

University of Missouri, St.-Louis

**ECOPHYSIOLOGICAL CONSTRAINTS ON
ENERGY PROVISIONING RATE BY SEABIRD PARENTS**

A dissertation submitted in partial satisfaction of the requirements for the
degree Doctor of Philosophy in Biology

by

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I dedicate this thesis to:

The memory of my father, to my mother for her unconditional love and support for my education and happiness, and to my stepfather for always being there for me.

To my youngest brother which help was not only beyond any call of duty,
but also made the work both possible and enjoyable simultaneously!

And to my family, my loving wife for and two sons for sharing this experience with me.

And to my advisor, who taught my science by leading an great example.

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ABSTRACT

This study investigates four possible constraints on the energy provisioning rate (EPR = meal mass \times food energy density \times feeding frequency) of Razorbills parents to their single chick. Razorbills, together with two other auk species have evolved a 'intermediate' nest departure pattern (NDP) where the chick leaves the nest when only between 20-30% of adult body mass.

The central objective is to identify possible causes of this unusual NDP. The activity specific energy and time budgets of Razorbill parents were measured simultaneously with the DLW method and using bird borne data-loggers. Mixture model multiple regression was used to partition the daily energy expenditure into four average activity-specific energy expenditures (AASMR's), solving a preexisting problem of statistical analysis. The analysis explained 96.2% (R^2) of the variance in DEE between individuals, strongly advocating its use for partitioning DEE and time budget data into multiple AASMR's.

Razorbill parents spend 20-30% of their total time swimming, which represents the only potentially available time to increase the EPR. An EPR simulation model of time-energy balanced Razorbill parents was constructed to quantitatively evaluate the role of digestion, occurrence of digestive bottlenecks, and the effect of the alternate foraging behavior of Razorbill parents (versus simultaneous foraging), among others factors. The model incorporates measurements and estimates of adult feeding rate (food availability), foraging distance (food distribution), digestion rate, nest attendance, activity-specific time allocation and metabolic rates.

The observed parental EPR capacity is compared to the estimated daily energy requirement of the chick, and is apparently insufficient to produce a greater chick mass at nest departure than observed. This stems from a combination of small meal size, but in particular low feeding frequency. Long duration of foraging trips is explained by high energy cost of locomotion, demanding great food consumption and long digestive time (which corresponds to the long swimming time and diving time). Digestive bottlenecks are probably uncommon. The alternate foraging behavior potentially reduces the EPR between 26-42%, and separates the 'intermediate' NDP species from the other nest dwelling species of the family.

Digestion duration is highly sensitive to the exact duration of feeding and egestion phases, factors which are only partly under the bird's control, and can cause as great variation in foraging duration as food availability, and it proposed that this mechanism generates the high rate of parental body mass loss (reproductive stress) measured. If prevalent, this high stress rate can prematurely terminate the nestling season on its own.

Finally, a theoretical model was constructed to investigate if diving birds in general need to spend time (swimming) to recover from anaerobic diving which surpass the aerobic diving limit (ADL). As currently calculated most deep diving birds surpass the ADL by a large margin. This gap between theory and observation has produced the explanation that birds sufficiently reduce their diving metabolism (hypometabolism).

Instead of assuming neutral buoyancy as classically done, the model investigates the effect of depth-dependent diving metabolic rate, by incorporating buoyancy effects. The model thus redefines the ADL which prediction is similar to as empirically observed, and suggests that birds do not generally surpass the ADL.

INTRODUCTION

Birds occupy a spectrum of life-histories from one extreme of high reproductive rate and short life span to the other extreme of low reproductive rate and long life span. As a group, pelagic seabirds represent extreme life histories, raising no more than one slowly-growing chick each year, but enjoying extremely long lives as adults (Ricklefs 1983b). Because seabirds are tied to land to raise their offspring but forage at great distances from the breeding sites, they function at the lower limit of food provisioning that can support successful reproduction (Ashmole 1963; Lack 1968). Reproductive rate of birds is determined in large part by the rate at which parents deliver food (energy and nutrients) to their offspring (Lack 1954; Lack 1968; Ricklefs 1968; Ricklefs 1983c). The principal energetic cost of reproduction in birds is in supplying food to the dependent chicks prior to fledging (King 1973; Ricklefs 1974; Ricklefs 1983a). Food provisioning is possibly also influenced by optimized levels of foraging and parental investment which balance reproductive rate against parental survival (Fisher 1999; Williams 1966).

Although there is a general relationship between foraging distance and clutch size in seabirds (Lack 1968), much of the energetic demand of seabird chicks is fine tuned through the growth rate, which are quite variable among seabirds (Ricklefs 1979; Ricklefs 1983a; Ricklefs 1983c; Starck and Ricklefs 1998a).

Asymptotic chick mass at nest departure has received relatively scant attention as a mechanism of fine tuning energy demand, in comparison to the overall growth rate. This is perhaps an understandable emphasis, given the general observation that most nidicolous birds leave the nest close to adult body mass (Starck and Ricklefs 1998a). It raises the question however, why is chick's nest departure at sub-adult body mass used by some

species and what conditions promote it? These questions were the primary motivation for undertaking the research presented in this thesis, and pertinent for the choice of the family and focal species.

Auk nest departure patterns

Auks (family Alcidae) are commonly stated to be the only case among birds in which several developmental modes are present within a single family (e.g., O'Connor 1984). It is perhaps a more accurate statement that there are three distinct 'nest departure patterns' (NDP) among auks (Starck and Ricklefs 1998b).

Razorbills (*Alca torda* L.) and the two species of Murres (*Uria* spp.) are distinct among auks in that their single chick departs the nest early in its development (about 20 days old), when only about 20-30% of adult body mass (Sealy 1973). This has been termed the 'intermediate' NDP, being intermediate between the four nidifugous *Synthliboramphus* Murrelets which leave the nest soon after hatching, and the nidicolous remainder of the family which remain in the nest until close to adult size (Sealy 1973). Strong evidence suggests that the nidifugous pattern is a response to heavy adult predation (Gaston 1992a; Gaston 1992b; Gaston and Jones 1998), and will not be discussed further here.

The intermediate NDP in auks is often stated to be unique both in the family and among birds in general (Birkhead and Harris 1985; Gaston 1992a; Gaston and Jones 1998; Hipfner and Gaston 1999; Hipfner and Gaston 2002; Houston et al. 1996; Ydenberg 1989), but similar patterns do seem to occur among doves and pigeons (Crome 1975a; Crome 1975b; Robertson 1988) and perhaps in other families as well.

Among the three intermediate species only one adult forages at a time, the other remains at the nest to guard the chick (alternate foragers), while in the other nidicolous species of the family both parents forage simultaneously after the chick can thermoregulate on its own. Although feeding frequency varies both seasonally (Dall'Antonia et al. 2001; Gaston et al. 1983), and between colonies (Benvenuti et al. 1998; Benvenuti et al. 2001; Dall'Antonia et al. 2001; Falk et al. 2000), it is commonly only once or twice daily in the large northern colonies (Gaston and Jones 1998), consisting of fish weighing only about 1.8% of adult body mass (De Santo and Nelson 1995). Auks in general provide small meal size to their chicks relative to adult body mass, compared to most other seabirds, but among auks, the 'intermediate' species provide the smallest meals (Gaston and Jones 1998).

It has been proposed that the food provisioning rates of the 'intermediate' species are constrained by their low transport capacity owing to a high wingload (Birkhead 1977; Lack 1968; Sealy 1973). However this hypothesis is critically undermined by two observations. Tufted puffins (*Fratercula cirrhata* Pallas) have 116% wingload that of the Razorbill (Spear and Ainley 1997), but they carry twice as large meal mass to their chick (Houston et al. 1996). They attend their burrow-dwelling chick only for the first few days, presumably until the chick is able to thermoregulate, and their chick does not fledge until about 70% of adult body mass (De Santo and Nelson 1995).

Murres, which are the heaviest of auks and have the highest wingloads of birds capable of flight (Greenwalt 1975; Spear and Ainley 1997), have about 10% higher body mass during incubation (*Personal observation*), than during chick provisioning, which shows that they are certainly able to carry a much greater mass than the meals they bring

to their chicks. This does not mean however that it is necessarily energetically sustainable to carry large meals during the nestling period, for example their foraging frequency is about one half during the incubation than during the nestling period. It has been argued using aerodynamical theory that meal size has relatively small effect on the aerodynamical cost of flight (Ricklefs 1983c). This was based on the assumption that the food's mass only affected induced power exerted against gravity, but the only way to carry greater mass is to increase speed (to increase airflow over the wings and produce more lift), which increases both parasite and profile powers (Pennycuik 1989). Even if the additive flight cost is relatively small, it becomes a potential constraint when foraging distances are great.

Furthermore, it is a doubtful inference to say that the small observed meal sizes of the intermediate species indicate carrying capacity limitation. This is because, after all, the intermediate chicks are not raised to great size, so their requirements are not as great as in the other species in the family which do raise them to near adult size (a number of studies show that meals are commonly smaller earlier in the development, presumably because of the chick's lesser needs and inability to ingest large meals, see Gaston and Jones (1998)).

The small meal size of auks has been suggested to be anatomically constrained by an inability to store food for long periods in the upper gut where it is subject to premature digestion, limiting the meal size by the bill (or the 'gular pouch' in the cases of the planktivores) carrying capacity (Gaston and Jones 1998). How auk meal size are determined is an important issue, but it is clear that in the lower range, among the 'intermediate' species, provisioning rate principally reflects the number of foraging trips and not meal size.

The intermediate NDP has also been hypothesized to represent a trade-off between relative growth rate and survival at the nest and at sea (Ydenberg 1989; Ydenberg et al. 1995). Survival is typically higher, and growth rate lower, at the nest. However if growth in the safety of the nest is constrained by a low energy provisioning rate (EPR), the leverage for the other parameters in the 'trade-off' is largely offset and subdued (Byrd et al. 1991; Gaston 1998; Hipfner and Gaston 1999; Ydenberg 1998).

An increase in 'intermediate' species EPR must principally reflect an increase in feeding frequency, rephrasing the question: "why is chick's nest departure at sub-adult body mass used by some species and what conditions promote it;" to "how parental chick feeding frequency is determined, and in particular, what factors constrain it?"

Razorbills allocate a large proportion, or 25-30% of their daily budget (Dall'Antonia et al. 2001), to swimming in so-called 'inter-diving bouts (IDB)' on the sea surface. IDB's are long periods between the diving bouts, the diving bouts being composed of a series of diving cycles (the collective term for a dive and the subsequent surface pause). The function of the IDB's is not adequately understood, but represents the only potential time in the time budget which can be reduced. Although not mutually exclusive, three possible explanations for long swimming time are examined.

Recovery from anaerobic diving, surpassing the aerobic diving limit (ADL) (Chapter 3). The ADL is defined as the maximum period without breathing that does not result in an increase in blood lactic acid concentration during or after a dive (Gentry and Kooyman 1986). If dives consistently exceeded ADL, the accumulation of lactic acid would result in progressive, exponential lengthening of the post-dive pauses or, depending on the extent, a suspension of diving until normal lactate levels were reestablished

(Kooyman 1989). Or in other words long times of swimming. A theoretical model applicable to all deep (>20 m) diving birds is developed in Chapter 3.

Digestive bottlenecks, or Digestion Do the frequently observed foraging ‘interruptions,’ correspond to digestive bottlenecks, limiting the food intake rate, and possibly setting a upper limit to the daily amount of ingested of food (Kirkwood 1983; Kleiber 1975)? Or is the swimming time simply necessary for *digestive* purposes? A digestive model was incorporated into the parental time-energy EPR model, using measured or estimated parameters (Chapter 2).

The potential reduction in the EPR because of the *alternate foraging behavior* (AFP) of the Razorbill is examined by comparison to hypothetical simultaneously foraging parents (as in the other nidicolous auk species parents) in a simulation model of the parental time-energy budget (Chapter 2). This model is also used to evaluate the actual parental EPR using empirical data and, to compare to allometric predictions of the daily energy requirement of the chick (Weathers 1992; Weathers 1996).

What causes the intermediate NDP in Razorbills?

The observed EPR apparently cannot but sustain growth of a larger chick than observed, except perhaps by greatly prolonging the growth period, where the chick would not attain adult size before onset of winter, i.e., surpassing the ‘termination criteria’ in Ydenberg’s (1989) trade-off model.

Parental EPR is the product of foraging trip frequency, meal mass, and the food’s energy density (i.e., ignoring the nutrient density of the food). This rate is partly a

function of the availability of food in the environment and partly a function of the adaptations of birds to exploit the food resource.

The low EPR observed stems from a combination of small meal size, but in particular low feeding frequency. Long duration of foraging trips is largely explained by high energy cost of locomotion (both flying and diving), demanding great food consumption and long digestive time (which corresponds to the long swimming time and diving time). The EPR model demonstrates a great dependence on foraging distance, which is to be expected in a species with high flight cost (Chapter 1). The observed range of feeding rates is however fairly narrow, possibly reflecting low sample size, but might also reflect that schools of fish might provide somewhat consistent yield. At a given foraging distance, feeding rate has relatively little effect on foraging frequency, except at very short distances (<5 km). Not surprisingly, most of the variation in energy expenditure seems to depend on foraging distance, the most energetically expensive activity (Chapter 1). There is not particular reason to believe however, that foraging range is consistently more variable in Razorbills than in other piscivores in the family, although that is a possibility.

Does Razorbill's EPR (or most avian divers) suffer from anaerobic recovery? Most deep diving birds surpass their theoretical ADL as generally formulated. This gap between observation and theory is currently considered best explained by a general hypometabolic capacity of birds, rather than to resort to an anaerobic explanation, but bird's anaerobic capacity is relatively poor (Boyd 1997). A third alternative, the 'buoyancy hypothesis', is proposed in Chapter 3 and the magnitude of buoyancy effects on diving metabolic rate and consequently the ADL examined. This hypothesis predictions fit

the observation well, closing the gap between observation and prediction, and suggesting that the current practice of assuming neutral buoyancy of deep divers is incorrect, and by falsely assuming a constant diving metabolic rate, independent of diving depth, produces the before mentioned gap. The “gap” was apparent in Razorbills, which unintentionally had their diving metabolic rate greatly increased through drag, but still dove much longer than expected (Chapter 1)!

Digestive bottlenecks are expected to occur rather infrequently, and certainly not explaining the ‘frequent foraging interruptions’ (Chapter 2).

According to the digestive model both diving time and swimming time were required for *digestion* purposes, not leaving any scope for potential EPR increase. Digestion duration (of the same amount of ingested food) is highly sensitive to the exact duration of feeding (diving) bouts and egestion (swimming) bouts, factors which are only partly under the bird’s control, and can cause as great variation in foraging duration. Together with food availability, this mechanism can generate the high rate of parental reproductive stress (body mass loss) measured.

The alternate foraging behavior potentially reduces the EPR between 26-42%, and segregates the ‘intermediate’ NDP species apart from the other nest dwelling species of the family. This behavior is common to the ‘intermediate’ species (a shared derived, or synapomorphic character), and is the primary candidate for the evolution of intermediate NDP, and is necessitated by the need to continuously guard the chick. This is understandable in the Murres (*Uria* spp.) case, as they breed colonially in the open. It is less obvious in the Razorbill which nests predominantly in crevices. Apparently however

Razorbill chicks are quite prone to be killed by non-breeding Razorbills if not guarded (*Personal observations*).

It should be mentioned that the high rate of parental body mass loss, or reproductive stress, observed in Razorbill parents (Chapter 2), is capable of termination of the nestling period prematurely, which would occur when the parental stress level reaches some critical minimum. However, further speculations have to await better knowledge if this is a prevalent phenomenon in the 'intermediate' species, and if the level of parental stress is inversely correlated with EPR level in the family. That is, if the level of parental stress dictates the nestling season duration in nidicolous auks.

EPR of seabird parents in relation to digestive specializations, and foraging ecology

To better understand the role of digestive specialization (perhaps better termed a handicap in the auks case), in the diversification in seabird foraging ecology, and its relation to reproductive rate, these aspects need to be put into perspective. Although seabird's parental EPRs are in the lower extreme, the range is nevertheless impressively large and reflects number of different specializations, especially in digestive physiology, which have opened up new dimensions in their foraging ecology, previously constraining the parental EPR.

Tube-noses (Procellariiformes) attained the ability to concentrate and accumulate fatty oils in their stomach, greatly increasing energy density of their meals (Imber 1976; Jacob 1982; Place et al. 1989; Roby et al. 1989; Roby et al. 1997; Taylor et al. 1997). This specialization allowed the exploitation of the extreme foraging ranges observed, by accounting for the lower feeding frequency associated with them, by the greater energy

content of meals (Jouventin and Weimerskirch 1990; Prince et al. 1992; Sagar and Weimerskirch 1996).

A recently documented, but apparently widespread food provisioning strategy, by tubenose parents which alternate between short and long foraging trips (both in terms of duration and distance), represents a behavioral modification that increases the chick's feeding frequency. This strategy enables the utilization of prey that is close to the colony for the chick, and hence increasing the feeding frequency, but offering too low energy acquisition rate to satisfy the parental expenditure (otherwise it would be the main prey). The parents make up for their temporary energy reserve loss endured in the short trip in a subsequent and longer foraging trip to more distant foraging area, offering higher energy acquisition rates (Chaurand and Weimerskirch 1994; Stahl and Sagar 2000a; Stahl and Sagar 2000b; Weimerskirch 1998; Weimerskirch and Cherel 1998; Weimerskirch et al. 2000; Weimerskirch et al. 1992; Weimerskirch et al. 1997). It would not be surprising if this would also be observed in auks in the future, especially in long distance feeders and 'intermediate' NDP species like the Thick-billed Murres (Benvenuti et al. 1998).

