1985) found that a large proportion of the Pygoscelid penguins marked with flipper bands on Ardley Island, Antarctica, during 1979 and 1980 (Bannasch and Odening 1981), had wounds by the breeding season of 1981-82. Ainley et al. (1983) first observed that bands "apparently caused some mortality... Mortality may occur from complications when the wing swells during moult and the band constricts blood flow." Ainley et al. (1983) assume that a consequent increased mortality of ca. 28% occurs during the first moult after banding, regardless of whether the penguin was banded as a chick or an adult. The authors were unable to determine whether bands affected survivorship thereafter (Ainley, pers. comm.).

During our expedition to Ardley Island in 1991/92 we were, for the first time, able to quantify the effects of flipper bands on swimming speeds and on the energetic costs incurred by penguins while swimming in the 21 m long, still water swim canal (Culik et al. 1993). A total of 7 Adélie penguins were equipped with a flipper band and then immersed in the canal to measure transport costs. Subsequently, the flipper bands were removed and the birds tested a second time. The order of the experiments was reversed for 3 of the 7 experiments to account for possible acclimation of the birds to the experimental setup.

Penguins equipped with the band swam slightly slower than controls (mean 1.58 vs 1.60 m s^{-1}, median 1.575 vs 1.605 m^{-1} s, n= 154 vs 194), although the difference was not significant (chi-square test, p= 0.6). This contradicts the conclusions of Wilson et al. (1986) and Gales et al. (1990). The mean amount of energy required for swimming at speeds between 1.4 and 2.2 m s^{-1}, however, was significantly higher (ANOVA, paired design, n= 7, p= 0.006) when the penguins were wearing a flipper band (21.1 Wkg^{-1}, n=115 measures)

than without (17.0 Wkg^{-1}, n=157 measurements). The mean power increment for swimming with a flipper band was 24%.

The power and transport cost increment (%) required by Adélie penguins in order to swim with a flipper band (Fig 13) reached a maximum of 36% at 1.4 m s^{-1} (n= 31 treatment vs. 41 control), 28 % at 1.6 m s^{-1} (n= 36 vs 48), a minimum of 9.4% at 1.8 m s^{-1}(n= 22 vs. 36), 14.3% at 2.0 m s^{-1} (n= 18 vs. 27) and 18.4% at 2.2 m s^{-1} (n= 8 vs. 5) as compared to the unbanded controls (Culik et al. 1993). Flipper bands increase hydrodynamic drag in a physical sense, and destroy most of the hydrodynamic characteristics of the penguin wing near the band (Bannasch, pers. comm.). There is, therefore, no possibility for the birds to acclimate to this given sufficient time: transport costs in banded penguins will always be higher than in unbanded individuals.
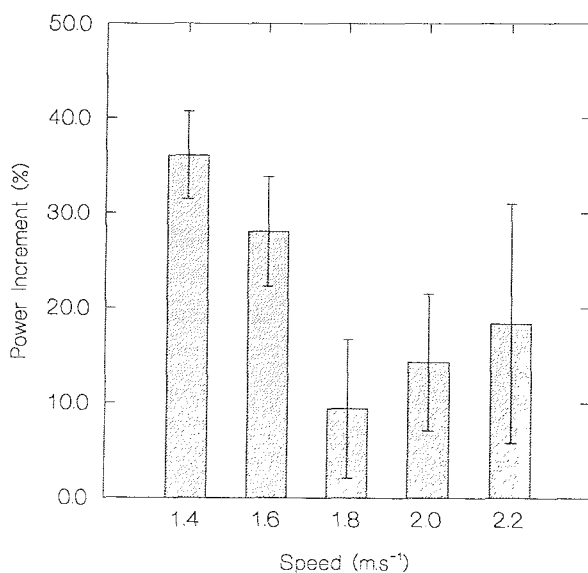
Fig. 13: Mean power increment (%) required by swimming Adélie penguins to maintain a particular speed when wearing a flipper band as opposed to controls. Energy expenditure in penguins wearing a band increased by a mean of 24% over the speed range of 1.4 - 2.2 m s^{-1}. Thin bars denotate SE.

Since Adélie penguins wearing flipper bands must expend a mean of 24% more energy when swimming, time-activity budgets were used to calculate the

overall increment in energy expenditure in these birds during the reproductive period. Energy consumption increases by 11% during incubation, 13% during brooding and 7% during the crèche phase (calculated from Culik 1995) compared to unbanded conspecifics. This may cause a reduction in breeding success, especially in years with low food availability.

Adélie penguins do not have to provide food for their chicks while incubating, and both parents have access to sufficient food towards the end of incubation. Therefore the amount of fat loss during that period may be considered negligible. From the data in Table 7 I estimate therefore, that the overall energy increment caused by flipper-bands on free living Adélie penguins throughout the year is of the order of 11%.