Penguins represent another example of digestive specialization, although little publicized. The loss of flight and consequent reduction by a magnitude in transportation speed, in combination with relatively long foraging ranges imposed a dramatic decrease in food provisioning rate. Penguins have been shown to have the unusual ability to cease digestion (Wilson et al. 1989), and are therefore able to carry very large meals intact back to the chicks, which more than compensates for their slow transportation speed (all but two species have a clutch size of two), analogous to flow of cargo over a fixed distance by a cargo aircraft versus a ocean tanker. It is not unlikely that this ability was a prerequisite

for the loss of flight, which permitted drastically increased body size and wing adaptations to swimming underwater, allowing the achievement of greater diving depth and duration, greatly expanding the choices of available prey.

This begs the question how the extinct Great Auk (*Pinguinus impennis* L.), a close relative of the Razorbill (Moum et al. 2002), evolved its flightlessness, assumingly being restricted to relatively small meals as other auks. The answer most likely is that their ancestors had 'intermediate' NDP, which was the precursor for the loss of flight, by greatly reducing the chick's energy demand.

As said before auks apparently lack the ability to cease digestion, in variance with penguins (Pütz 1994; Wilson et al. 1989), which precludes the use of the stomach for food transport by premature digestion (Gaston and Jones 1998). The overall small meal size carried by auks to their chicks, is limited to transporting food in the bill (piscivores), or in special 'gular sacks' (planktivores), and the corresponding volume capacity (Gaston and Jones 1998). Meal mass of the 'intermediate' species is considerably smaller than their aerodynamic carrying capacity, judged from intra-specific body mass difference during incubation versus nestling periods (e.g., Gaston and Perin 1993).

Future studies

The Mixture Model Multiple Regression (MMMR) as a AASMR calculation method should largely solve the preexisting statistical calculation problem of extracting multiple AASMR's from daily energy expenditure (DEE). This method has the capacity of elevate field studies which use DLW and also measure detailed time allocation, to new levels of sophistication and complexity of hypotheses which can be tested, away from the DEE (or

field metabolic rate, FMR) reporting currently practiced (see a review by Speakman 1997). Especially are AASMR promising in modeling parental foraging ecology, particularly EPR, and thus producing a comparative framework of foraging ecology and reproductive energetics.

The role which digestion plays in foraging ecology has certainly not been given the attention it deserves. The field is abound with opportunities of investigation, especially in the laboratory but also field experiments. The preferential choices of when to start feeding again (IDB) as a function of previous ingestion rate or amount ingested. The results of such experiments should appeal both to physiologists and ecologists alike. Perhaps the most important aspect of digestive physiology in relation to foraging ecology and time-energy balance is the large influence is can have on time allocation, much of with not under the bird's control, that is, a potential 'parental stress generator.' However it remains to see how and why that relates (if it does) inversely to EPR, pending on data from a greater number of species.

The ADL simulation model is experimentally testable, and in particular calls for adequate measurements of bird buoyancy. The canal respirometry experiments need experimental field counterparts, preferably using the same species, streamlined loggers and MMMR for analysis. The suggested suppression effect of digesta on respiratory volume lends itself to experiments using force-feedings and subsequently measuring respiratory capacity.

The EPR simulation can undoubtedly be enhanced with propagation error analysis, to investigate which components are candidate generators of parental stress, and the effects of environmental stochasticity, among other things.

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Partitioning the Field Metabolic Rate Into Multiple Activity-Specific Metabolic Rates Using a Mixture Model Multiple Regression

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Summary

Daily energy expenditure (DEE) of Razorbill parents during the nestling period was measured with the DLW method. Precise and exhaustive time allocation was measured simultaneously with data-loggers, separated into four activity-specific time categories, flying, diving bouts, ‘inter-diving bouts’ at the sea surface, and at the nest. A previously overlooked method was used to partition the DEE into four corresponding average activity-specific energy expenditures (AASMR’s), the mixture model multiple regression. The model explained 96.2% (R^2) of the variance in DEE between individuals, and its general outstanding performance, strongly advocates its use for partitioning DEE and time budget data with more than two categories. The metabolic rate at the nest and in inter diving bouts were statistically indistinguishable at 2xBMR. Metabolic rates (MR) of both flight (MR_F , 17.7xBMR), and diving bouts (MR_{DB} , 11.8xBMR) were high, but not statistically different. The MR_F estimate is 168% of an allometric prediction, and the MR_{DB} 355% of an allometric prediction from compiled laboratory studies. This difference is primarily attributed to instrument drag, affecting diving to a substantially greater extent. Razorbill’s oxygen reserves available for diving are high (57.2 mL O₂ kg⁻¹) as in other auks and in penguins. The inadvertently increased MR_{DB} lowered the calculated aerobic diving limit (cADL) to only 16 s, but was still “surpassed” in 60.4% of the dives! The behavioral ADL (bADL) was estimated at ≈70 s, which only 0.3% of dives surpassed. Diving pause duration was virtually independent of dive duration until 30 s, after which it increased linearly to the bADL. The apparently large ‘discrepancy’ between observed and expected aerobic diving capacity appears to be an theoretical artifact, by falsely assuming MR_{DB} independence of depth, and subsequently extrapolating costly shallow dives.

Introduction

Empirical time-energy budget is perhaps the most appropriate currency to quantitatively test such diverse ecological theories as, parental food provisioning effort and investment, foraging strategies, and resource competition (Goldstein, 1988; Goldstein, 1990). Central to this approach are average activity-specific metabolic rates (hereafter AASMR's). AASMR's calculated from time partitioned daily energy expenditure (DEE), measured with doubly labelled water (DLW) method (Speakman, 1997), enable the examination of both observed, and any conceivable hypothetical time budgets (e.g., foraging schemes). The statistical methodology for AASMR calculation, has however received undeservedly scant attention, and has generally been somewhat ambiguous to date. One approach has been to subtract the time and energy expenditure at the nest from the DEE, when direct measurements are available, (e.g., Arnould et al., 1996). This procedure is bound to affect the variances estimates for the at sea activities, and discards information about the average metabolic rate measured under natural conditions at the nest, and its variance. It seems more informative approach to compare these data to the available direct measurements. More common approach to AASMR calculation has been to use univariate linear regression of time spent in a focal locomotor activity (e.g., flying or swimming) versus total energy expenditure over the measurement period (i.e., DEE), the slope of the regression being the cost of the focal activity per unit time over and above the intercept, which involves all energy expenditure in the absence of the focal locomotor activity (Ballance, 1995; Birt-Friesen et al., 1989; Costa and Prince, 1987; Flint and Nagy, 1984; Nagy et al., 1984). Wilson and Culik (1993) pointed out that in this analysis, the intercept cannot remain constant, and independent of the amount of time

allocated to the focal locomotor activity, as inherently assumed, because of the fact that the activities are mutually exclusive. In fact this approach is a clear example of using a univariate technique to a multivariate problem. Even with the use of ‘ordinary’ multiple regression as suggested by Wilson and Culik (1993), the previously mentioned intercept problem still remains at large. This is because the statistical properties of exhaustive and mutually exclusive activities, like time allocations in time-energy budgets, are ignored, instead of being utilized in the choice of an analysis method. To solve this problem, we advocate the mixture model multiple regression analysis (MMMR, Kvålseth, 1985; Marquardt and Snee, 1974; Wilkinson et al., 1996). The MMMR partitions the effects of mixtures of mutually exclusive, ‘independent’ variables (activity specific time allocations), on a dependent variable (daily energy expenditure, DEE). The main difference of the MMMR from the ordinary multiple regression is that the independent variables sum to a constant value (i.e., 24 h commonly used in DLW studies), and the residual sums of squares have therefore one less degree of freedom than ordinary multiple regression models. This also explains the nonexistence of a non-zero intercept, MMMR on *exhaustive and mutually exclusive* activity mixtures, have by definition a zero-intercept (also termed ‘no-intercept’)! In other words, it is by definition (by principle of allocation) impossible for an animal not to spend all its time in some of the *mutually exclusive* activity categories, because they compose an *exhaustive* total time budget.

We used a data-logger on Razorbill parents, during the chick provisioning period, simultaneously executing an doubly labelled water (DLW) study. The aims of this study were as follows. (1) The determination of daily energy expenditure (DEE) using the

DLW method. (2) Simultaneous measurement of their exhaustive time budgets, divided into five mutually exclusive activities, flying, at nest, diving, surface diving pauses, and on the sea surface (i.e., not following dives). (3) The identification of the mixture model multiple regression as the most appropriate statistical method for partitioning DEE into average activity-specific metabolic rates (AASMR's).. (4) To use MMR to partition the DEE of Razorbill parents into AASMR's of flying (MR_F), nest (MR_N), 'diving bouts (MR_{DB}),' and 'inter-diving bouts (MR_{IDB}).' (5) To compare the observed MR_F to a allometric prediction (Masman and Klaassen, 1987). (6) Compile laboratory studies on avian diving metabolism from the literature, and produce an allometric regression equation, in order to provide an preliminary prediction for comparison to our observed MR_{DB} . (7) Determine the frequency distribution, average and standard deviation of: dive duration; diving pause duration; and diving depth. (8) Evaluate the relationship between dive pause duration and dive duration, and estimate the 'behavioral aerobic diving limit' (bADL, Kooyman and Kooyman, 1995). (9) Estimate the oxygen stores available for diving. (10) To determine the 'calculated ADL' (cADL, dividing 3 by 5), and compare to the bADL.

Material and methods

The study site, Látrabjarg, NW-Iceland (65°30'N, 24°32'W), is the world's largest Razorbill colony (*Alca torda islandica*), of about 230.000 pairs (Garðarsson, 1985). The study birds were snared from the cliff's edge, using a 7-m noose-pole, during

the chick-provisioning period, 3-14 July 1998. All experimental birds were attending chicks between 1-11 days old.

Sexing. Four- μ L blood samples were normally collected for sex determination when the birds were recaptured and immediately put in cell lysis solution (Purgene, Genra Systems Inc., MN 55447), in which they were stored at 5° C until analysis. Sex was determined by PCR amplification using sex-specific primers P2 and P8 (Griffiths et al., 1998) and 2550F and 2718R (Fridolfsson and Ellegren, 1999). The results were verified by controls using known males and females. All but two individuals were sexed, either directly or by association to a mate of determined sex (Appendix A).

Daily energy expenditure (DEE). Fourteen adult parents were caught, hooded to calm them down, and injected intravenously (IV) into the brachial vein with 0.9547 ± 0.0004 SD mL of DLW. The injected DLW dose was estimated by repeating the field protocol in the laboratory and carefully weighing an empty syringe (1.0 mL ‘Tuberculin Once’), a syringe filled with 1 mL of doubly distilled and deionized H₂O, and an emptied syringe, including the ‘dead space.’ Weighing was repeated in triplicate to the nearest 0.1 mg on a recently calibrated analytical balance (Denver Instrument Company, XE-Series, Model 100A). DLW enrichments were, ¹⁸O 1.0274 p.p.m., and ²H 1.0264, p.p.m.. After injection, the birds were banded with a one g steel band, the flattened wing cord was measured to the nearest mm, and body mass was obtained to the nearest 5 g using a 1000-g Pesola spring balance. Birds were then fitted with a data-logger (see below). An ‘initial’ blood sample (4-5 x 40 μ L) was collected by puncturing the brachial vein with a sterilized needle, or by using a syringe to draw blood from an unidentified vein in the leg (from the opposite side of injection), and placed into 100 μ L

heparinized microcapillary tubes. The microcapillary tubes were flame-sealed immediately with a propane torch and stored at 5° C from the day of sampling until the isotope analysis. Birds were released after the bleeding had been stopped. An attempt was made to capture each bird after 24 h. Upon recapture, another set of blood samples was taken as described above ('final' sample), body mass measured, the data-logger was removed, and the recorder's data were downloaded to a laptop PC via the serial port.

The IV injection was chosen in preference over intramuscular (IM) and intraperitoneal (IP) injections to achieve the shortest isotope equilibrium time possible. The average equilibration time was 10.46 ± 3.15 min ($n=13$), and was determined practically by the time needed to attach the data-logger, band the bird, and take its body measurements. This short equilibrium time was implemented to minimize time away from the chick and handling stress. Meanwhile, the chick needed to be continually guarded (remotely) by a researcher until the parent was released and returned to the nest, normally within 5 minutes. This was necessary because of aggressive non-breeders, which on one occasion killed an unguarded chick within minutes of its parent's capture.

An isotope equilibrium study was performed by injecting four incubating birds and sampling them twice, during 25-27 June 1999. This study compared the difference in isotope enrichment levels after 11.13 ± 1.44 min from injection, and after the one-hour equilibration period (54.5 ± 7.59 min, Table 1) typically employed in comparable doubly labeled water studies (Speakman, 1997). The equilibrium study subjects were kept in ventilated, darkened cardboard boxes between taking the blood samples.

Average background isotope levels were measured in eight non-experimental birds at the same location, collected between 3-12 July 1998. Mean background of ^{18}O was 2005.2 ± 6.05 (SD) p.p.m. and of ^2H 154.7 ± 2.52 (SD) p.p.m..

Isotope Analysis. For each sample, $^2\text{H}/^1\text{H}$ and $^{18}\text{O}/^{16}\text{O}$ isotope ratios were determined in triplicate, when possible, at the Centre for Isotope Research, Groningen, Netherlands, using VG-ISOGAS SIRA 10 and SIRA 9 isotope ratio mass spectrophotometers (IRMS) for each isotope, respectively. The ^{18}O and ^2H enrichments were determined by the CO_2 equilibrium and uranium reduction methods, respectively (Speakman, 1997). For details of isotope analysis see Visser and Schekkerman (1999).

‘Initial’ total body water pool (TBW, N , mol) of each individual was calculated using the principle of isotope dilution for both ^{18}O and ^2H (N_{O} and N_{D} , respectively), using eq. 3 in Visser and Schekkerman (1999), and is referred to as the ‘plateau’ method (Speakman, 1997).

Fractional isotope turnover rates for ^2H and ^{18}O , k_{D} and k_{O} , respectively (d^{-1}), were calculated using eqq. 4 and 5 in Visser and Schekkerman (1999). The average background concentration for ^2H was 154.7 ± 2.52 p.p.m., and for ^{18}O was 2005.2 ± 6.05 p.p.m. ($n=8$).

Water flux rate ($r\text{H}_2\text{O}$) was calculated assuming that body water pool W (mL), is a constant percentage of body mass with regard to change in body mass over the measurement period, in which case water influx and efflux differ, depending on extent of loss or gain of body mass (eqq. 4 and 6 in Nagy and Costa, 1980). In this scenario, the initial body water pool (mL) was calculated by eq. 3 in Visser and Schekkerman (1999), and the final water pool (mL) was estimated using the same percentage, but of the final

body mass (kg). The water flux calculations were corrected for isotope fractionation effects caused by evaporative water loss, using eq. 7.6 in Speakman (1997). Proportion of water flux assumed to be lost in evaporation (r_G), and the equilibrium fractionation factor (f_1 , ^2H ; H_2O vapour/ H_2O liquid) were assigned values of 0.25 and 0.941 respectively, (Speakman, 1997; Visser, 2001).

Water flux rate, assuming a constant water pool (water influx equaling the efflux), was additionally computed using eq. 3 in Nagy and Costa (1980), and subsequently corrected for fractionation, also using eq. 7.6 in Speakman (1997). Individual water turnover rates under both assumptions are given in Appendix A, but the constant percentage assumption (see above) is used throughout the text.

The rate of carbon dioxide production ($r\text{CO}_2$, L STPD) was measured with the ‘two-sample technique,’ assuming a ‘single water pool,’ and 25% evaporative water loss, using eq. 17.7 in Speakman (1997), using a pooled correction factor $f_p=0.0249$ (see Table 7.1 in Speakman, 1997). Carbon dioxide production (L, STPD) was converted to energy equivalent (kJ) using a conversion factor of 27.33 kJ L^{-1} (Gessaman and Nagy, 1988a).

Activity-specific time budgets. We used a data-logger with 128 kB memory capacity, equipped with two active sampling channels (Benvenuti et al., 1998; Benvenuti et al., 2001; Dall'Antonia et al., 2001). (1) Depth gauge, with operative range 0-70 m, with 0.3 m resolution, and 4-second sampling interval. (2) A modified mini microphone serving as a ‘flight’ sensor (including underwater ‘flight’), with a 6-second sampling interval. As configured, the event-recorders discriminate between four distinct basic types of activities: (1) diving, (2) flying, (3) on the sea surface, and (4) at the nest (see Benvenuti et al., 1998), and conform to the main ‘natural’ activities of provisioning

Razorbill parents. The temporal sequence of the activities conveys additional information, allowing that surface time to be split into diving pauses, and so-called ‘inter-diving bouts (IDB).’ Diving bouts are a continuous sequence of diving cycles, composed of a dive and subsequent diving pause. We separated the diving pauses and the IDB’s from each other in the time budget, using a critical limit of 90 s, being lesser and greater than, respectively (Dall’Antonia et al., 2001). This limit was determined by a visual inspection of the data, although somewhat arbitrary as such, IDB’s of much longer duration predominate, not justifying more sophisticated analyses (e.g., Mori and Sato, 2001; Sibly et al., 1990; Slater and Lester, 1982). We are confident that allocation bias between the two categories is diminutive, due to the large duration difference and the fortunate rarity of ‘medium’ length surface periods.