Considering that 1) about 22.3 % of marked King penguins (*Aptenodytes patagonicus*) lost their flipper bands during the first year after banding, and 4.5% during the second year (Weimerskirch et al. 1991), 2) Flipper bands cause irritation, feather wear and wounds (e.g. Sallaberry and Valencia 1985), 3) penguins with flipper bands have to expend 24% more energy for swimming and 11% more energy overall (this study) and 4) flipper bands cause 28% increased mortality in Adélie penguins during the first year after banding (Ainley et al. 1983), it seems necessary to reconsider the necessity and the usefulness of penguin banding programs, such as the one proposed by CCAMLR. This suggestion was put forward at a recent international conference and led to a general consensus among participants that alternative marking techniques should be developed rapidly (Workshop on Researcher-Seabird Interactions, Monticello, USA, 1993).

Individual identification of study birds may be achieved, for instance, using transponder technology. Le Maho et al. (1993) recently published first results of a study conducted since 1991 where they report on the use of a new individual identification system (TIRIS, Texas Instruments) which allows animals to be tagged by subcutaneous injection of passive transponders. The transponder tags used are small (30 x 3 mm, mass 0.8 g) and do not require batteries. Using a special detector (hand-held or built into a gate), they allow identification of the bearer from distances of up to 0.7m.

Although it is too early to assess problems associated with the new method, it offers clear advantages over externally-attached markers. Transponder-tagged birds cannot be identified using binoculars as can flipper-banded penguins, but this inconvenience on the part of the researchers is more than balanced by the advantages to the birds and the resulting quality of the data obtained.

4.2 Penguin instrumentation

Marine animals are particularly difficult to study because they often range far from the coast and thus cannot be observed from land, or behave unnaturally if approached by boats or divers. To elucidate the marine ecology of fish, mammals and birds, many researchers consequently attach external transmitting or recording devices (e.g. Wilson and Culik 1992; Wilson et al. 1993a). For example, Mc Govern and McCarthy (1992) attached acoustic transmitters (56 x 12 mm, 22 g in air) to the backs of eels (*Anguilla anguilla*), and Hammond et al. (1992) e.g. studied grey seal (*Halichoerus grypus*) activity in the North Sea by glueing radio transmitters (size and mass not given) to the animals' heads. Birds have been studied using remote-sensing technology by attaching depth gauges (64 x 11 mm, 6 g in air) to Adélie penguins (Wilson et al. 1991b), and Ancel et al. (1992) used satellite transmitters (mass 250 - 475 g, size not given) on Emperor Penguins (*Aptenodytes forsteri*). Despite innumerable such telemetric studies (c.f. Priede and Swift 1992) remarkably little has been published on the possible deleterious effects of the devices on the study animals.

Penguins are an exception to this generalization. Sadleir and Lay (1990) for instance reported that Adélie penguins peck at attached radio transmitters, and Wilson and Wilson (1989b) have quantified this behaviour in both African and Adélie penguins by attaching a purpose-designed peck-activity recorder to the birds. Adélie penguins pecked at the devices mostly when at sea, which was probably responsible for the increased duration of their absence from the nest. In a subsequent study (Wilson et al. 1990) it was determined that the colour of the device should match the colour of the plumage if pecking was to be kept at a minimum.

Although drag and therefore power input presumably increase due to instrumentation, results from doubly-labelled water studies (Wilson et al. 1986; Gales et al. 1990; Culik and Wilson 1992) showed that foraging African, Little Blue and Adélie penguins did not spend more energy per unit time than controls. It was proposed that instrumented animals swim either slower to achieve this (and the results in the swim canal would oppose this conclusion) or make more pauses while at sea, resulting in a slower mean speed. Since the length of the foraging trip in African and Little Blue penguins did not seem to increase after instrumentation, this ultimately must have resulted in a reduced foraging range, a reduced chance of encountering prey (the latter is dependent on the distance travelled; Wilson and Culik 1992), and therefeore presumably a reduction of food intake.

In the case of Adélie penguins, the time spent foraging by these birds increased after instrumentation (Wilson et al. 1989b; Culik and Wilson 1992). The extra time at sea was most likely used to compensate for instrument effects. As a result, chick feeding frequency and brood survival were thought to be reduced (c.f. Williams et al. 1992; Sadleir and Lay 1990).

Device mass is considered of little importance to marine animals because of buoyancy (Wilson et al. 1991b), but the drag of the instrument in water is important. Most aquatic animals are highly streamlined, and may have drag coefficients as low as $C_d = 0.037$ (e.g. penguins; see Bannasch et al. 1994). Wilson et al. (1986) noted that swimming speed in free-living penguins was related to the cross-sectional area of the device. In the swim canal, we determined (Culik and Wilson 1991b) that penguins wearing an elongated but rounded data-logger mounted on their back expended 42% more energy than untreated conspecifics.

Using methods normally only available to aircraft and ship designers, a wind tunnel and a water flume, we were recently able to improve drastically the streamlining and positioning of externally mounted devices (Culik et al. 1994a; Bannasch et al. 1994). Using wingless models of Chinstrap penguins it was determined that the device should be attached to the lower back, as far below the line of maximum girth as permitted by the base of the tail (in other species, a different positioning might be required). Furthermore, the device should blend in with the body, in order to prevent flow separation and turbulence formation.

The mean drag increment of the device was thus reduced to 17.4% at speeds between 1.2 - 2.4 m s^{-1}.