The data-logger’s four-second sampling interval is 15.9% of the 25.1 s average duration of diving (the activity of the shortest duration). This is above the 10% guideline suggested by Boyd (1993) and by Wilson *et al.* (1995), above which they reported an introduction of bias in the dive duration information. However, neither of these studies examined whether this proposed guideline was independent of the activity’s absolute duration. The cumulative effect of the ± 4 s imprecision for the total time budget is negligible, since all deviate moments within the 8 s range are equally probable, and largely cancel out, producing much higher accuracy in the total diving time measurement than in the individual dive durations.

The data-loggers were attached to the mid-back (between the wings) by three brass wires threaded under a fine nylon mesh which had been glued with cyanoacrylate to trimmed back-feathers (for further attachment details see Benvenuti et al., 1998). Logger

detachment by clipping and removing the wires only took few seconds. Although the recorder's position maximizes parasite or fuselage drag (Bannasch et al., 1994), it also minimizes any changes to the center of gravity during flight. Radio transmitters attached to the tail, in contrast to the back, on Razorbills and Common Guillemots (*Uria aalge*) inflicted abnormal behavior (Wanless et al., 1985; Wanless et al., 1988; Wanless et al., 1989). Our data-loggers were streamlined by rounded front and edges, but had a flat, instead of tapered end (Obrecht III et al., 1988), and were not shaped to conform to the bird's back contour. (Culik et al., 1994a). The physical characteristics of the data-logger were: mass 28 g (4.5% of average body mass, M_b 616g); volume 28 mL; density 1.0 g cm³; buoyancy 0.008 N; maximum cross sectional area (S_i) 4.15 cm²; or 7.0% of the estimated cross-sectional area of a 616 g bird (59 cm²) (eq. 3.5 in Pennycuick, 1989); height: 13-18.5; width: 22-31; and length: 80 mm.

Average activity-specific metabolic rates. Since oxygen reserves are replenished during the diving pauses, their metabolic rates, and metabolic rate of the idle inter-diving bouts are likely to differ. Separation schemes of the diving metabolic rate (MR_D), and diving pause metabolic rate (MR_{DB}) are available (Culik et al., 1996), provided that information on their covariation is available (as in respirometry studies). This is not the case for DLW partitioning, although the temporal component of the information is available, the approach is limited to partitioning the rate energy consumption into activity-specific averages. The choices are thus limited to the calculation of (1) all five possible AASMR's, (2) to calculate the four 'basic' activities, i.e., to treat both surface categories (diving pauses and inter-diving bouts) as the same, although against better knowledge, or (3) to account for their physiological inter-dependency by combining them

into a single rate (diving bout, DB). We performed analyses 1 and 3, starting with all five AASMR's. The results of analysis (1) demanded the combination of dives and pauses into a single category, i.e., analysis (3), otherwise their physiological interrelationship was manifested by a “negative” metabolic rate of diving (insignificantly different from zero), and an unrealistically high diving pause metabolism ($674 \text{ J g}^{-1} \text{ h}^{-1}$). Analysis (1) produced a correlation coefficient of -0.97 between the partial regression coefficients of diving pauses and dives, and a condition index of 20.714 for diving pauses, statistically confirming the notion of physiological interdependency between the two. The results of analysis 3 are provided in Table 3.

The average activity-specific metabolic rates of the ten birds with complete information were calculated using MMR (Wilkinson et al., 1996). The individual activity-specific time allocations were proportionally scaled to 24 h before the analysis, $24 = T_N + T_F + (T_P + T_D) + T_{IDB}$ (eq. 1), where T is the time (h) spent daily in each activity (Table 2), and the capital subscripts N, F, P, D, and IDB, denote the time spent at nest, in flight, pauses on the surface, diving, and inter-diving bouts respectively. Pauses and dives durations were combined into diving bouts (DB). The regression model is specified by $DEE = b_N T_N + b_F T_F + b_{DB} T_{DB} + b_{IDB} T_{IDB}$ (eq. 2), where DEE is mass-specific daily energy expenditure ($\text{J d}^{-1} \text{ g}^{-1}$) and the b_i 's are the partial regression coefficients corresponding to AASMR's ($\text{J h}^{-1} \text{ g}^{-1}$). Scaled individual activity-specific time budgets and corresponding mass-specific DEE's used in the analysis are provided in Table 2.

The aerobic diving limit (ADL). The ‘calculated’ aerobic diving limit (cADL, Kooyman, 1989), was calculated by dividing the estimated oxygen stores available for diving (see below), with the estimated average diving metabolic rate (MR_D , Table 3).

The *ad hoc* concept ‘behavioral aerobic diving limit (bADL)’ was estimated using the ‘tracing of the minimum diving pause at depth’ following Kooyman and Kooyman (1995). bADL corresponds to a ‘sharp increase’ in the minimum pause duration when plotted as a function of dive duration (Fig. 3A). The bADL estimate was more clearly illustrated in another study on the slightly larger subspecies of the Razorbill (*A. t. torda*), using the same instruments as here (see Fig. 9C in Benvenuti et al., 2001). The frequency distributions of diving duration, diving pause duration, and maximum diving depth are provided in Fig. 4, together with the cADL and the bADL.

Linearity test (Zar, 1999), of replicated linear regression between diving pause durations (replicated) per second of dive duration (groups), found the relationship highly significantly nonlinear ($F_{72, 9986} = 9.476, P \ll 0.000001$). The data show an initial ‘flat phase,’ where diving pause duration increases very little with dive duration, and a following ‘sloping phase,’ where the diving pause duration increase with increased dive duration (Fig. 3A). The relationship was examined with respect to this by fitting a four parameter ‘piecewise’ linear regression (or ‘broken-stick’ regression), whereas the least square fit of two but combined linear regressions are maximized simultaneously by the choice of a optimal breakpoint, separating the two linear functions (Wilkinson et al., 1996).

Oxygen reserves available for diving. The oxygen reserves for Razorbill and four other alcid species are compiled in Table 4, using both published, and our own unpublished data. The compilation follows Stephenson *et al.* (1989), and assumptions therein, except when noted otherwise. Plasma volume in four adults Razorbills was measured by I.V. injection of 0.1 mL of 2.5 g L⁻¹ Evans Blue (T-1824) dissolved in

doubly distilled water (Linden and Mary, 1983). Blood samples were collected from the opposite wing (or leg) to the side of injection at 3, 6 and 9 minutes from injection. The blood samples were stored at 4° C from the day of collection until analysis. Absorbance was measured photospectrometrically at 624 nm, and compared to a calibration curve of five known dye dilutions in razorbill plasma. The protocol of Thornberg (1958) was used due to occasional hemolysis, but gave virtually identical results. The Evans Blue dye reached an equilibrium between 6 and 9 minutes. Blood volume was calculated as plasma volume divided by 1-Hcit (Hcit: hematocrit) which is the proportion of blood cells of the blood. Mean Hcit (in duplicates at minimum for each individual, but normally in quadruplicates or more), were obtained in the field by centrifugation of blood in microcapillary tubes at 10,000 rpm for 5 min, shortly after collection. Hemoglobin (Hb) concentration was measured using the Sigma diagnostics total hemoglobin procedure No. 525. Identical results were obtained whether using 100 µL sample volume as with the original protocol's 2 mL sample volume. Hb carrying capacity was assumed to be 1.356 mL O₂ g⁻¹ Hb (Lenfant et al., 1969), instead of 1.24 mL O₂ g⁻¹ Hb (Viscor et al., 1984). 96% of the blood's oxygen was assumed usable (Hudson and Jones, 1986). Muscle mass of all five species was assumed to be 30% of body mass (Kooyman, 1989). Muscle myoglobin (Mb) capacity was assumed to be 1.24 mL O₂ g⁻¹ Mb, and 100% usable. Razorbill's Mb concentration was assumed to be the same as the Brünnich's Guillemot's pectoral muscle's (Croll et al., 1992). Total respiratory volume (lungs and air sacks) was estimated by the allometric equation of Calder (1984), $V_R=155M_b^{0.92}$, where M_b is body mass in kg. Average volume fraction of oxygen in respiratory system

was assumed 17.6% (20.95% in air STPD), and that 75% was usable (Torre-Bueno, 1978).

Total oxygen reserve of four other species of auk were also compiled for comparison, Brünnich's Guillemot (*Uria lomvia*), Little Auk (*Alle alle*), Atlantic Puffin (*Fratercula arctica*), and Black Guillemot (*Cepphus grylle*), using a combination of literature values and own measurements (E.S. Hansen *unpubl.*). Blood volume has only been measured in one other alcid species, the Brünnich's Guillemot (Croll et al., 1992), which had practically the same blood volume proportion of body mass as in the Razorbill, or 12.3% and 12.4% respectively. The blood volume of the three other alcid species were assumed to be the 12.3% of body mass. The muscle myoglobin concentration of the Little Auk was assumed to be the same as Atlantic Puffin's (Davis and Guderley, 1987).

Results are reported as average \pm S.D. of the mean, except where otherwise noted, and significance assumed at $\leq 5\%$ probability (α), SYSTAT was used for statistical analysis (Wilkinson et al., 1996). Logger data was downloaded into a custom made software (A. Ribolini *unpubl.*) for primary analysis, and secondary data management performed in Excel.

Results

The birds' sex, number of foraging trips, age of their chick (d), body mass (g) and times of capture and recapture, total body water (%), and daily CO₂ production and water turnover under the two different assumptions about body water change, are

provided in Appendix A. The sex of 12 of the 14 birds was determined as five females and seven males.

Two of the 14 data-loggers failed to produce data (birds No. 2 and 7), and one bird escaped before blood sampling (No. 11), reducing the sample size to 11 individuals of which time and energy budgets were both known. Bird No. 1 was incubating an egg, and had a significantly lower DEE than the other birds (Studentized residual = -2.212, $P < 0.05$), reflected in consistently the lowest AASMR values. It is possible that this result is somehow associated with incubation, but this outlier was certainly not representative of the group and was therefore excluded from further analyses. Water turnover indicated that bird No. 7 did forage and that bird No. 2 did not (failed data-loggers). Six of the 12 individuals with known time budgets went on one (No. 10, 11, 12 and 14), two (No. 4 and 9), or three (No. 13) foraging trips during the measurement period, while six did not forage (No. 1, 2, 3, 5, 6, and 8). This pattern of foraging/non-foraging was independent of sex (Fisher's Exact test, $P=1$). Two of the six foragers (birds No. 4 and 10) experienced a reduced food intake rate (negative energy balance), based on their water influx values, which were intermediate between the foragers and non-foragers. Consequently they suffered an energy deficit (less energy intake in food, than expenditure).

The parents which foraged undertook on average one daily foraging trip (1.2 ± 0.7 , $n=7$). The behavior of the six non-foragers is at apparent variance with the 15 instrumented-only individuals (Dall'Antonia et al., 2001), all of which foraged. It should be noted however that the time budgets of the instrumented-only individuals and that of the 'suppressed' foragers are indistinguishable, leaving open the possibility that some of

the instrumented-only birds might have suffered reduced food intake as well. The fact remains however, that despite the I.V. injection and short handling time, the combined treatments of DLW and the data-logger instrumentation lead to total cessation of foraging in one half of the birds (6 out of 12), but apparently in none of the cases of the data-logger alone!

Isotope equilibrium. Two direct measurements of TBW were made by desiccation (dried at 60° C until constant mass) of two adult males, one collected in the beginning (TBW 57.8% of body mass), and the other at the end, of the chick-provisioning period (TBW 60.3% of body mass). Their average, 59.0 ± 1.8 TBW% was 1% lower than the average of the ‘plateau’ TBW estimates from the ‘short period’ birds, although not significantly different ($60.0 \pm 2.0\%$, $n=14$, Student’s 2-tailed t -test: $t=0.514$, $df=14$, *n.s.*, Appendix A), suggesting that an equilibrium had been attained after the ‘short’ period.

On average the ^{18}O enrichment was $2.65 \pm 0.76\%$ lower after the 54.5 ± 7.6 minutes or the ‘normal’ equilibrium period (one hour), than after the ‘short’ period of 11.1 ± 1.4 minutes from the IV injection, and in an identical comparison the average ^2H enrichment was $2.27 \pm 0.70\%$ lower (Table 1). The reduction in isotope enrichment indicates that equilibrium had been attained after the short period, the difference between the short and ‘normal’ periods predominantly reflecting the metabolic activity over the average 43 min.

Average activity-specific metabolic rates

The MMR analysis explained 96.2% of the variance (R^2) in mass-specific DEE between individuals, and the standard error of the estimate was 0.099 (Table 3)! The

regression was highly significant (ANOVA, $F_{3,6}=51.336$, $P<0.000114$). The residuals appear homoscedastic (Fig. 1), but the small sample size diminishes the statistical power enough to render a Goldfeld-Quandt test for heteroscedasticity inconclusive. Bird 10 was identified as an significant outlier (Studentized residual = -2.3548, Fig. 1), but was included because of no sound basis for its omission, and to avoid artificially inflating the performance of the MMMR.

All four partial regression coefficients (AASMR's) were highly significantly different from zero (Table 3). The MR_N ($\pm SE$) at the nest was $44.7 \pm 6.1 \text{ J h}^{-1} \text{ g}^{-1}$, and the MR_{IDB} on the sea surface $45.4 \pm 3.5 \text{ J h}^{-1} \text{ g}^{-1}$, did not differ significantly ($F_{1,6} = 0.007$, *n.s.*), and are virtually identical at $45 \text{ J h}^{-1} \text{ g}^{-1}$ ($2 \times \text{BMR}$), assuming $\text{BMR} = 22 \text{ J h}^{-1} \text{ g}^{-1}$ (Bryant and Furness, 1995). Although the MR_F $388.9 \pm 60.3 \text{ J h}^{-1} \text{ g}^{-1}$ ($17.7 \times \text{BMR}$), was 150% of that of MR_{DB} $258.8 \pm 25.1 \text{ J h}^{-1} \text{ g}^{-1}$ ($11.8 \times \text{BMR}$), they did not differ significantly ($F_{1,6} = 3.295$, *n.s.*).

Partial residual (also termed 'adjusted residuals') plots for each of activity category are produced in Fig. 2. The partial regression residual represent the relative contribution of an specific activity duration to an individual's DEE, while statistically holding the effects of the other activities constant. All four metabolic partial residuals conform as linear functions of the partial residuals of time (Fig. 2).

Aerobic diving limits and diving behavior

The estimated oxygen reserve for diving in the Razorbill is $57.2 \text{ mL O}_2 \text{ kg}^{-1}$, and is itemized in Table 4, together with four other alcid species.

The diving bout AASMR ($71.9 \text{ J s}^{-1} \text{ kg}^{-1}$, Table 3) was converted to oxygen consumption assuming $20.0832 \text{ mL O}_2 \text{ J}^{-1}$ (Schmidt-Nielsen, 1997), becoming $3.58 \text{ mL O}_2 \text{ kg}^{-1} \text{ s}^{-1}$. The cADL thus estimated is only 16 seconds ($57.2 \text{ mL O}_2 \text{ kg}^{-1} / 3.58 \text{ mL O}_2 \text{ kg}^{-1} \text{ s}^{-1}$), and was exceeded by 60.4% of dives (Fig. 3A)! The bADL was estimated $\approx 70 \text{ s}$ (ca. $4.4 \times \text{cADL}$), which only 0.3% of the dives surpassed (Fig. 3 and 4, see also Fig 9C in Benvenuti et al., 2001).

The piecewise regression of diving pause duration as a function of diving duration, identified a ‘breakpoint’ at 29.5 s diving duration, separating a virtually ‘flat phase’ ($<29.5 \text{ s}$), and a ‘sloping phase’ ($>29.5 \text{ s}$, Fig. 3). Although the increase in pause duration was significantly greater than zero, the slope was quite low or only 0.041 s per second diving until the breakpoint or 1.2 s over the whole phase’s range (Fig. 2A). In contrast, in the sloping phase, pauses increased by 0.5 s per second increase in diving.

Minimum dive duration (D_{\min} , s) as a function of depth was examined (Fig. 3B). Minimum dive duration was approximately linear and equal to $1.75 \times \text{dive depth}$. Given zero bottom time and equal descent and ascent speeds, the fastest vertical diving speed to depth is 1.14 m s^{-1} ($2 \times 40 \text{ m} / 70 \text{ s}$). Using the data from 18 instrumented Razorbills in Latrabjarg 1998 (see Dall’Antonia et al., 2001), mean dive duration was $25.1 \pm 15.9 \text{ s}$, mean pause duration $16.5 \pm 10.8 \text{ s}$, and mean dive depth $9.5 \pm 7.3 \text{ m}$ ($n=10060$, Fig. 4).

Discussion

The average daily field metabolic rate (DEE) of the five Razorbills, which were determined to be in energy balance (estimated energy supply similar to expenditure) was

2064 J g⁻¹ d⁻¹ (Table 5). The mean DEE of Razorbill's ranks the sixth 'highest' out of a total of eleven DLW studies, on seven alcid species during the nestling period, falling in-between the ranges of the three lowest ranking species (each represented by two studies), the Common and Brünnich's Guillemots, and the Atlantic puffin (Table 5). Evidently the mass-specific FMR of Razorbills is on the lower side among auks, which is thought provoking in the light of the large instrument effects on locomotion estimated here.