We tested the new device and its attachment on free-living penguins in Antarctica. For that purpose we again used the swim canal and determined, using respirometry, the energy expenditure of Adélie penguins with and without the instrument attached. As opposed to the experiments with flipper bands, the order of the experiments could not be reversed here, because the tape used in attachment will not adhere to wet feathers (Culik et al. 1994a). The duration of the experiments in the canal allowed for the birds to calm down after capture and ended after the birds had swum continuously for at least 40 min.
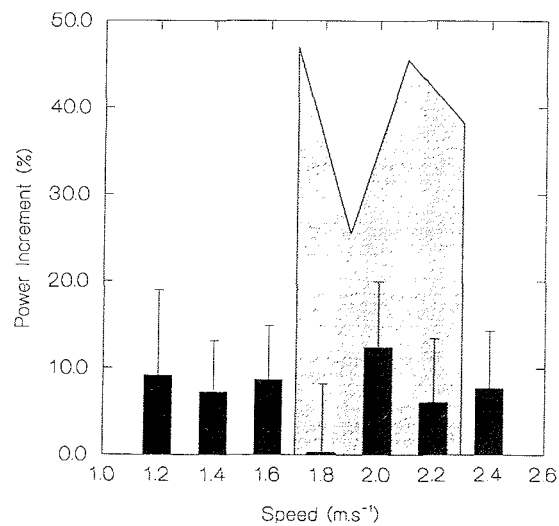
Fig. 14: Mean power increment (%) required by swimming Adélie penguins to maintain specific speeds while carrying an externally-mounted instrument as opposed to controls (black bars). Energy expenditure in penguins wearing a caudally-fastened streamlined instrument increased by a mean of 5.4% over the speed range of 1.2 - 2.4 m s^{-1} (Culik et al. 1994a). Thin bars denotate SE. For comparison, in a previously conducted experiment (Culik and Wilson 1991b) a much smaller, but not streamlined, device was attached dorsally at the point of maximum girth of the birds, leading to a power increment of 42% (shaded area).

Penguins equipped with the instrument swam significantly slower than controls (mean 1.57 vs 1.70 m s^{-1}, median 1.53 vs 1.57 m^{-1}s, n= 185 vs 118; t- test, p= 0.018). The mean amount of energy required for swimming at speeds between 1.2 and 2.4 m s^{-1}, however, was not significantly higher (t-test, p= 0.37) for penguins carrying the device (P$_i$= 17.0 W kg^{-1}, n= 157) than for those without (P$_i$= 16.1 W kg^{-1}, n=109). The power increment for swimming with the device attached to the lower back averaged only 5.4%.

The data-logger previously tested (Culik and Wilson 1991b) was only 500 mm^2 in frontal cross-section (2.1% body cross-sectional area), with a mass of only 35 g in air (0.9% bird body mass), but attached dorsally between the flippers. When swimming with this instrument, Adélie penguins expended on average 42% more energy (Fig. 14) than controls (22.5 vs. 15.8 W.kg^{-1}). Streamlining and attachment of the new and much larger instrument (5 times the volume of the old device) in a caudal position where cross-sectional area of the bird, at the line of maximal girth, was not increased, greatly improved these values. The new instrument did not have a blunt, rounded frontal edge as did the old data-logger. Instead it was rather wedge-shaped, a design common in sports cars.

Since drag increment is directly proportional to power input (if the speed is to be maintained, Culik and Wilson 1991b), we would have expected power in live Adélie penguins (Culik et al. 1994a) to increase by the same value (17.4%) as in the model experiments. Several explanations can be offered for the observed discrepancy. 1) Cross-sectional area in Adélie penguins is 6.3% larger than in Chinstrap penguins (Oehme and Bannasch 1989), thereby reducing the effect caused by the device. 2) The model used in the water flume (Bannasch et al. 1994) was wingless. Drag induced by the wings in live Adélie penguins would therefore further reduce instrument effects. 3) Adélie penguins in the wild do not have a static body surface, such as the glass-fibre model of the Chinstrap penguin, but one that is presumably able to adjust to turbulence and flow variations by adjustment of the feathers, which would tend to maintain laminar flow. 4) Before removal of the devices, we always observed that the points of attachment as well as the leading edge were partly covered with the tips of adjacent feathers. This may further have reduced drag.

In Adélie penguins, maximum dive depth recorded previously with the smallest instruments available (140 mm^2 in cross section) was ca. 180 m (Whitehead 1989). Wilson (1989b) found a negative correlation between maximum dive depth per foraging trip and device cross-sectional area for Adélie and Gentoo penguins. This was attributed (Wilson and Culik 1992) to the increased power requirements of instrumented birds, which would cause oxygen stores to be depleted faster during the dive. According to the equation given by Wilson (1989), Adélie penguins wearing an instrument with a cross-sectional area of 2100 mm^2 (the size of the logger used here) should not dive below 10 m. However, Adélie penguins equipped with our instrument regularly dived to about 100 m (Wilson et al. 1993b).

Adélie penguins diving to depths of 100 m choose dive and surface angles of 60° (Wilson et al. 1993b), which results in 115 m swum by the bird to reach that particular depth. Taking into account the power increment, and resulting incremental oxygen consumption due to the device (6.1% at 2.2 m s^{-1}), dive depth without the instrument would have been 106 m instead of 100 m. Adélie penguins equipped with a time depth recorder shaped like our old device (Culik and Wilson 1991b), however, would have only reached 58 m. Although these calculations are very much simplified, they serve to illustrate the point. It would thus appear, that device shape can affect even the most basic of biological data gained from time depth recorders (see also Wilson 1989b).

It is clear from the data reviewed here, that instrumentation effects are considerable and it is imprudent to ignore them. In the past it seemed intuitively important to reduce mass and cross-sectional area (Wilson 1989b) of externally attached instruments. The results presented here, however, demonstrate that these parameters are less relevant to the animals in the water than streamlining.

Another possible solution to problems associated with externally attached instruments is miniaturization and implantation of these into the study animal's body cavity. This approach was used successfully by Boyd and Sladen (1971) on Emperor and Adélie penguins, by Butler and Woakes (1984) on Humboldt penguins and here on Adélie penguins (Culik et al. 1990a, b, 1991b; Culik and Wilson 1991b; Wilson and Culik 1991; Wilson et al. 1991c; Culik 1992). However, this method only allows the use of sensors which do not require

contact with the surrounding medium. This excludes the use of speed sensors, such as the one employed in our hydrodynamically designed data-logger (Wilson and Culik 1993; Wilson et al. 1993a, b; Bannasch et al. 1994; Culik et al. 1994a, b). Furthermore, implantation prohibits the rapid recovery of the instrument after deployment. Problems associated with implantation are 1) the requirement of a permit by the responsible ethics committee, 2) surgery requiring skill and experience, 3) a possible shift in the position of the implanted device, which can move sensors to a non-optimal position so that data (e.g. heart rate) cannot be recorded, and 4) long-term effects to the study animal, such as dammage to air sacs.

On the other hand, Adélie penguins implanted with heart rate/temperature transmitters (Culik et al. 1990a, b, 1991b; Culik and Wilson 1991b; Wilson and Culik 1991; Wilson et al. 1991c; Culik 1992) recovered very well from surgery. After implantation, adults were returned to their colony, where they successfully resumed incubation and subsequently chick rearing. Behaviour of these birds in the canal was, however, somewhat altered, the penguins showing less unrest and jumping behaviour than non-instrumented controls (the time allocated to swimming and resting in the canal, however, was not different in the two groups). A similar observation was made on penguins which had been induced to swallow stomach temperature loggers: they were less active than untreated conspecifics (Matthias, pers. comm.). Furthermore, energy consumption of two implanted Adélie penguins during rest in cold water was 40% lower than in controls. While swimming, the implanted birds consumed on average 20% less energy than controls. However, these differences were attributed to the frequent handling and the repeated use in experiments involving the water canal. Presumably, the implanted study birds were better acclimated to human presence than controls, which resulted in stress-reduction during the experiments (Culik and Wilson 1991b).

In summary, our experiments with implanted and externally attached instruments on Adélie penguins showed that both had a measurable effect on the performance and energy consumption of the bearer. Both methods have their advantages and disadvantages which should be kept in mind prior to the beginning of a study.

4.3 Doubly-labelled water

Adélie penguins injected with doubly-labelled water (DLW; Culik and Wilson 1992) showed a 5% loss of body mass during the period of the experiments, irrespective of the time of the breeding season or whether the birds were carrying externally attached instruments or not. Although this mass loss coincided with a general decrease in body mass in all adults in the colony (c.f. Fig. 2 above), which has been attributed to the high energetic demands of the growing chicks (Wilson et al. 1991b), we also observed that the chicks were not fed equally well by the manipulated bird as opposed to its non-manipulated partner.

Mass losses in penguins used in DLW experiments have been reported in almost all studies to date (Nagy et al. 1984; Costa et al. 1986; Davis et al. 1989; Gales et al. 1990; Nagy and Obst 1992) irrespective of whether the birds were on shore or (presumably feeding) at sea. This has been attributed to paucicity of prey items (Costa et al. 1986), but Nagy et al. (1984) suggested, that manipulation of the birds might have had some effect on their feeding behaviour. Obstruction of the pectoralis muscle after injection and/or in the foot after blood sampling might prevent the animals from foraging optimally. Nagy and Obst (1992) noticed "reluctance in some individuals to leave their nest after being relieved of nest duty" after DLW-injection.

This aspect of DLW studies has recently been further investigated (unpublished data). Gentoo penguins (n= 14) were equipped with externally-attached, streamlined data-loggers (Culik et al. 1994a; Bannasch et al. 1994), which logged swimming speed, dive depth and bird heading at intervals of 10-15 s. The devices were removed after 32-50 h, when the birds were considered to have been to sea at least once to forage. Following the methods employed by Nagy et al. (1984), Nagy and Obst (1992) and Chappell et al. (1993a), 7 of the birds were additionally injected with 5ml of DLW in one spot of the pectoralis muscle. Three other birds also received DLW, but the 5ml portion was injected in 1.25 ml quantities in 4 different localities in the pectoralis. This was done because it was considered that a volume of 5 ml in one locality might cause noticeable damage to the surrounding muscle fibres. The remaining 4 penguins were not injected and served as controls. The nests of all birds and adjacent beaches were either surveyed continuously with the aid of a remote-

controlled video camera, or nominally checked every 3 hours by an observer (at night, darkness made it sometimes impossible to check properly for 8 hours).