A number of studies on penguins have reported two times higher 'RMR on water' than 'RMR on land' (range 1.4-2.6 times), the latter perhaps better known as BMR (e.g., Bethge et al., 1997; Culik et al., 1996; Culik and Wilson, 1991a), reflecting a greater heat loss in water than in air (De Vries and Van Erden, 1995). In this context it is interesting that Razorbill's MR_N and MR_{IDB} are virtually equal (2 x BMR, Table 3), supporting the notion that 'wasted' heat, produced as 'heat increment of feeding (HIF)' (e.g., Rothwell et al., 1990), also called 'specific dynamic action,' can compensate for the thermoregulation component of the water surface metabolism (Hawkins et al., 1997; Pütz et al., 1998; Wilson and Culik, 1991). HIF has been suggested as a reheating mechanism following peripheral body cooling endured in foraging diving bouts (Bevan et al., 1995; Handrich et al., 1997; Hawkins et al., 1997; Wilson and Culik, 1991; Wilson and Grémillet, 1996).

Razorbill's flying and diving bout's metabolic rates reported here are very high (17.7 and 11.8 xBMR respectively, Table 3). Unfortunately the current and applicable aerodynamic or hydrodynamic theories, do not offer accurate flight cost predictions, primarily due to poorly known and highly species-specific 'fudge' factors, particularly

the drag coefficient (Lighthill, 1969; Pennycuick, 1995; Pennycuick, 1997; Pennycuick et al., 1996; Rayner, 1994; Rayner, 1995).

Only three studies to our knowledge have attempted to measure instrument effects on aerial flight energetics using the DLW method, and these preliminary studies have reported somewhat mixed results. Mass-specific DEE of common terns (*Sterna hirundo*) was increased by 5.5% on average due to instrumentation, although not significantly higher than non-instrumented controls (Klaassen et al., 1992). The instrument's 2.1 cm² cross sectional area (S_i) was 9.21% of the bird's (S_b), or 40% larger than our logger's proportion! Klaassen *et al.* (1992) interpreted this result to indicate no instrument effects, although acknowledging that flight time was neither measured or controlled for, which rendered the study incapable of addressing the question by design.

Gessaman's and Nagy's (1988b) study on harnessed homing pigeons (*Columba livia*), reported a substantial decrease (25-31%) in flight speed, 141-152% higher flight cost, combining in a 185-200% increase in cost of transport ($32.4 \times \text{RMR}$). The instrument's cross sectional area was relatively small ($S_i = 1.13 \text{ cm}^2$, or 2.5% of the bird's S_b), indicating that the harness was the culprit.

Gessaman *et al.* (1991) repeated this study but using larger instruments on smaller tipler pigeons ($S_i/S_b = 7.3\%$). They also found a similar reduction in flight speed (21-26%), but the energy expenditure of instrumented birds was insignificantly higher than controls due to very large individual variance. They attributed the latter result to relatively small ¹⁸O reduction incurred in the short experiment, which produces a large estimation error (Gessaman et al., 1991; Nagy and Costa, 1980). Gessaman *et al.* did however find greatly (and significantly) increased water-turnover in experimental birds,

which further augmented the estimation error of CO₂ production (Nagy and Costa, 1980). They attributed this to greatly increased respiratory evaporative loss due to increased breathing frequency, as a compensation for a constricted tidal volume induced by the harness.

It is truly bewildering why research on instrumentation effects on flight energetics in particular is so scarce, especially since instrumentation is a frequently employed research method (radio tracking etc.). The common claim of small instrument effects in avian telemetry studies (reviewed in Calvo and Furness, 1992), has rarely been quantitatively tested, and thus has a dogmatic flavor. This is not to say that all telemetry studies are necessarily effected by instrumentation, only that most of the evidence to the contrary is commonly subjective and unconvincing.

Measurements of the cost of instrumented flight in wind-tunnels indicate that instrument drag is of greater importance (Pennycuick, 1995; Pennycuick et al., 1988), than instrument mass (Caccamise and Hedin, 1985; Pennycuick, 1995), for the energetic cost of sustained flapping flight, given the range in mass and shape of commonly used devices. The exact instrument shape and location on the body has been shown to be of crucial importance for reducing instrumentally induced cost of penguin 'underwater flight' (Bannasch et al., 1994; Culik et al., 1994a; Culik and Wilson, 1991b).. Although aerial flyers might be more sensitive to changes in center of gravity due to the instrument than penguins, these results have equally applicable implications for drag increase in aerial flight.

Allometric regression of non-instrumented avian flight metabolic rate (MR_F , W), was produced using the data compilation made by Norberg (Table 7.3, 1996). The

original data was measured using one of three different methods, (1) DLW and time budget (8 studies, i.e., less Gessaman and Nagy [1988]), (2) wind tunnel respirometry (13 studies), and (3) body mass loss during migration (17 studies). The each of the three datasets were compared using analysis of covariance (ANCOVA). The slopes were found to be homogenous ($F_{2, 32} = 0.208, P=0.813$), and the intercepts did not significantly differ ($F_{2, 35} = 2.963, P=0.065$). The data was subsequently combined, $\text{Ln}_{10}(\text{MR}_F) = 1.772 (\pm 0.071 \text{ SE}) + 0.828 (\pm 0.054 \text{ SE}) \text{Ln}_{10}(M_b)$, where M_b is body mass in kg (Fig. 5). In back-transformed form: $\text{MR}_F (\text{W}) = 59.2M_b^{0.83}$. ANOVA: $F_{1, 36} = 235.7, P<0.000001, R^2 = 86.7\%$, and standard error of the estimate 0.212. Both the intercept ($t = 24.755, P<0.000001$), and the slope ($t = 15.351, P<0.000001$) were significantly different from zero. Thus expected MR_F of an 622.5 g Razorbill is 40.0 W ($231.3 \text{ J h}^{-1} \text{ g}^{-1}, 10.5\times\text{BMR}$). The observed MR_F ($388.9 \text{ J h}^{-1} \text{ g}^{-1}, 17.7\times\text{BMR}$) is 163% of this value, indicating considerable instrumentation effects. However because Razorbills have higher wing load (1.342 g m^{-2}), or wing pressure (132 Pa, Spear and Ainley, 1997), than the species used in the regression, it expected that their real MR_F value is somewhat higher than predicted. This excessive cost is of proportionally similar magnitude as reported in instrumented Adélie Penguins (161%) diving in a respirometry canal (Table 5, Culik and Wilson, 1991b).

To evaluate the Razorbill's diving bout metabolic rate ($\text{MR}_{\text{DB}}, \text{W}$), we produced an allometric relationship of avian diving bout metabolic rate with body mass (Fig. 5), by compiling 14 laboratory-respirometry studies on 12 species from the literature (listed in Appendix B). We chose three criteria for inclusion in the allometric regression. (1) That an estimate of instrumented 'free-ranging' diving speed in the wild was available (or

vertical speed if true speed was not available) excluding the benthivorous ducks, and that the MR_{DB} was measured at, or reasonably extrapolatable to this speed. (2) Not instrumented, excluding the little penguin (*Eudyptula minor* J. R. Forster 1781), in which case no difference was detected between the control and instrumented birds (Bethge et al., 1997). (3) That MR_{DB} was calculated using the VO_2 -1 method (see Appendix B), i.e., dividing the total respiration during a pause with the sum of the pause duration and the preceding dive duration (see Culik et al., 1996), corresponding to the AASMR of diving bouts used here. We made an subjective exception to criteria (3), again for the little penguin, simply to fill an otherwise evident gap in the range of body mass. Bethge *et al.* (1997) used the VO_2 -2 method (see Appendix B), subtracting the ‘RMR on water’ from the total respiration, and dividing the excess by the preceding dive duration (this method produces an roughly 40% higher MR_{DB} estimate than the VO_2 -1 method, Appendix B).

We examined if there was an difference in the relationship between MR_{DB} and body mass (kg), with respect to the two diving propulsion modes, (1) foot-propelled (six studies on three species), and (2) wing-propelled (eight studies on eight species), using ANCOVA. The slopes were statistically homogenous ($F_1=0.0728$, $P=0.79$), as were the intercepts ($F_1=0.0511$, $P=0.82$), and the data subsequently combined: $\text{Ln}_{10}(MR_{DB}) = 1.267 (\pm 0.0160 \text{ SE}) \times 0.808 (\pm 0.0340 \text{ SE}) \text{ Ln}_{10}(M_b)$, or $MR_{DB} (W) = 18.5M_b^{0.81}$ back-transformed. ANOVA, $F_{1,12}=561.8$, $P<0.0000001$, Fig. 5, $R^2=97.9\%$, and standard error of the estimate 0.0546. The intercept ($t=79.002$, $P<0.000001$), and the slope ($t=23.7$, $P<0.000001$) were both significantly different from zero. For a 622.5 g Razorbill this equation predicts $MR_{DB} = 12.6 W$ or $72.9 \text{ J g}^{-1} \text{ h}^{-1}$ ($[12.6 \text{ J s}^{-1} \times 3600 \text{ s}]/622.5 \text{ g}$). The observed MR_{DB} ($258.8 \text{ J g}^{-1} \text{ h}^{-1}$, Table 3), is 355% of this prediction, and 11.9% higher

than the predicted flight metabolic rate ($231 \text{ J g}^{-1} \text{ h}^{-1}$)! Whatever the actual diving metabolic rate, it is clear that the instruments had a much greater effect on diving metabolism than on flight metabolism (see Fig. 5).

The allometric curves for flight and diving metabolism were compared using ANCOVA (Fig. 5). The slopes were not significantly different ($F_{1,48}=0.123, P=0.72$), but the intercept of flight metabolic rate was significantly higher than the diving bout metabolic rate's ($F_{1,49}=363.3, P<0.0000001$).

The application of the MMMR method was successful and particularly well suited to the general problem at hand, especially the extraction of highly precise AASMR's estimates. Thus there is no particular reason to believe the high MR_{DB} is an statistical artifact. However this is the first comparison of partitioned field data to that of the laboratory data to date. Undertaking more DLW-time partitioned studies seems an obvious and exciting future course of action, utilizing the powerful MMMR analysis, especially on the species for which the laboratory data exists (see Appendix B), and employing the available virtually zero-drag instruments (Bannasch, 1995; Bannasch et al., 1994). This research programme is the most straightforward way to evaluate and examine any possible differences between laboratory and field data, and opens up new, even more important aspects beside that comparison, such as the effect of depth on MR_{DB} , but perhaps most importantly it ambitiously encourages the achievement of unprecedented levels of sophistication in field experimental studies.

The aerobic diving limit

All studies to date on avian divers have demonstrated that a considerable proportion of dives exceed the cADL (Boyd, 1997; Kooyman, 1989), in contrast to mammals (Boyd, 1997), but see Schreer *et al.* (2001). Exponential lengthening of post dive-pauses (i.e., >bADL) in birds has been demonstrated clearly in six avian species to our knowledge, the Blue-eyed Shag *Phalacrocorax atriceps* (Schreer *et al.*, 2001), the Emperor Penguin *Aptenodytes forsteri* (Kooyman and Kooyman, 1995), the King Penguin *A. patagonicus* (Kooyman *et al.*, 1992), but see Culik *et al.* (1996), the Razorbill (this study), the Brünnich's Guillemot (Croll *et al.*, 1992), and the Common Eider *Somateria mollissima* (Ydenberg and Guillemette, 1991). In some of those cases the bADL exceeds the cADL multiple times. In the razorbill's case 4.4 times, despite the large increase in the MR_{DB} ! The initial flat phase in the relationship between diving pause durations and dive duration of razorbills shows that the birds were well within their aerobic capacity until 30 s (the breakpoint), just short of double the cADL! It is even more interesting that the birds were still within their replenishable respiratory capacity until 70 s (bADL, Fig. 3A).

This cADL-bADL discrepancy immediately demands the exclusion of methodological error, that the oxygen reserves are not underestimated, and the diving metabolic rate (MR_D) is not overestimated. Assuming a that either methodological error is negligible, dives surpassing the cADL have been hypothesized either to be extended anaerobically with consequent lactate production, or aerobically by hypometabolism (Boyd, 1997). The hypometabolism hypothesis is currently the generally favored explanation, because of better support by a diverse body of evidence, which in summary do not reflect adaptations to anaerobiosis (Boyd, 1997). It is generally agreed that

oxygen reserves are fairly robustly estimated (Boyd, 1997; Kooyman, 1989; Stephenson et al., 1989), and any conceivable variability in the reserves is certainly nowhere near the magnitude of the cADL-bADL gap. However, diving metabolic rate is assumed constant and independent of depth as a computational convenience in calculating cADL (Boyd, 1997; Kooyman, 1989), contrary to better knowledge (Clowater and Burger, 1994; Lovvorn and Jones, 1991b; Wilson et al., 1992)!

Interestingly the hypometabolism hypothesis fit to the empirical data has not yet been quantified (but see Hansen and Ricklefs, *in press*), that is, if the proposed mechanisms can sufficiently reduce the diving metabolic rate to explain or account for the cADL-bADL discrepancy. In this context it might be noted that in respirometry canals, most hypometabolic conditions and processes are operative, or at least not suppressed. The exact contribution of buoyancy to metabolism in the respirometry canals (and as compared to free-ranging) is currently unknown, but the birds can behaviorally adjust buoyancy somewhat by inspiration-expiration. Net power efficiency (E_{net}), is the ratio of total mechanical power output to metabolic power input less basal metabolic rate (Blake, 1991). Assuming maximal buoyancy, E_{net} (dimensionless) was calculated using respirometry canal data for Adélie and little penguins, as 0.137 and 0.147 respectively (Hansen and Ricklefs, M.S.). The effect of reducing the plumage volume by one half, reduced E_{net} by 21 and 26% respectively (to 0.108), which more than counterbalances the reduction in the mechanical power output due to buoyancy! This provides an assessment that buoyancy is either maximal in the respirometry canals, or that net power efficiency of experimental birds is low, probably lower than occurs in free-ranging birds. Of the two, the former is more likely to be the case.

It has been quantitatively demonstrated that buoyancy reduction not only can, but is a much more prominent candidate than the hypometabolism hypothesis, simply because it is a number of times larger component than the BMR (which reduction is the focus of the hypometabolic hypothesis), and does reduce greatly with depth (Hansen and Ricklefs, *in press*). This is not to say that hypometabolic processes do not occur, just that they are not a sufficient explanation.

For some reason buoyancy has largely been discounted as an explanation in the literature (e.g., Kooyman, 1989), although often, especially regarding penguins, neutral buoyancy has been assumed in the absence of direct measurements (e.g., Bannasch, 1995). Wilson *et al.* (1992) present one of few direct measurement known to us, and has been cited as supportive evidence for this assumption, but their measurement methods have been criticized for producing underestimation bias (Stephenson, 1993; Stephenson, 1995)!

Aside from unconvincingly assuming neutral buoyancy, the simple dynamics of depth dependent diving metabolism are currently not generally appreciated for their superior fit to observation! The cADL-bADL “discrepancy” simply disappears altogether when buoyancy is accounted for (Hansen and Ricklefs, *in press*)! The use of average diving metabolic rate at face value, to calculate cADL of greater duration than is present in the original data is only appropriate when the depth profile remains unchanged, that is, when the birds are simply dwelling longer at the same depth. In almost all studies on avian diving, duration and depth are highly correlated, and the cADL calculation ignores therefore the buoyancy change with depth, and the associated reduction in diving

metabolism. The current practice seems only to be useful for the demonstration of its demise, vividly portrayed by the huge cADL-bADL “gap.”

More direct measurements of buoyancy are needed (Lovvorn and Jones, 1991a), in addition to improved (standardized) measurement methodology (Stephenson, 1993; Stephenson, 1995). Measuring diving metabolic rate in pressurized water tunnels (at least to 3 ATA, 20 m depth), might be a future possibility attempting to quantify the magnitude of the buoyancy contribution directly.

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Figure legends

Fig. 1. Residuals plotted on estimates of daily energy expenditure from AASMR mixture model multiple regression (see Table 3). The bird identification numbers are provided.

Fig. 2. Partial residual plot of each activity influence on the daily energy expenditure in mixture model multiple regression (see Table 3). Each individual bird's activity-specific partial residual value represents the relative DEE contribution, given the relative duration of the respective activity (of the total average), and after the effects of the other three variables have been statistically controlled for.

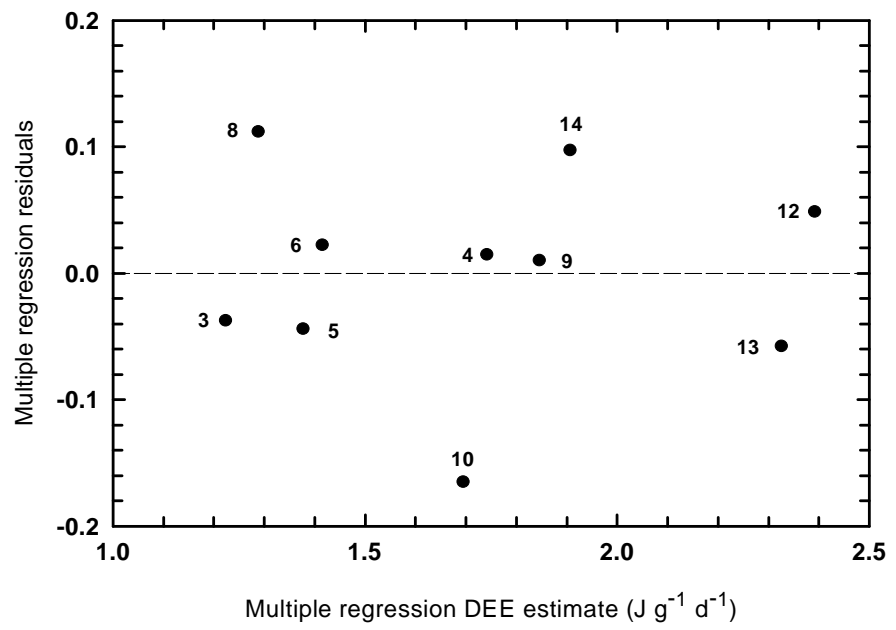
Fig. 3. Relationship between (A) pause duration (T_p) as a function of dive duration (T_d), and (B) dive duration as a function of maximum depth. Dive cycles where $T_p > 90$ s, were omitted from the analysis (see text). The data constitutes 10060 dive cycles and the respective maximum depths reached by 18 birds. Piecewise linear regression was fitted to (A), and a breakpoint was found at $T_d = 29.45$ s (± 0.731 Asymptotic S.E.), separating

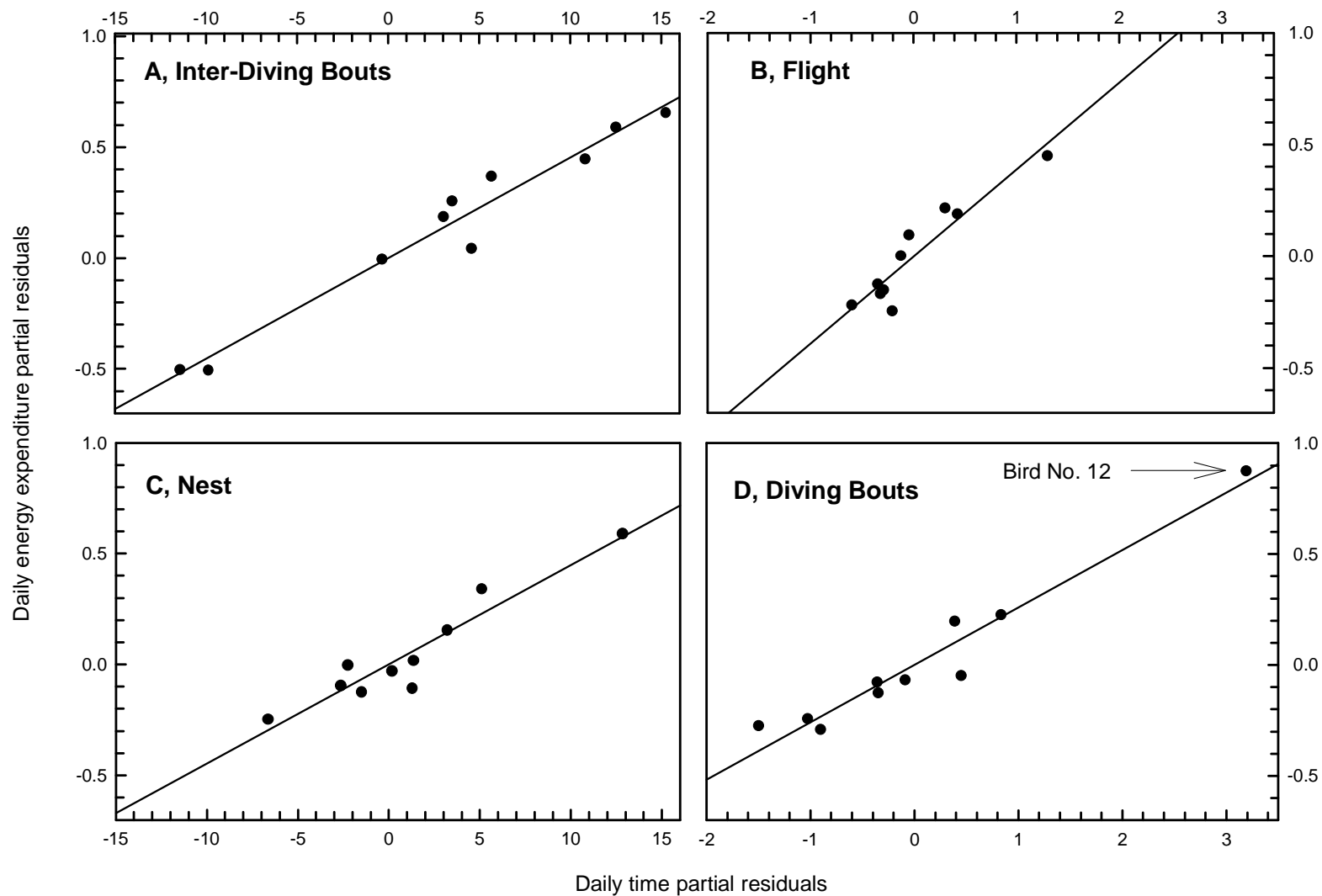
the response into two parts, a virtually ‘flat’ phase (T_d : 0-29.45 s), and a ‘sloping’ phase ($T_d > 29.45$ s). The nonlinear fit R^2 was 21.5% (observed vs. predicted). *Flat phase*: $T_p = 12.987 (\pm 0.257 \text{ A.S.E.}) + 0.041 (\pm 0.015 \text{ A.S.E.}) \times T_d$. *Sloping phase*: $T_p = 14.206 + 0.501 (\pm 0.022 \text{ A.S.E.}) \times T_d$. The minimum dive duration (D_{\min}) at depth is approximately linear ($D_{\min} = 1.75 \times \text{depth}$) is shown in (B), as well as the estimated bADL (≈ 70 s). D_{\min} and bADL intersect at 40 m depth, the maximum diving duration at depth contracts steadily while approaching this intersect. The observed D_{\min} represents a maximum average vertical diving velocity of 1.14 m s^{-1} . The ‘calculated aerobic diving limit,’ cADL = 16 s, (see text), the ‘behavioral aerobic diving limit,’ bADL ≈ 70 s (see text), and the ‘piecewise regression breakpoint’ (29.4 s) are indicated by broken lines.

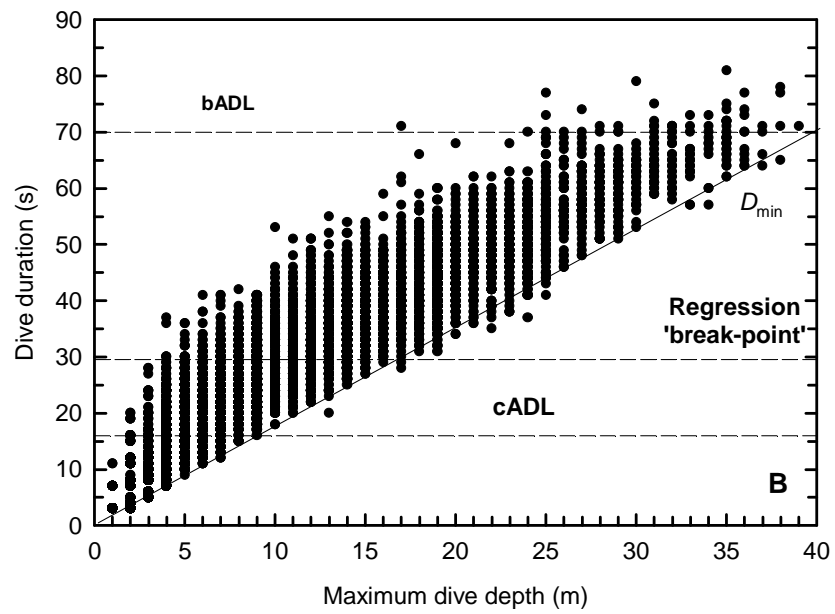
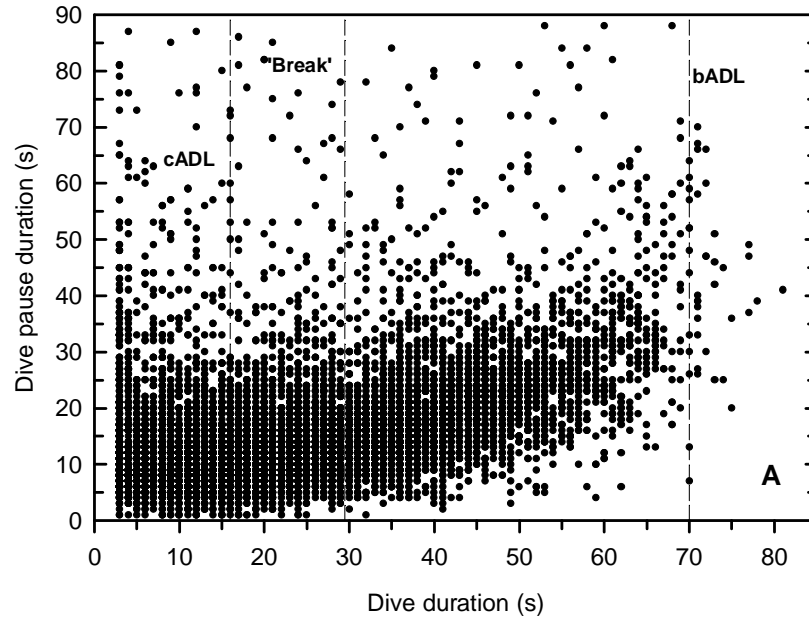
Fig. 4. Frequency histograms of, (A) dive duration, (B) pause duration, and (C) maximum depth, of 10060 dive cycles and the respective maximum depths reached by 18 birds. Dive cycles where pause duration > 90 s, were omitted from the analysis (see text). cADL (16 s), and bADL (≈ 70 s) are presented with vertical broken lines in (A). 60.4% of dives exceeded the cADL, but only 0.3% the bADL.

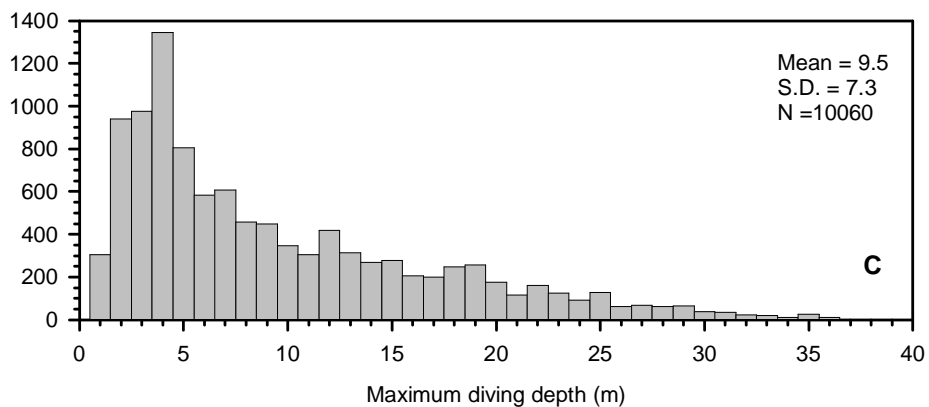
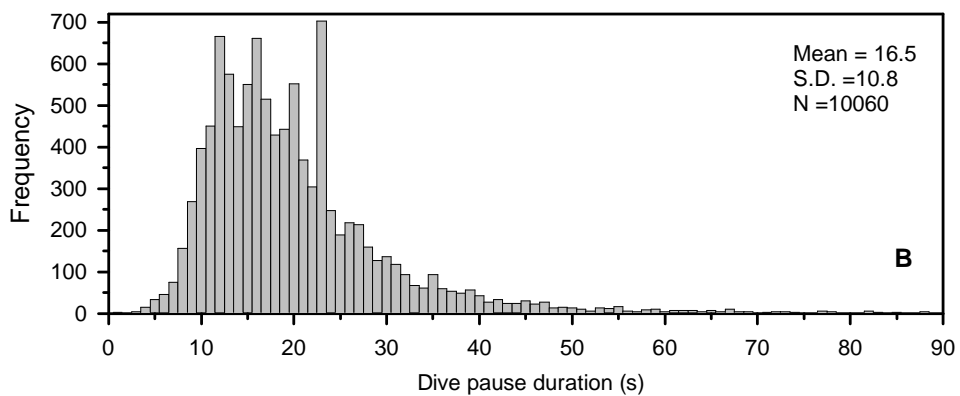
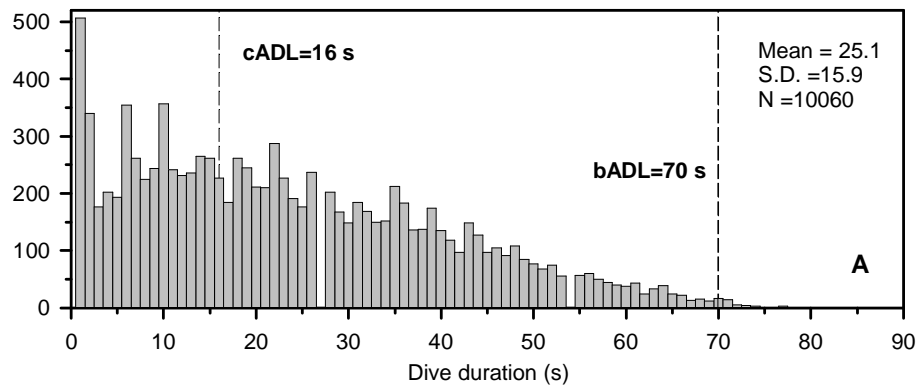
Fig. 5. The allometric relationship between avian flight metabolic rate (MR_F , W, upper regression line) based on data compiled in Norberg (1996), and diving bout metabolic rate (MR_{DB} , W, lower regression line) and body mass (M_b , g) in 14 laboratory studies on 11 species (see Appendix B). No difference was found between foot-propelled divers (filled circles) and wing-propelled divers (filled squares) in a analysis of covariance (ANCOVA, see text), and the data combined: $MR_{DB} = 18.5 \times M_b^{0.81}$, ANOVA $F_{1, 12} = 561.8$, $P < 0.0000001$, $R^2 = 97.9\%$, SE of the estimate = 0.0546. 95% confidence limits around the regression line are given. Flight metabolic rate was examined using ANCOVA with respect to three methods of measurement (see text), and did not significantly differ. The combined data is shown in the figure: open squares signifying doubly labelled water studies, open circles, wind tunnel respirometry studies, and open diamonds, migratory body mass loss studies. The back transformed function is: $MR_F = 59.2 \times M_b^{0.83}$ (see text). The slopes of flight and diving metabolism are statistically not significant different ($F_{1, 49} = 0.123$, $P = 0.73$), but the flight metabolism intercept is significantly higher ($F_{1, 49} = 363.3$, $P < 0.0000001$). The estimated AASMR of flight and

diving bouts for the Razorbill's (*Alca torda islandica*) are shown with filled, downward (MR_F), and upward (MR_{DB}), pointing triangles, respectively (see text).









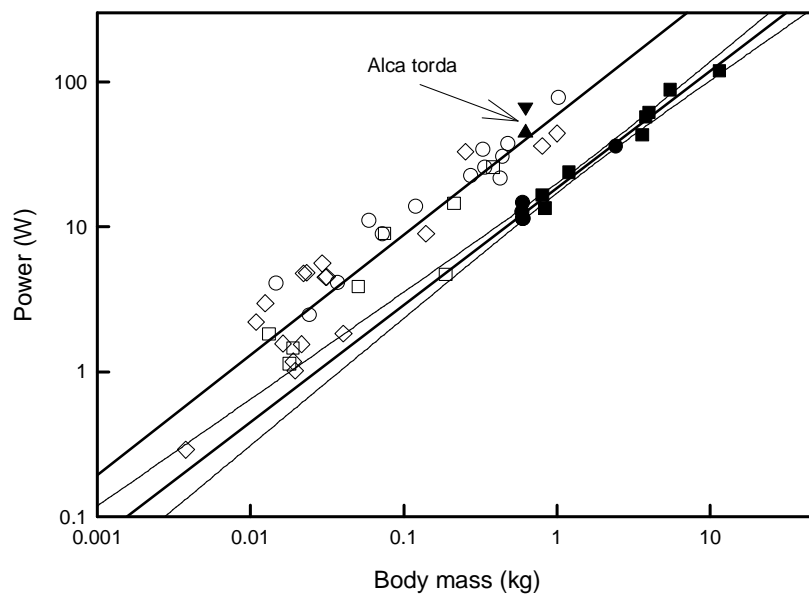


Table 1. Comparison of isotope enrichment after of the employed 'short'(11.1 min), and 'traditional' (54.5 min) equilibrium periods, mean background of ^{18}O was 2005.2 ± 6.05 (SD) p.p.m. and of ^2H 154.7 ± 2.52 (SD) p.p.m.

| Bird No. | M_b (g) | Duration (min) | | $\delta^{18}\text{O}$ (V-SMOW) ^a | | | $\delta^2\text{H}$ (V-SMOW) ^a | | |
|----------|-----------|----------------|--------|---|-----------------------|------------|--|-------------------------|------------|
| | | Short | Normal | Short | Normal | $\Delta\%$ | Short | Normal | $\Delta\%$ |
| C1163 | 685 | 11 | 62 | 712.75 (1) | 696.91 (1) | -2.222 | 4464.95 (1) | 4353.79 (1) | -2.489 |
| C1292 | 690 | 9.5 | 60 | 726.55 \pm 0.86 (3) | 712.49 \pm 9.62 (3) | -1.935 | 4594.98 \pm 42.43 (3) | 4537.92 \pm 22.07 (3) | -1.242 |
| C1210 | 635 | 13 | 47 | 644.69 \pm 4.98 (2) | 621.09 \pm 2.49 (3) | -3.661 | 4074.31 \pm 10.28 (2) | 3960.91 \pm 23.13 (3) | -2.783 |
| C2400 | 680 | 11 | 49 | 736.21 (1) | 715.60 \pm 9.62 (2) | -2.799 | 4690.45 (1) | 4515.37 \pm 4.86 (2) | -2.562 |
| Mean | 672.5 | 11.1 | 54.5 | 705.05 | 686.52 | -2.654 | 4456.17 | 4342.00 | -2.269 |
| SD | 25.3 | 1.4 | 7.6 | 41.37 | 44.38 | 0.7612 | 270.93 | 266.96 | 0.696 |
| CV | 3.8% | 12.9% | 13.9% | 5.86% | 6.5% | 28.7% | 6.1% | 6.2% | 30.7% |

^aVienna Standard Mean Oceanic Water (e.g., Speakman, 1997).