Visual checks showed no apparent difference in colony attendance between the different bird groups, with generally 1-2 absences per 24 h. However, as shown by the data-loggers, no bird injected with DLW actually went to sea within the first 12 h after the injection, whereas the 4 control birds did. Furthermore, swimming speeds in the birds which had received a single dose of DLW were considerably lower than in the 2 other groups. There were also significant differences in foraging ranges: 2.8, 3.2 and 6.2 km were recorded in the once, 4 times injected and control birds, respectively (Fig 15). Dive duration, depth and descent angles were also significantly different in the once injected birds with respect to the 2 other groups (unpublished data).

The effects of the injection are not manifest in the rhythm adhered to by the penguins while on land. Nest relief schedules were not affected, showing that observations made at the nest site alone are inadequate to document the possible ill-effects of DLW injection. However, the reluctance of Gentoo penguins to swim after injection, and the reduced swimming speeds, foraging range and -duration in the birds that had been injected once, presumably lead to reduced food uptake in comparison to the other 2 groups. This would explain the body mass losses observed in most DLW experiments (see above). Furthermore, if based on observations made on land, such birds are considered to forage normally and the field metabolic rate interpreted accordingly, calculated activity-specific daily metabolic rates will be wrong.

The differences between the once and the 4 times injected birds suggest that disturbance results directly from the quantity of liquid injected per locality in the muscle, with larger volumes stressing the muscle more. It is therefore advisable to inject small quantities, of physiological saline solution, preferrably into muscles which are not used in swimming or to inject intraperitoneally. From this study, it also appears necessary to ascertain that the animals used in DLW studies behave normally even when absent from the nest-site. This can only be achieved using telemetric or data-logging devices.
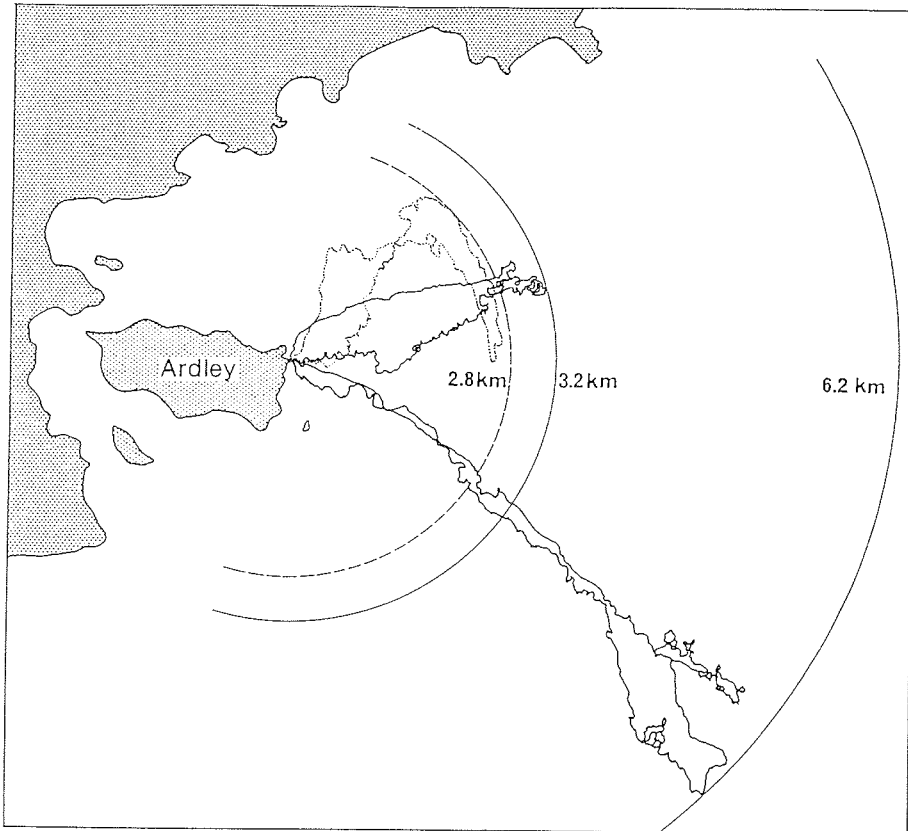
Fig 15: Mean foraging ranges of 3 Gentoo penguins representing birds that had been injected once (2.8 km), or 4 times with doubly labelled water (3.2 km) as opposed to the non-injected control group (6.2 km). Foraging ranges were determined using externally-attached data-loggers recording speed, direction and depth (Wilson et al. 1993a; Culik et al. 1994a).

5. EFFECTS OF HUMAN INTERFERENCE ON PENGUINS

In Antarctica, ice-free areas near the coast that are suitable for penguin colonies are rather rare. These areas are also often used as sites for research bases, which leads to local, but circumpolar conflict with wildlife (Culik et al. 1990b). Antarctic stations and their supply ships pollute the environment with raw sewage and fuel (Culik et al. 1991b). Oil and other surface-active agents such as detergents and faecal matter destroy the water-proofing quality of the feathers and cause loss of buoyancy and insulation (Clark and Gregory 1971; Ambrose 1990). Penguins are more vulnerable to oil spills than flying birds, since they must regularly swim from their breeding colonies to their foraging grounds. This aspect of human interference will be discussed in part 1) below.

Aircraft used in logistics are clearly highly stressful to Adélie penguins and even short exposure to this sort of stimulus causes massive panic at distances of up to 1 km (Wilson et al. 1991c). Furthermore, human proximity and handling may lead to increases in the body temperature of penguins, which may be maintained for several hours after the event (Boyd and Sladen 1971; Wilson et al. 1989b; Reins, pers. comm.). Even though incubating penguins show no visible behavioural response to the approach of a man to 30 m, heart rate rises significantly (Culik et al. 1989, 1990b). Visually assessed birds appear to be unconcerned until the human approaches to 3 m, by which time heart rate has risen by 50%. Such stress may cause changes in time/activity budgets and thus affect foraging success of pengins at sea. These aspects will be discussed in 2) (Aircraft, tourists, scientists), and some recommendations given on how these could be minimized.

5.1 Oil

Four adult Adélie penguins not attending nests were captured near Esperanza and implanted with heart rate/body temperature transmitters and subsequently kept in an enclosure. The birds were fed once daily with 400 g food consisting of deboned cod, duck food pellets and vegetable oil (16:3:1) in gelatine. Oiling of the birds occurred accidentally by preening after being fed, thereby

spreading food remains and vegetable oil over the feathers. Within 2 days, the birds feathers lost their waterproofing qualities, and the penguins got thoroughly wet whenever it rained. Energy consumption and HR of these birds were compared to those of a control group, 2 Adélie penguins which, after transmitter implantation, had been returned to their nest site where they were alternatively incubating eggs and foraging at sea (Culik et al. 1991b).

Although the duration of various activities in the swim canal were similar in oiled and control penguins, oiled birds swum significantly shorter distances in a straight line fashion (133 m) than controls (222 m) per 5 Min interval, and at slower speeds (1.6 vs 1.8 m s^{-1}). Preceeding a dive, HR in oiled birds averaged 321 bpm as opposed to 252 bpm in controls and reached 315 as opposed to 297 bpm after surfacing. More important, oiled birds while swimming consumed on average 18.8 as opposed to 12.7 W kg^{-1}, yielding mean transport costs of 12.1 J kg^{-1} m^{-1} as opposed to 7.0 J kg^{-1} m^{-1} in the control group, a difference of 73% (Fig 16). At their preferred travelling speed (2.2 m s^{-1}) oiled birds consumed on average 55% more energy than controls.

Oiled Adélie penguins in this experiment had a strong tendency to leave the water, and their swimming was erratic. They were repeatedly observed to shiver at the surface and their feathers were completely wet after each experiment, having lost all insulative properties. From this it must be concluded that, although the birds were lightly oiled, they were suffering from substantial heat loss in the water. Metabolic rate and heart rate were significantly higher in oiled birds, suggesting that these animals might have been unable to physiologically adjust for diving. High metabolic rates while swimming have also been observed in other species after oiling (c.f. Culik et al. 1991b), largely due to heat loss, but also to drag increase. Bannasch (pers.comm.) found that small changes in the surface properties of cast penguin models, such as the attachment of woolen threads for flow visualisation, caused the drag coefficient to increase by 25%.

Adélie penguin live in an extreme environment, and even on land often find conditions outside their thermoneutral zone (c.f. Culik et al. 1989). Low thermal conductance of the feathers is essential for their survival, and destruction of these properties by surface-active agents causes excessive heat loss, especially in sea-water around 0° C. Ultimately, this prevents the penguins

from foraging, which in breeding birds results in reproductive failure and death of the young. Fat loss due to fasting, even if metabolic rates on land are reduced with respect to non-polluted penguins, may not be recuperated: oiled penguins require on average 60 d for recovery, and oil is easily transfered from premoult to postmoult feathers (Kerley et al. 1985). When this happens, even freshly moulted birds die in the water when hunger eventually forces them to return to the sea (Randall et al. 1980).
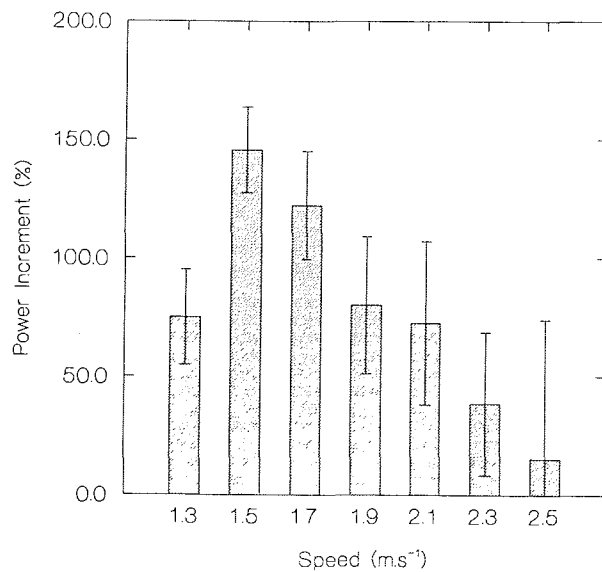
Fig 16: *Mean power increment (%) required by oiled Adélie penguins to swim at the same speed as controls. Energy expenditure in oiled penguins increased by a mean of 73% over the speed range of 1.3 - 2.5 m s⁻¹. Thin bars denotate SE.*