Table 2. Daily energy expenditure (DEE), and daily activity-specific time budgets, of ten instrumented Razorbill parents. DEE is calculated using two different assumptions of body water change with body mass change, fixed, and fixed percentage change.

| Bird No. | DEE (J g ⁻¹ d ⁻¹) | | Activity-Specific Time Allocation (h d ⁻¹) | | | | |
|----------|--|-----------|--|--------|--------------------------|--------|------------------|
| | 'Fixed' | 'Fixed %' | Nest | Flight | Diving Bout ^a | | IDB ^b |
| | | | | | Diving | Pauses | |
| 3 | 1227.7 | 1185.9 | 4.908 | 0.191 | 0.191 | 0.142 | 18.567 |
| 4 | 1778.8 | 1756.5 | 19.723 | 0.625 | 1.543 | 0.569 | 1.540 |
| 5 | 1379.0 | 1333.0 | 7.083 | 0.302 | 0.692 | 0.191 | 15.732 |
| 6 | 1525.6 | 1438.0 | 4.904 | 0.881 | 0.051 | 0.074 | 18.090 |
| 8 | 14659 | 1400.3 | 10.229 | 0.599 | 0 | 0 | 13.173 |
| 9 | 1900.3 | 1855.7 | 12.170 | 0.641 | 1.636 | 0.912 | 8.640 |
| 10 | 1567.0 | 1530.3 | 9.537 | 0.612 | 1.223 | 0.660 | 11.968 |
| 12 | 2516.1 | 2440.9 | 7.678 | 0.923 | 2.778 | 1.864 | 10.756 |
| 13 | 2396.5 | 2267.8 | 14.014 | 2.297 | 1.346 | 0.791 | 5.552 |
| 14 | 2108.1 | 2003.6 | 8.696 | 1.107 | 1.082 | 0.992 | 12.123 |

^a'Diving Bout (DB)' time here is the accumulated diving cycles durations. Diving cycle is composed of a dive and a subsequent diving pause. Diving pauses need to be of lesser duration than 90 s to be termed so.

^b'Inter-Diving Bout (IDB)' time is accumulated surface time of greater duration than 90 s. IDB's were predominantly of much longer duration than 90 s.

Table 3. *Partial coefficients (b_i) from a mixture model multiple regression (which has a zero intercept), representing the partitioning of mass-specific daily energy expenditure (DEE) into average activity-specific metabolic rates (AASMR's), their respective standard errors, AASMR's presented as BMR multiples, two-tailed t-tests ($b_i=0$), standardized partial regression coefficients (b'_i), and the regression's ANOVA, standard error of estimate = 0.099, $R^2=96.2\%$.*

| | Average Activity Specific Metabolic Rates | | | |
|--|--|-----------------------|------------------------|---------------|
| | Nest | DB^a | IDB^b | Flight |
| b_i (J h ⁻¹ g ⁻¹) | 44.7 | 258.8 | 45.4 | 388.9 |
| SE (J h ⁻¹ g ⁻¹) | 6.1 | 25.1 | 3.5 | 60.3 |
| ×BMR ^c | 2.0 | 11.8 | 2.1 | 17.7 |
| t | 7.315 | 10.309 | 13.020 | 6.447 |
| P | 0.00033 | 0.00005 | 0.00001 | 0.00066 |
| b'_i | 1.216 | 1.397 | 1.451 | 0.970 |
| Regression: | | | | |
| Source of variation | SS | MS | F | P |
| Regression ($df=3$) | 1.51358 | 0.504527 | 51.3365 | 0.000114 |
| Residual ($df=6$) | 0.058967 | 0.009828 | | |

^aDiving Bouts (DB)' are the sum of diving and a diving pauses (<90 s).

^bInter-Diving Bout (IDB)' represent surface periods >90 s. IDB's were predominantly of much longer duration.

^cGiven 22 J h⁻¹ g⁻¹ mass-specific BMR (Bryant and Furness, 1995).

Table 4. *Estimated oxygen reserves available for diving in five species of auks. The calculation follows Stephenson et al. (1989), except where noted otherwise. Blood volume (V_B , mL) was calculated as $V_B = V_P / (1 - H_{cit})$, where V_P is measured plasma volume (mL), and H_{cit} is hematocrit. Plasma volume was measured with Evans Blue dilution (Linden and Mary, 1983; Thornberg, 1958). The blood volumes of Brünnich's guillemot, and Razorbill were both 12.3% of body mass, and the other three species were assumed to have the same proportion. Fractional arterial and venous blood volumes were assumed to be one third, and two thirds of the total, respectively (Rothe, 1983). Hemoglobin concentration was measured using the protocol of Austin and Drabkin (1935). Oxygen binding capacity of hemoglobin (Hb) was assumed $1.356 \text{ mL O}_2 \text{ g}^{-1} \text{ Hb}$ (Lenfant et al., 1969). Oxygen saturation of arterial and venous blood is 100 and 70%, respectively. 96% of the blood's oxygen was assumed useable. Muscle mass was assumed to be 30% of body mass (Kooyman, 1989). Myoglobin concentration values were taken from the literature. The oxygen binding capacity of myoglobin (Mb) was assumed to be $1.24 \text{ mL O}_2 \text{ g}^{-1} \text{ Mb}$, Mb saturation, and the usable proportion of muscle oxygen assumed 100%.*

Total respiratory volume (V_R , mL O_2) was estimated using $V_R = 155 M_b^{0.92}$ (Calder, 1984), where M_b is body mass in kg, Mean fractional oxygen concentration assumed to be 17.6% of volume, and the usable proportion 75%. Total body water mass was assumed 60% of M_b , and its oxygen concentration $5 \text{ mL O}_2 \text{ L}^{-1}$. Values are reported as mean \pm SD (n), {estimates}

| Oxygen reserves | <i>U. lomvia</i> | <i>A. torda</i> | <i>F. arctica</i> | <i>C. grylle</i> | <i>A. alle</i> |
|---|----------------------------|----------------------------|----------------------------|----------------------------|----------------------------|
| Blood Reserve (mL): | 27.0 (46.3%) | 15.6 (45.2%) | {12.0, 49.0%} | {11.0, 43.8%} | {2.7, 42.9%} |
| Plasma vol. (mL) | 59.7 (20) ² | 29.3±1.4 (4) ¹ | - | - | - |
| Hematocrit (%) | 52.8±2.3 (20) ² | 60.7±5.7 (43) ¹ | 60.8±3.5 (8) ¹ | 50.7±0.7 (6) ³ | 56.8±1.9 (26) ⁴ |
| Blood vol. (mL) | 126.5 (20) ² | 74.6±3.4 (4) ¹ | {52.5} | {52.9} | {13.6} |
| Hb conc. (g Hb dL ⁻¹) | 18.0±1.8 (20) ² | 17.6±2.7 (42) ¹ | 19.4±2.8 (10) ¹ | 17.7±3.7 (4) ³ | 17.0±0.9 (26) ⁴ |
| Muscle Reserve (mL): | 7.3 (12.5%) | {4.3, 12.5%} | 2.0 (8.2%) | 3.4 (13.5%) | {0.5, 7.9%} |
| Mb conc. (% g ⁻¹) | 1.9 ² | {1.9} | 1.25±0.26 (5) ⁵ | 2.16±0.42 (5) ³ | {1.25} |
| Respiratory Reserve (mL): | 21.0 (36%) | 12.8 (37.1%) | 9.3 (38.0%) | 9.4 (37.4%) | 2.7 (42.8) |
| Body mass (g) | 1029 ² | 603 ¹ | 424 ¹ | 427 ³ | 110 ⁴ |
| Respiratory vol. (mL, STPD) | 159.1 | 97.3 | 70.4 | 70.8 | 20.3 |
| Body water O ₂ Reserve (5 mL O ₂ /L) ^a | 3.1 | 1.8 | 1.3 | 1.3 | 0.3 |
| Total Reserve (mL O ₂) | 58.3 (100%) | 34.5 (100%) | 24.5 | 25.1 | 6.3 |
| Total Reserve (mL O ₂ kg ⁻¹) | 56.7 | 57.2 | 57.8 | 58.7 | 56.8 |

Studies cited: (1) this study; (2) Croll *et al.* (1992), (3) Haggblom *et al.* (1988); (4) Kostelecka-Myrcha (1987); (5) Davis and Guderley (1987). ^aAssuming 60% TBW of *M_b*.

Table 5. Comparison of mass-specific daily energy expenditures, among eight species of food provisioning alcid parents

| Species ^a | M_b | DEE | | | Lat. °N | Study |
|--|-------|-------------------|-------|----|---------|-------|
| | g | $J g^{-1} d^{-1}$ | SD | N | | |
| Least Auklet (<i>Aethia pusilla</i>) | 83 | 4308 | 528.6 | 24 | 56 | (1) |
| Little Auk (<i>Alle alle</i>) | 164 | 4252 | 633.5 | 13 | 79 | (2) |
| Cassin's Auklet (<i>Ptychoramphus</i> <i>aleuticus</i>) | 174 | 2374 | 338.4 | 9 | 37 | (3) |
| Black Guillemot (<i>Cepphus grylle</i>) | 380 | 2263 | 460.8 | 10 | 79 | (4) |
| Atlantic Puffin (<i>Fratercula arctica</i>) | 395 | 2213 | 381.6 | 9 | 56 | (5) |
| | 460 | 1843 | - | 9 | 70 | (6) |
| Common Guillemot (<i>Uria aalge</i>) ^a | 940 | 1903 | 280.8 | 4 | 47 | (7) |
| | 1025 | 2143 | 561.6 | 11 | 70 | (8) |
| Razorbill (<i>Alca torda</i>) ^a | 603 | 2064 | 285.6 | 5 | 65 | (9) |
| Brünnich's Guillemot (<i>U. lomvia</i>) | 980 | 1898 | 216.0 | 5 | 67 | (10) |
| | 1078 | 1654 | - | 12 | 57 | (6) |

^aInstrumented.

Studies cited: (1) Roby and Ricklefs (1986); (2) Gabrielsen *et al.* (1991); (3) Hodum *et al.* (1998); (4) Mehlum *et al.* (1993); (5) Wernham (1993); (6) Ellis and Gabrielsen (2001); (7) Cairns *et al.* (1990); (8) Gabrielsen (1996); (9) this study (birds No. 4, 9,12-14, see text); (10) Croll and McLaren (1993).

APPENDIX A. *General results. Sex, foraging status, chick age, date and mass at capture and recapture, total body water (TBW), daily CO₂ production, and water turnover of Razorbills, under two different assumptions of body water change*

| Bird | No. | First capture | | | Second capture | | | Duration | TBW | Fixed TBW | | Fixed % TBW | | |
|------|-----|---------------|---------|------------|----------------|------------|------------------|----------|------|----------------------|----------------------|---------------------------------|----------------------------------|----------------------|
| | | Chick | Date & | M_{b1} | Date & | M_{b2} | rCO ₂ | | | rH ₂ O | rCO ₂ | rH ₂ O _{in} | rH ₂ O _{out} | |
| No. | Sex | Trips | Age (d) | time | (g) | time | (g) | (h) | (%) | (L d ⁻¹) | (g d ⁻¹) | (L d ⁻¹) | (g d ⁻¹) | (g d ⁻¹) |
| 3 | M | 0 | 1 | 3.7 16:28 | 660 | 4.7 15:40 | 615 | 23.200 | 63.3 | 29.649 | 88.2 | 28.639 | 85.6 | 115 |
| 4 | M | 2 | 3 | 4.7 15:08 | 595 | 5.7 11:50 | 580 | 20.483 | 58.9 | 38.727 | 156.7 | 38.240 | 154.8 | 165.1 |
| 5 | M | 0 | 10 | 4.7 16:20 | 675 | 5.7 15:00 | 630 | 22.667 | 60.1 | 34.058 | 87.2 | 32.924 | 84.7 | 113.3 |
| 6 | F | 0 | 3 | 4.7 18:20 | 610 | 6.7 09:30 | 540 | 39.167 | 59.7 | 34.050 | 53.7 | 32.097 | 51 | 76.6 |
| 8 | F | 0 | 2 | 8.7 13:17 | 615 | 9.7 21:29 | 560 | 32.200 | 60.7 | 32.986 | 47.8 | 31.511 | 46 | 70.8 |
| 9 | F | 2 | 3 | 9.7 14:41 | 635 | 10.7 21:20 | 600 | 30.560 | 58.3 | 44.153 | 202.7 | 43.117 | 198.1 | 211.8 |
| 10 | M | 1 | 6 | 9.7 15:38 | 640 | 10.7 16:00 | 610 | 24.200 | 57.6 | 36.696 | 132.4 | 35.836 | 129.5 | 146.5 |
| 12 | M | 1 | 7 | 10.7 16:23 | 585 | 12.7 14:45 | 550 | 46.367 | 59.7 | 53.857 | 374.4 | 52.247 | 363.3 | 374.1 |
| 13 | M | 3 | 5 | 11.7 11:06 | 605 | 13.7 11:55 | 540 | 48.833 | 59.9 | 53.052 | 208.6 | 50.201 | 197.4 | 216.6 |
| 14 | F | 1 | 5 | 11.7 17:50 | 605 | 13.7 17:40 | 545 | 47.833 | 61.4 | 46.667 | 205.1 | 44.354 | 195 | 213.5 |

Appendix B. *The energetic cost of diving in birds.*

| Species | | Instruments | | | Experiments | | | Analysis | | Study |
|----------------------------|-----------------|-------------|----------------------------|--------------|-------------------|------|-------------------|---------------------|-----------------------------------|-------|
| | | M_b | Style ^b : S_i | M_i | T_w | V | E_d | | | |
| Foot-propelled divers | ID ^a | kg | cm ² (% S_b) | g (% M_b) | Type ^c | °C | m s ⁻¹ | Method ^d | J g ⁻¹ h ⁻¹ | |
| <i>Aythya affinis</i> | 1 | 0.591 | - | - | T-1.5 | 12 | - | VO ₂ -1 | 77.4 | 1 |
| <i>A. fuligula</i> | 2 | 0.597 | - | - | T-1.7 | 13.6 | - | VO ₂ -1 | 68.6 | 2 |
| | - | 0.578 | - | - | T-0.6 | 22.9 | - | VO ₂ -1 | 49.8 ^e | 3 |
| | 3 | 0.605 | - | - | T-0.6 | 7.4 | - | VO ₂ -1 | 67.8 | 3 |
| | 4 | 0.6 | - | - | T-2.2-5.5 | 23 | - | VO ₂ -1 | 68.4 | 4 |
| | 5 | 0.6 | - | - | T-2.2-5.5 | 7 | - | VO ₂ -1 | 88.2 | 4 |
| <i>Phalacrocorax carbo</i> | 6 | 2.43 | - | - | C-13 | 12.6 | 1.92 | VO ₂ -1 | 53.1 | 5 |
| | - | 2.43 | B: 3.23 (2.2) | 36 (1.5) | C-13 | 12.6 | 1.92 | VO ₂ -1 | 65.8 | 5 |
| Wing-propelled divers | | | | | | | | | | |
| <i>Uria lomvia</i> | 7 | 0.803 | - | - | P-8 | 20 | - | VO ₂ -1 | 74.3 | 6 |
| <i>U. aalge</i> | 8 | 0.836 | - | - | P-8 | 20 | - | VO ₂ -1 | 58.2 | 6 |

| | | | | | | | | | | |
|-----------------------------|----|-------|----------------------------|------------|------|-----|-----|--------------------|-------------------|----|
| <i>A. torda</i> | - | 0.616 | T: 4.15 (7.0) ^f | 28.5 (4.5) | W | 10 | 1.0 | DLW _P | 258.8 | 8 |
| <i>Eudyptula minor</i> | 9 | 1.2 | B: 2.25 (2.4) | 35 (2.9) | C-18 | 10 | 1.8 | VO ₂ -2 | 71.4 ^g | 9 |
| <i>Spheniscus humboldti</i> | 10 | 3.6 | - | - | C-20 | 19 | 1.7 | VO ₂ -1 | 43.2 | 10 |
| <i>Pygoscelis adeliae</i> | 11 | 4 | - | - | C-21 | 4 | 2.2 | VO ₂ -1 | 55.7 | 11 |
| | - | 3.9 | - | - | C-21 | 4 | 2.2 | VO ₂ -2 | 77.7 | 12 |
| | - | 3.9 | B: 21 (10.4) | 200 (5.1) | C-21 | 4 | 2.2 | VO ₂ -2 | 83.8 | 12 |
| | - | 4.42 | I- | 20 (0.5) | C-21 | 4 | 2.2 | VO ₂ -3 | 33.7 | 13 |
| | - | 4.2 | - | - | C-21 | 4 | 2.2 | VO ₂ -3 | 43.0 | 13 |
| | - | 3.9 | 2×T: 10 (5.0) | 70 (1.8) | C-21 | 4 | 2.2 | VO ₂ -3 | 69.1 | 13 |
| <i>P. antarctica</i> | 12 | 3.8 | - | - | C-21 | 4 | 2.4 | VO ₂ -1 | 54.3 | 11 |
| <i>P. papua</i> | 13 | 5.5 | - | - | C-21 | 4 | 1.8 | VO ₂ -1 | 57.9 | 11 |
| <i>Aptenodytes</i> | 14 | 11.5 | - | - | C-30 | 9.1 | 2.2 | VO ₂ -1 | 37.6 | 14 |
| <i>patagonicus</i> | - | 11.5 | - | - | C-30 | 9.1 | 2.2 | VO ₂ -2 | 53.9 | 14 |
| | - | 11.5 | - | - | C-30 | 9.1 | 2.2 | VO ₂ -4 | 36.8 | 14 |

^aID: studies used in the regression analysis of MR_{DB} on body mass shown in Fig. 5 (see text).

^b*Instrument styles.* B: ‘Bannasch-style’ (Bannasch et al., 1994). C: ‘Cairns-style’ (Cairns et al., 1987). I: internal. T: ‘torpedo-style,’ a general collective category of approximate cylindrical or elongated shapes, such as radio transmitters and time-depth recorders. S_i is cross sectional area of external instruments, S_b is the cross sectional area of the bird (Pennycuick, 1989), and M_i is total instrument mass.

^c*Experiment type’s.* C: canal (length, m). P: pool (depth, m). T: Tank (depth, m). W: wild. T_w is the water temperature, and V is observed swimming speed in nature with instruments.

^d*Analysis methods, for estimating energy consumption.* Respirometry analysis methods (Culik et al., 1996; de Leeuw, 1996). VO_2-1 constant average over the whole diving cycle (dive and pause). VO_2-2 ‘RMR in water’ subtracted from the diving pause (until reaching the resting value), and the remainder allocated to the dive. VO_2-3 ‘uncorrected-regression’ i.e., for abnormal jumping (escape) behavior. VO_2-4 two parameter mixture regression, AASMR’s of dives and pauses. DLW_P : mixture regression (AASMR) partitioning of doubly labelled water energy budget.

^eThis observation is an significant outlier in, and omitted from the allometric regression of MR_D on body mass (Fig. 5).

^fA neutrally buoyant instrument.

^gSince MR_D was not influenced by the instruments (Bethge et al., 1997), it was incorporated in the allometric regression of MR_D on body mass (Fig 5.).

Studies cited: (1) Stephenson (1994); (2) Woakes and Butler (1983); (3) Bevan and Butler (1992); (4) de Leeuw (1996); (5) Schmid *et al.* (1995); (6) Croll and McLaren (1993); (7) Cairns *et al.* (1987; 1990); (8) this study; (9) Behtge *et al.* (1997); (10) Luna-Jorquera and Culik (2000); (11) Culik *et al.* (1994b); (12) Culik *et al.* (1994a); (13) Culik and Wilson (1991b); (14) Culik *et al.* (1996).

DIGESTION AND REPRODUCTIVE ENERGETICS:
ENERGY PROVISIONING CAPACITY OF RAZORBILL PARENTS

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RUNNING HEAD: *Digestion and parental energy provisioning capacity*

Abstract. Three species of auk exhibit a unique ‘intermediate’ nest departure pattern, whereby the chick departs the nest when it has attained only between 20-30% of adult body mass. This pattern is examined from the perspective of parental energy supply and the chick’s energy demand. A model of the energy provisioning rate ($EPR = \text{meal mass} \times \text{food energy density} \times \text{feeding frequency}$) of time-energy balanced Razorbill parents is developed. This EPR capacity model quantifies the relative roles of, and incorporates the measurements and estimates of adult feeding rate (food availability), foraging distance (food distribution), digestion rate, meal mass, energy density of food, nest attendance, activity-specific time allocation and metabolic rates. The simulated razorbill’s parental EPR capacity is compared to the estimated daily energy requirement of the chick. The observed EPR capacity of razorbill parents is apparently insufficient to produce a greater chick mass at nest departure than observed. This stems from a combination of small meal size, but in particular low feeding frequency. The alternate foraging behavior, a shared derived trait by the three ‘intermediate’ species, potentially reduces the feeding frequency in Razorbills by 26-42% from that if the parents foraged simultaneously, as the nidicolous species in the family. The model illustrates that the long observed swimming time is required for digestion, which is very sensitive to diving and inter-diving bout duration, and prolonged by more frequent and shorter bouts. Digestion and nest attendance-foraging pattern are at least equally important in the EPR determination, as foraging distance and feeding rate.

KEYWORDS: foraging behavior; digestion; energy provisioning rate; parental care; time-energy budget; fledging strategies; body mass loss.

INTRODUCTION

Among families of birds the auks are considered exceptional as they represent the only case in which several developmental modes are present within a single family (O'Connor 1984). The diversity of nest departure patterns is an unusual phenomenon, and represents highly specialized modifications between parental care and chick development. Three nest departure patterns have been described. (1) The four 'precocial-4' and nidifugous (nest fleeing) *Synthliboramphus* species depart the nest 2-4 d after hatching and are fed by both parents at sea (Gaston 1992a). Several workers have suggested that early departure pattern is an adaptive response to the high predation rates the adults suffer on the breeding grounds (Jones et al. 1990, Gaston 1992a, b, Gaston and Jones 1998). (2) Fifteen of the family's 22 species, are semi-precocial. That is, chicks remain in the nest for 25-75 d and depart at 42-100% of adult body mass, after which they are independent (Gaston 1985, Ydenberg 1989, Gaston and Jones 1998). (3) The so-called 'intermediate' pattern (Sealy 1973), is exhibited by three species: the razorbill (*Alca torda* L.) and the two murre species (*Uria aalge* Pont. and *U. lomvia* L.). 'Intermediate' is in reference to patterns (1) and (2) above; the single chick departs the nest with its male parent after 15-35 d, it has attained between 20-30% of adult body mass. The explanation of this departure pattern is the central focus of this paper.

Gaston and Jones (1998) reviewed the ideas about clutch size and nest departure patterns in the 'nidicolous,' or nest-keeping auks. These compose two main, but not necessarily mutually exclusive, theories. The first states that chick's age and body mass at nest departure is proportional to the parental 'energy provisioning rate (EPR)' (Lack

1968, Sealy 1973, Birkhead and Harris 1985). Parental EPR is the product of the average, feeding frequency, prey energy density, and meal mass. Alternatively, departure time optimizes a trade-off between chick's survival and chick's growth. Accordingly, survival is higher, but growth is slower in the nest, whereas survival is lower but growth is faster at sea (Ydenberg 1989). As proposed this theory suffers from assuming that chick's growth rate is independent of both food availability and parental foraging decisions (Byrd et al. 1991, Houston et al. 1996, Gaston 1998, Ydenberg 1998).

Alcids provide small meals to their chicks, relative to other seabirds having similar adult body mass, and low food provisioning frequency, ranging between 1-10 daily feedings per parent (Ricklefs 1983, De Santo and Nelson 1995, Gaston and Jones 1998). The three 'intermediate' species provide relatively smaller meals than the semiprecocial species (Gaston and Jones 1998). Two hypotheses have been proposed to explain the small meal size of alcids, and its apparent inverse relation to adult body mass. *Premature digestion* (Gaston and Jones 1998). This hypothesis states that alcids are unable to store food for long periods in the upper gut where it is subject to premature digestion, thereby limiting meal size to the bill carrying capacity in piscivores, and 'gular pouch' volume in planktivores. Comparing larger to smaller species, bill length does not increase as rapidly as body mass. It should be noted that the habit of murrelets to carry a single fish lengthways in the bill, reduces their bill utilization efficiency further. *Limited load carrying capacity* (Lack 1968, Sealy 1973, Birkhead 1977). The meal carrying capacity is inversely related to wingloading, which is the mass of the bird per unit of wing area. The 'intermediate' species are the largest auks and they have the highest wingloads, suggesting that carrying capacity may limit food delivery. However, the

semiprecocial tufted puffin (*Fratercula cirrhata*, Pallas) has a wingload that is 116% that of the razorbill's, and it can nonetheless carry twice the meal mass of the razorbill (Houston et al. 1996, Spear and Ainley 1997, Gaston and Jones 1998), suggesting that the razorbill might be carrying smaller meal mass than expected by either hypothesis. Why alcid meal size is small is an important aspect of the EPR, but it is clear that the foraging frequency is the most important component of EPR in the intermediate species as they operate at the lower EPR extreme (<5 daily feedings per parent).

Among auks, the intermediate species are unique (synapomorphic, or 'shared derived' trait) in that only one adult forages at a time, while the other remains at the nest attending the chick (e.g., Birkhead and Harris 1985). Alternate foraging in the 'intermediate' alcids reduces the EPR to the chick by approximately one half compared to what it would be if both parents foraged simultaneously. This is because alternating foraging parents (AFP) must collect energy reserve to fuel the subsequent nest shift, and thus must both collect more food, and spend more time collecting it, than simultaneously foraging parents (SFP). Furthermore, the time budgets of AFP are interdependent, i.e., the foraging trip duration of parent A determines the concurrent nest shift duration of parent B, and vice versa; furthermore, unequal sharing deviations disrupts the time-energy budget, and increases the variance in the duration of foraging and nest attendance shifts, and increases energy requirements of the adults.

The activity-specific time allocation of species with low foraging frequency is of special interest in the search for their constraints, in particular two activities, 'shared nest time,' and swimming, deserve special attention as they can potentially be reduced and used to increase the foraging trip frequency. The time which the parents share in the nest,

which represents unutilized potential foraging time and has been considered available 'buffer time' against variable prey abundance (Burger and Piatt 1990).

Studies on parental time allocation by the intermediate species, have demonstrated that during the nestling period a large proportion of the time at sea is spent swimming, but the 'buffer time' constitutes a considerably smaller proportion, and quite variable (Davoren and Montevecchi 2003). Razorbill parents in Græsholmen, Baltic Sea (55°19'N, 15°11'E), spent on average 31.2 % of their daily time swimming, while also spending unspecified time together in the nest (Benvenuti *et al.* 2001). Razorbills in Látrabjarg, Iceland (65°30'N, 24°32'W), spent on average 24.7 and 27.1% of daily time swimming in two seasons, but shared hardly any time in the nest (Dall'Antonia *et al.* 2001). Thick-billed murre parents on Hakluyt Island, Greenland (77°26'N, 72°42'W), spent 15.6% of their total time swimming, and shared virtually no nest time (Falk *et al.* 2000). Common murre parents on Great Island, Witless Bay, Newfoundland (47°11'N, 52°49'W) spent 57.5% of their total time swimming, but Cairns *et al.* (1990) did not report shared nest time (but see Davoren and Montevecchi 2003).

The idea that digestive bottlenecks possibly set an upper limit to the daily amount of ingested food (Kleiber 1975, Sibly 1981, Kirkwood 1983) has been gaining experimental support (Kenward and Sibly 1977, Levey and Grajal 1991, Dykstra and Karasov 1993b, a, Guillemette 1994, 1998). Digestive bottlenecks result in frequent and long lasting foraging interruptions (Diamond *et al.* 1986, Karasov *et al.* 1986, Temeles 1989, Kersten and Visser 1996, McWhorter and del Rio 2000). The foraging patterns of auks (and most avian divers), are indeed characterized by a series of diving bouts (composed of series of dives and intermittent short diving pauses), 'interrupted' by 'inter-

diving bouts (IDB)' of idle swimming (Monaghan et al. 1994, Falk et al. 2000, Benvenuti et al. 2001, Dall'Antonia et al. 2001). It is likely that the swimming time is to some extent utilized for digestive purposes, although which dynamics are not adequately understood.

The digestive physiology of auks has been the focus of a number of recent investigations by Hilton et al. (1998, 1999, 2000b, 2000a). In this paper swimming time utilization for digestive purposes by razorbill parents is evaluated, which provides a preliminary but fundamental insights towards understanding the determination of time-energy budgets of parental auks in terms of physiological and ecological interactions, and the relation of the time-energy budgets to nest departure patterns. We implicate that the long swimming time is required for digestion, and that digestion plays a major role in the determination of the time-energy budget and constrains the energy provisioning capacity of parent razorbills, and is undoubtedly an important factor for many seabird species beside auks. Furthermore we argue that the reduction in the EPR attributable to the alternate foraging by the intermediate auk parents is the single main cause for the intermediate nest departure pattern.

The objectives of this paper are: (1) to construct a model (using 2, 3 and 4) of digestion time in parent Razorbills, and to use this model to predict the digestion time (swimming time), required by a given feeding rate; (2) to estimate Razorbill feeding rates using doubly labelled water turnover and diving time; (3) to measure the stomach evacuation rate of razorbills in force-feeding and stomach pumping experiment; (4) examine how the number of diving- and inter-diving bouts, affect the digestion duration; (5) to construct a parental time-energy model, composed of time and energy allocation to

four basic behaviors: flying, diving, at the nest, and swimming (using 1). Use (5) to calculate the daily parental foraging trip frequency, we shall examine how foraging distance (food distribution), feeding rate (food accessibility), and digestive time (using 1), affect the parental energy-provisioning rate (EPR). Two parental foraging behavior organization scenarios are evaluated: alternate foragers and simultaneous foragers; and contrasted for three different combinations of flight and diving metabolic rates. The model EPR results are compared to the predicted peak and mean metabolic energy demands by chicks of different sizes, showing a good match between the low levels of EPR and small chick mass at nest departure. The low EPR is due to a combination of relatively small meal size, but in particular, low foraging frequency. Energetically expensive foraging, long digestive time, and especially the alternate foraging organization together cause the low foraging frequency. The maximum observed daily foraging frequency is 2.4 trips by alternately foraging parents, but 4.5 trips by parents experimentally induced to forage simultaneously (Lloyd 1977). The alternate foraging parent's EPR is a far below the estimated requirements to raise a chick to adult size in the nest (Weathers 1992, 1996). This result emphasizes that the growth rate in the nest is severely suppressed, supposedly being such an 'overwhelming' selective pressure in the context of the hypothetical growth-survival trade-off (Ydenberg 1989), that the effects of the other factors are presumably diminished in comparison.

Furthermore, we demonstrate increasing parental physiological stress with chick age, and propose that if this pattern is prevalent, it will ultimately constrain the duration of the nestling period to what is sustainable by the parents, constituting a third and a new hypothetical explanation for the early nest departure in the 'intermediate' species.

MATERIALS AND METHODS

The energy provisioning rate (EPR) is the product of food energy density (E_m), meal mass (M_m) and feeding frequency (N_t). The reported range (\pm SD) of mean Razorbill chick's meal mass (g) is 8.0 (\pm 1.0) to 11.4 (\pm 1.7) (Harris and Wanless 1986, 1989, Chapdelaine and Brousseau 1996), corresponding to EPR_{\min} and EPR_{\max} respectively. Reported total daily feeding frequency ($2N_t$) ranges from 1.6 (this study) to 4.7 (Lloyd 1977, 1979).

The principal component of EPR: the parental feeding frequency (meal delivery rate) is calculated using a time-energy balanced model. Two EPR scenarios are calculated with respect to: alternate foraging parents (AFP); and simultaneously foraging parents (SFP). The feeding frequencies are examined with respect to foraging distance (prey location), feeding rate (prey availability), and different metabolic rates of flight and diving. The model results, together with minimum and maximum observed chick's meal size, and an assumed energy density of food, are used to calculate the minimal and maximal EPR with feeding frequency. These results are compared to average and peak daily metabolic energy requirements (DME, Weathers 1992, Weathers 1996) as a function of chicks body mass (M_f) at nest departure.

Parental feeding frequency model

A premise of the model is that parents are in energy balance (Eq. 1), that is, their energy expenditure (E_{out} , kJ) is balanced by their net food energy intake (E_{in} , kJ): $E_{\text{in}} = E_{\text{out}}$ (1). In alternate foraging parents (AFP), the energy acquisition in each foraging trip must

equal the flight cost of a round trip, the diving (both for parent and chick) and swimming costs, and the cost of the subsequent nest shift. The nest shift is on average of the same duration as the foraging trip: $T_{\text{sea}} = T_{\text{N}}$ (2), where T_{sea} is time at sea (the sum of flight time (T_{F}), diving time (T_{D}), and swimming time (T_{S}), and T_{N} is the nest time. This ‘internal’ time constraint satisfies both continuous nest attendance and equal duties between the sexes. In simultaneously foraging parents (SFP) no time is spent at the nest ($T_{\text{N}} = 0$), and ‘internal’ time balance is inapplicable. SFP parents do not have to synchronize both their time and energy budgets between each other; they only have to maintain energy balance (i.e., satisfy Eq. 1).

We classify the AFP time balance as an ‘internal’ constraint, distinct from artificially fixed ‘external’ time constraints, say a 24 hour time frame (e.g., Houston et al. 1996): $T_{\text{F}} + T_{\text{D}} + T_{\text{S}} + T_{\text{N}} = 24$ h. The importance of this distinction is best appreciated by a simplistic example. A parent making foraging trips of equal distance and duration, and facing a fixed 24 h external time frame constraint, can only make two 12 h foraging trips a day (or a combined trip and nest shift in the case of AFP), but can only make one 13 h trip, where the 11 remaining hours would be spent in ‘inactivity’ (not foraging). The more realistic ‘internal’ time constraint (i.e., able to exceed the time frame), would allow the same parent to make 1.85 daily 13 h trips (24/13). We chose to use the internal time constraint to avoid the assumption of long periods of inactivity, which would introduce a large bias at low feeding frequencies.