This problem can be circumvented by carefully transfering fuel, and by the collection and treatment of sewage before discharging it to the sea. Risks such as those of oil spills associated with accidents involving ships can be minimized, if cruises are dedicated to a specific objective, e.g. either tourism **or** refueling. In the case of the wreckage of the Bahía Paraíso near Palmer Station in 1989 (Barinaga and Lindley 1989; Eppley and Rubega 1989), for example, the ship was carrying both tourists and supplies, including fuel, for Antarctic stations. Had the trip only involved tourism, the ship would not have carried over 1 million litres of fuel. On the other hand, Palmer station would have never

been visited on a purely supply-oriented mission to Argentinian Antarctic stations.

5.2 Aircraft, tourists, scientists

Adélie penguins react strongly to humans approaching their nest sites on foot during the breeding season, although judging from their activities, they seem unconcerned. Heart rate in one penguin increased from 76 bpm to 135 bpm when approached by single human from a distance of 50 m to within 4 m of the nest. When the human approached to within 1 m, HR rose further to 140 bpm. Subsequent capture and weighing caused the bird to struggle and HR to rise to 287 bpm (Wilson et al. 1991c). Similarly, HR in a chick rose by 30% when the animal was approached and captured (Culik et al. 1990b).

Increases in HR during handling of penguins were previously thought to be a good stress-indicator, but not to affect metabolic rate to any significant extent (Culik et al. 1990a). It was thought that a rise in HR would only affect basal metabolism, and become unnoticeable once the animal engaged in energy consuming activities such as swimming or walking. However, this has been found recently not to be the case. Apart from the discussed increase in HR, human proximity and handling may lead to increases in the body temperature of penguins, which may be maintained for several hours after the event (Boyd and Sladen 1971; Wilson et al. 1989b; Reins, pers. comm). According to Wilson (pers. comm.) capture of a Chinstrap penguin and subsequent external attachment of a data-logger (handling time 6 Min, human presence due to instrumentation of neighbouring birds 22 Min) caused the animal's body temperature to rise from 38 °C to 40.5 °C within 10 Min, as measured with a stomach temperature sensor (Wilson et al. 1993a). The body temperature increase of 2.5 °C corresponds to 34 800 J of stored thermal energy (assuming a mass of 4 000 g and a body heat capacity of 3.48 J g^{-1} $°C^{-1}$). Since muscles generate 70% heat and 30% mechanical energy (Schmidt-Nielsen 1983), this corresponds to 45 240 J produced by the Chinstrap penguin in 10 Min, or the energy equivalent of 50 Min of resting.

In December 1987, 50 Adélie penguins in the vicinity of Esperanza station were marked, avoiding flipper bands or other external markers which could

affect hydrodynamic drag, by clipping 1 cm from the birds tail feathers. Tails were clipped whilst the birds remained on the nest and there was no contact between the researcher and the birds except for the scissors. The whole process took 10 s per bird. Since Adélie penguins without tail feathers were breeding normally at the same locality, we judged that the loss of a small section of the tail feathers would enable us to mark the birds with minimal disturbance. However, tail clipped birds leaving their nests on Dec 23 (n= 7) stayed significantly longer at sea than unmarked controls (n= 11) on the same date (47 vs. 34 h, respectively, Wilson et al. 1989b). The reason for this was unclear, since the birds did not have to drag an external device through the water, and the change in bird behaviour was attributed to what was termed "psychological disturbance". The implications were, however, altered nest relief intervals and reduced feeding rates of the chicks. Since the duration of the
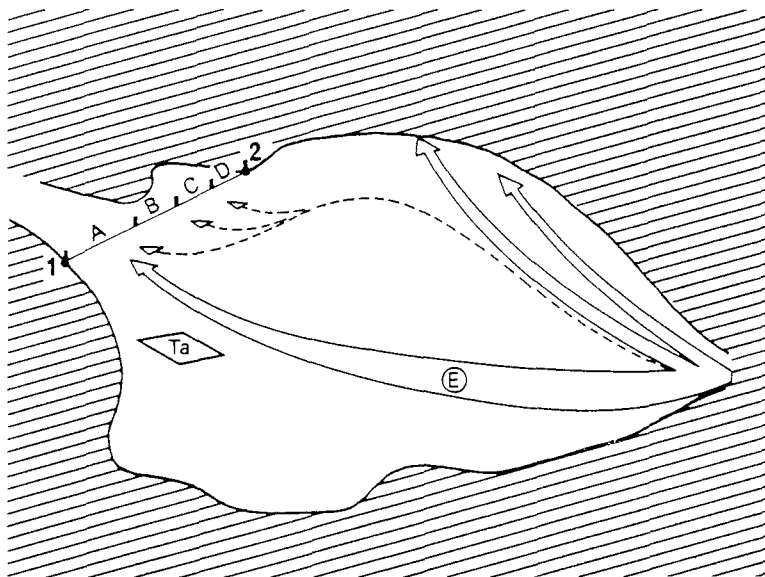
Fig 17: Schematic diagramm of the snow field over which penguins travelled to move between their colonies and the sea. Solid arrows show normal routes taken and dotted arrows show the detour made by the birds normally following route "E" after being exposed to a single human in area "Ta". Numbers of commuting birds were counted in sectors A through D (Wilson et al. 1991c).

foraging trip is a key parameter in Table 7 (Chapter 3), the overall energetic budget and reproductive success of the breeding pair thus treated were affected.

On December 12 1989, we recorded the reactions of Adélie penguins commuting between their colonies and the sea on a well-trodden path (Fig 17), to the presence of a single human "tourist" (190 cm, male) repeatedly frequenting and sitting in an area ca. 20 m distant (total duration of disturbance: 5 h). For observation we used a remote-controlled video camera and a time-lapse recorder (Wilson et al. 1991c). Presence of the "tourist" caused the birds to progressively deviate from their normal route, so that in the end they made a detour of 70 m. Birds continued using this new route as long as 4 hours after the "tourist" had left the area. This single event caused 12 000 birds to deviate on their return journey, amounting to an extra 835 penguin kilometers walked, corresponding to 95 000 kJ or 26 kg of krill spent.

In a special issue on Antarctica, Nature (350: 294; 1991) reported Wayne Trivelpiece as suggesting that a 10-20% decline in Adélie and Chinstrap penguin populations near the Polish research base Arctowski, King George Island, South Shetlands, was possibly due to overfishing of krill stocks in that area (Culik and Wilson 1991a). Trivelpiece et al. (1990) further suggested that penguin numbers could be used to monitor krill stocks.

The total annual catch of krill by commercial fisheries in the Antarctic has oscillated around 400 000 tons per summer over the past five years (Nicol, 1990). Fisheries in area 48.1, ie. the Antarctic Peninsula, Bransfield Strait and around Elephant Island and the South Shetland Islands take ca. 71 000 tons from December to March each year (D. Croll, pers. comm.), with a historical maximum of 105 600 tons. The total Adélie Penguin population in that area amounts to ca. 322 000 breeding pairs (colonies 55 through 63, Wilson 1983), which corresponds to a krill consumption per breeding season of 56 000 tons (174 kg per pair, see above), or only 80% of the annual catch taken by the fisheries. It is somewhat disconcerting to realize that, even in this remote part of the world, it is not one penguin species or some other Antarctic animal species that is the dominant predator, but mankind.

However, the observed decline of penguin populations in the vicinity of Antarctic stations may also have other reasons. Aircraft operations near the large Adélie penguin colony at Esperanza caused birds to panic, even if the plane (Hercules) was more than 1000 m away. Three days of continuous helicopter operation at the same locality for re-supplying of the base caused HR in adults to rise from 86 to 145 bpm (Culik et al. 1990b), the number of birds returning from the sea to their colonies to drop by 50%, and 8% of penguin nests to be abandonned (Wilson et al. 1991c). Adélie penguins at the joint US-NZ base at Cape Hallett, Antarctica, declined by 41% between 1959 and 1968, to 37000 pairs, and a sharp decrease in penguin numbers was also reported for Cape Royds, attributed to frequent visits by tourists and helicopters. Near Australia's Casey station, Adélie penguin populations increased by a mean of 209% everywhere but in the vicinity of the base, where numbers were stagnating (Culik and Wilson 1991a, and references therein).

However, it is also worth mentioning that at a recent conference, Fraser and Patterson (pers. comm.) presented data on Adélie penguin populations in the vicinity of Palmer station, which do not match the general pattern. Torgerson island was declared Specially Protected Area in 1978, which ended tourism and reduced research to insignificant levels. Nevertheless, the penguin population decreased there by 56% between 1975 and 1992. Lichfield island, on the other hand, was frequented every summer by tourists and scientists, and the decrease in penguin populations amounted to only 13%.

To conclude, there are numerous reports on decreasing penguin numbers in areas where human disturbance is high, be it through base operation, tourism or scientists (c.f. Culik et al. 1990b). It seems therefore, that human activities should at least be regulated in these areas, and recommendations have been elaborated for that purpose (Wilson et al. 1991c). Finally, scientists studying the wildlife in Antarctica should be aware of the fact that the utility of the data collected is not solely dependent on the accuracy of the technology used to determine the parameters of interest. It is also critically dependent on how "normally" birds behave. This implies that handling be skilful, minimal and involving minimally disturbing experimental and other procedures.

ACKNOWLEDGEMENTS

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