The energy expenditure is the sum of the products of activity-specific time allocation (T_i , h), and the corresponding average activity-specific metabolic rate (MR_i kJ/h, Eq. 3):

$$E_{\text{out}} = T_{\text{F}} MR_{\text{F}} + (T_{\text{D}} + M_{\text{m}}/\lambda_{\text{in}}) MR_{\text{D}} + T_{\text{S}} MR_{\text{S}} + T_{\text{N}} MR_{\text{N}}, \quad (3)$$

where total diving time is the sum of diving time for self (T_{D}) and time spent foraging for the chick's (given by the term $M_{\text{m}}/\lambda_{\text{in}}$), where M_{m} is the meal mass and λ_{in} is the feeding rate (g/h).

Daily energy expenditure (DEE) equals the product of daily foraging trip number (N_{t}) and energy output (or energy input if in energy balance): $\text{DEE} = N_{\text{t}} E_{\text{out}}$ (4). DEE measured with the doubly-labeled water (DLW) method (Lifson and McClintock 1966, Speakman 1997), can be statistically partitioned into any number of non overlapping activity-specific behavioral categories (Chapter 1). DEE is the sum of the products of daily activity-specific time allocation (T_{i} , h), and the corresponding average activity-specific metabolic rate (MR_{i} kJ/h). The time budget of parent alcids has been described by four mutually exclusive activities, flying, diving, swimming, and at the nest (Chapter 1), denoted with the capital subscripts F, D, S, and N, respectively.

The daily net food energy intake required to remain in energy balance is: $E_{\text{in}} = T_{\text{D}} \lambda_{\text{in}} AE E_{\text{M}}$ (5), where AE is the energy assimilation efficiency (75%, Brekke and Gabrielsen 1994), and E_{M} is the average energy density of sandeels (*Ammodytes* spp.) 6.25 kJ g^{-1} (Gabrielsen 1996).

The number of daily foraging trips per parent (N_{t}) in energy balance, and corresponding DEE was calculated as a function of foraging range (R_{F} , km one-way), for three feeding rates, λ_{in} : 70; 90; and 110 g/h. As explained below, both N_{t} and DEE are greatly affected by the number of inter-diving bouts per trip (N_{IDB}), which affect the digestive dynamics and time utilization, portrayed by an example in Figs. 3 and 4. The N_{t}

corresponding to the highest N_{IDB} , and lowest DEE (shown by arrows in Fig. 3) was the criteria used for N_t in all remaining analyses (Figures 5 and 6).

The daily foraging frequency corresponding to minimal (EPR_{min}) and maximal (EPR_{max}) EPR is presented in Fig. 5. Also presented is the chick's body mass at nest departure (M_f , g) corresponding to the predicted mean daily energy requirement (DER), and the predicted peak DER, using the allometric equations of Weathers (1992, 1996). This comparison illustrates the correspondence between the parental EPR supply and the estimated chick energy demand, and provides a guide to the model simulation results. The N_t results of the model are reproduced for three different combinations of locomotion metabolic rates in Figures 6 and 7, for AFP and SFP, respectively.

Determination of the parental time budget. – Three of the four time categories, at nest, diving and flying, are either known by definition, or easily predicted by known terms (see later). Swimming time (T_s) is the only activity that is not straightforwardly expressed by other parameters. In what follows, the determination of each time category is portrayed, ending with a digestion model of swimming time.

Nest time. – Two nest attendance/foraging schedules were examined. (1) *Alternate foraging parents* (AFP). Throughout both incubation and nestling periods, the egg or chick is always accompanied by one or the other parent and nest attendance is shared equally. To remain in time balance, the nest time has to equal the time at sea (Eq. 2). Nest time vary from the average, depending on the duration of the partner's foraging trip. The residual surplus time may be used either as shared nest time ('buffer time,' Burger and Piatt 1990) or idle swimming time, but the time deficit results in greater energy requirement and lost foraging time of the other parent. Our model ignores such

variations and instead focuses on a balanced average. (2) *Simultaneously foraging parents* (SFP). The effect of abandoning alternate foraging: ($T_N = 0$), in favor of simultaneous foraging, is explored to evaluate the EPR ‘sacrifice’ associated with this foraging organization.

Flight time. – Is given by $T_F = 2R_F/v$ (6), where R_F is one half the total foraging trip flight distance (km), including to and within foraging areas, v is the flight speed relative to the ground in zero wind (58.3 km/h, Pennycuick 1987).

Diving time. – T_D is defined here as the sum of both underwater time and the following short dive pauses. This definition is required because diving metabolism occurs partially in both time periods, most adequately presented as a single rate (Culik et al. 1996, Hansen et al. *M.S.*). Consequently the total swimming time (T_S) presented here, is less the total diving pause time. Substituting Eq. 3, and 4 into Eq. 1 illustrates that diving time (T_D) occurs on both sides of the equation, requiring an iterative numerical solution by computer. This is because the determination of total diving time is dependent on how much food needs to be collected, but part of the food needed stems from the cost of acquiring it, namely diving. Required diving time (to remain in energy balance) can be found by solving Eq. 1 for $T_D = [E_{out}/(\lambda_{in} AE E_M)] + M_m/\lambda_{in}$ (Eq. 7), but the calculation is intrinsic to solving Eq. 1 above.

Swimming time. – The problem of determining swimming time is appreciated when one realizes that swimming activity (apart from the short diving pauses) is a response to three main processes: (1) resting after flight; (2) digestion bouts, also called ‘inter-diving bouts (IDB),’ interspersed between diving bouts, and (3) distinctively long IDB’s,

typically occurring towards the end of long trips (often overnight), which are used for both digestion and resting.

The determination of swimming time (T_S) was approached from two perspectives. (1) *Digestive time utilization*. Four razorbill parents for which we had DEE and time budgets measurements (Table 3), were evaluated by using an empirically based ‘Digestion model’ (Table 4, see below). Because both diving and swimming bouts are highly variable in duration, and presumably also the feeding rate, we used average duration and estimated average feeding rate of each bird (Table 3). We performed two analyses, firstly using only inter-diving bouts (IDB) of ‘typical’ duration, and secondly incorporating also the ‘long’ IDB’s (Table 4). In addition we performed the latter approach on average time budgets from two colonies, differing greatly in population size and foraging distance (see ‘Digestion model,’ Tables 4 and 5). The results indicate that the ‘long’ IDB’s are also required for digestive purposes (as well as resting), and are the basis for the second perspective.

(2) *Digestion time requirement*. We developed a ‘digestion model’ to predict the average inter-bout duration (T_{IDB}) required to pass a known amount of digesta from the stomach (see below). Swimming time is the product of number of inter-diving bouts (N_{IDB}) and the IDB duration (T_{IDB}): $T_S = N_{IDB} T_{IDB}$ (Eq. 8).

Average activity-specific metabolic rates. – Three sets of values for diving (MR_D) and flying (MR_F) metabolic rates were compiled. (1) Allometrically predicted, 72.9, and 231 J g⁻¹ h⁻¹, respectively (Hansen et al. *M.S.*). (2) 140% of the allometrical prediction (1), representing an educated guess of the ‘real’ values. (3) Observed, but while experiencing large instrument effects while carrying a data-logger, 259 and 389 J g⁻¹ h⁻¹

respectively (Hansen et al. *M.S.*). Hansen et al. (*M.S.*) found the nest metabolic rate (MR_N) and swimming metabolic rate (MR_S) to be the same ($45 \text{ J g}^{-1} \text{ h}^{-1}$), which the value used here.

Digestion model

We used the model to estimate required digestion time, which we could then compare to the observed swimming time available (i.e., digestion time utilization). The model is divided both temporally and functionally into two parts: ingestion phase; and subsequent egestion phase (Fig. 1). The ingestion phase corresponds to a diving bout, during which both feeding and egestion occur. The amount of food ingested is the product of diving bout duration (T_{DB}) and feeding rate (λ_{in}).

Stomach egestion rate (λ_{out}) has been shown to be a positive function of the digesta volume (V_S) in the stomach (Stubbs 1977, Sibly 1981). As the digesta in the stomach is accumulates, the egestion rate is accelerates, which in turn dampens the accumulation of digesta in the stomach and the acceleration in the egestion rate (Fig. 1). The total amount of digesta egested (V_{out}) during the ingestion phase is calculated by the sum:

$$V_{out}(t) = \sum_0^{T_{DB}} \sum_{t-1}^t [(\lambda_{in} + V_{t-1}) - V_t \lambda_{out}], \quad (9)$$

where V_t is the digesta volume in the stomach at time t , V_{t-1} is the stomach's digesta volume one time interval before V_t . The function was summed over 0.1 min increments for four combinations (the four parents) of feeding rates and mean diving bout durations (Tables 3 and 4), and corresponding estimates from the colony data (Tables 5 and 6). Furthermore, Eq. 9 was summed for the three feeding rates (70, 90 and 110 g/h) used in the T-E model, over a 90 min period, and the results fitted to a third order polynomial,

$V_{\text{out}}(T_{\text{DB}}, \lambda_{\text{in}}) = X_1 T_{\text{DB}} + X_2 T_{\text{DB}}^2 - X_3 T_{\text{DB}}^3$ (Eq. 10), using multiple regression: $V_{\text{out}}(T_{\text{DB}}, \lambda_{\text{in}} = 70) = 0.013654 T_{\text{DB}} + 0.007844 T_{\text{DB}}^2 - 0.000024 T_{\text{DB}}^3$; $V_{\text{out}}(T_{\text{DB}}, \lambda_{\text{in}} = 90) = 0.017555 T_{\text{DB}} + 0.010085 T_{\text{DB}}^2 - 0.000031 T_{\text{DB}}^3$; $V_{\text{out}}(T_{\text{DB}}, \lambda_{\text{in}} = 110) = 0.021456 T_{\text{DB}} + 0.012326 T_{\text{DB}}^2 - 0.000038 T_{\text{DB}}^3$. These three functions evaluate the amount egested during the diving bout (or the ingestion phase), in order to calculate the amount of digesta residing in the stomach (V_i) at the beginning of the egestion phase.

The egestion phase corresponds to the inter-diving bout, where egestion occurs at a decelerating rate as the digesta volume decreases in the stomach (Fig. 1). The amount egested during the egestive phase is determined by:

$$V_{\text{out}}(T_{\text{IDB}}) = V_i - V_i (1 - \lambda_{\text{out}})^{T_{\text{IDB}}}. \quad (11a)$$

The volume residing in the stomach at the end of the evacuation bout is termed residual digesta volume (V_R) and needs to be evaluated for a reasonable T_{IDB} estimate. The V_R value is partly an artifact of using averaged feeding rates and diving bout durations, and partly reflecting real behavior of resuming feeding before completely clearing the stomach since the last diving bout (increasing the evacuation rate during the subsequent ingestion phase). We ‘rounded’ the average V_R from Table 4 (9.25) to 10 g for AFP. V_R was assumed 5 g for SFP, but this reduction was necessitated because in foraging scenarios costing little energy V_i became very close to or even less than V_R . Unfortunately this complicates the comparison of AFP and SFP time budgets, but this assumption makes intuitive sense, part of the greater time availability is utilized for digestion, presumably increasing assimilation efficiency. Incorporating V_R and solving Eq. 11 for T_{IDB} :

$$T_{\text{IDB}} = \text{Ln} \left(1 - \left(\frac{V_i - V_R}{V_i} \right) \right) / \text{Ln}(1 - \lambda_{\text{out}}). \quad (11b)$$

Individual feeding rates. – Activity specific time budgets (Dall'Antonia et al. 2001), and water flux (Hansen et al. *M.S.*), were measured simultaneously by using dataloggers and the DLW method (Speakman 1997), for 12 parents provisioning 3-7 day old chicks, 3-14 July 1998 in Látrabjarg, Iceland, the world's largest Razorbill colony (230.000 pairs, Garðarsson 1995). The birds were snared from the cliff's edge, using a 7 m noose-pole. The 'Egestion rate' experiment was conducted at the same location at the end of the incubation period 25-27 June 1999.

The summer diet of razorbills off the west coast of Iceland is predominantly sandlance (*Ammodytes* spp.) (Lilliendahl and Sólmundsson 1997). Sandeel energy density is assumed 6.25 kJ g⁻¹ (Gabrielsen 1996). Four razorbill parents were selected on the basis that they were roughly in energy and time balance (Table 3). Average feeding rates (both individual and colony specific) were estimated by dividing the total consumed food mass (M_F , g) with the total diving time (T_D): $\lambda_{\text{in}} = M_F/T_D$. The average individual feeding rates are given in Table 4, and 'colony' specific rates in Table 5.

Total ingested food mass was estimated from total water intake (W_{in} , mL), by dividing the total water intake by a food conversion coefficient ($C_F = 0.85$ mL H₂O g⁻¹ sandlance, wet), $M_F = W_{\text{in}}/C_F$. The food conversion coefficient is the sum of sandlance water content (0.707 g H₂O g⁻¹) and the metabolic water generation (0.147 g H₂O g⁻¹ food, wet). The metabolic water is the sum of fat (1.07 g H₂O g⁻¹ fat) and protein (0.5 H₂O g⁻¹ protein, uric acid excretion) metabolic water production coefficient and the mass specific proportions of fat and protein (Schmidt-Nielsen 1997).

Colony specific feeding rates. – Average feeding rates based on the average time budgets for two different seasons in Látrabjarg (1997 and 1998, Dall'Antonia et al. 2001), and in the small colony of Græsholmen, Baltic Sea (Benvenuti et al. 2001), were estimated by 'assuming' energy balance (Tables 5 and 6).

Egestion rate experiment. – Farm raised 0-group salmon (*Salmo salar* L.) were stored frozen (-20°C), and thawed immediately prior to feeding (fed at 5-10° C), blotted dry on paper towels, weighed to the nearest 0.1 g using an electronic balance (ACCULAB VI-1200), moistened, and force fed. Prior to the main experiment, three birds were force fed, and stomach-pumped ten minutes later. Their meals were still mostly intact, approximately corresponding to the initial 'lag' period, during which the chemical and mechanical breakdown initialize (Sibly 1981, Hilton et al. 1998). With respect to these results, stomach-pumping time was chosen to be 20 minutes after feeding. The stomach was 'pumped' using a 100 mL syringe filled with water, connected to 20 cm long catheter (diameter: 5 mm external; 3.5 mm internal), (Wilson 1984, Ryan and Jackson 1986, Gales 1987, Jackson 1992). The water and digesta started flowing out of the bill after injecting about 60 mL, then the bird was inverted head first over a plastic collection sheet, gentle pressure applied on the anterior of body, and while firmly holding the legs, quickly jerked up and down. Three randomly chosen birds in the main experiment were stomach-pumped twice in succession to examine if any food remained after single pumping, which did not occur, indicating that the relatively small meal's remains were easily retrieved.

Eight adult birds were caught and fasted for 12 h in ventilated cardboard boxes lined with newspapers, prior to the feeding experiments. The stomach evacuation rate

(λ_{out} , g/min) was measured in replicate, in absorptive birds, and again when post-absorptive. Two meal sizes were used, and four experimental groups were thus formed.

(1) *Absorptive, small meal.* – Six birds were force-fed ‘small meals’ consisting of single fish averaging 17.7 ± 2.7 (\pm SD) g, and stomach-pumped after 20 minutes. (2) *Post-absorptive, small meal.* – The same birds as in the first experiment were force fed the second time and allowed to digest for 50 minutes. They were then force fed for the third time, and stomach-pumped 20 minutes later. The same six birds as in Group 1 received 31.8 ± 3.1 g total in the two feedings. (3) *Absorptive, large meal.* – Two birds were force feed ‘large meal’ consisting of two fish, 30.5 and 42.2 g, respectively, but received otherwise the same treatment as Group 1. (4) *Post-absorptive, large meal.* – The same birds as in Group 3 received the same treatment as in group (2), their large double meals being 67.4 and 78.8 g in total, respectively.

In all treatments the λ_{out} was calculated by dividing total meal size by total time since first feeding until stomach pumping (i.e., 20 and 70 min respectively). The relationship between λ_{out} and meal mass in the two treatments, was examined using ANCOVA (Fig. 2).

Stomach-esophagus volume. – V_S was measured in one adult collected under permit, by dissecting the upper gut and filling it with water. The gut volume was estimated to be the product of gut length, and mean gut cross sectional area, measured at three locations along the gut, approximately 30 cm apart.

RESULTS

Digestion model

Egestion rate. – The egestion rate of digesta (λ_{out} , g/min) as a function of meal mass (M_{m} , g) was estimated as the slope of regression through the origin, and was done separately for absorptive (Groups 1 and 3) and non-absorptive birds (Groups 2 and 4). The slope coefficient of non-absorptive birds (0.0165 g/min \pm 0.000260 SE) was significantly higher (t -test, $t = 2.716$, $P < 0.05$) than in absorptive (0.0143 g/min \pm 0.000897 SE). However, to simplify the prediction of egestion rate, a regression was performed on the pooled data: $\lambda_{\text{out}} = 0.015$ (\pm 0.0004 SE) M_{m} , ANOVA: $F_{1, 16} = 1338.5$; $P < 0.0000001$; $R^2 = 98.9\%$; SEE = 0.600 (Fig. 2).

Inter-diving bout number per foraging trip (N_{IDB}). – The number of daily foraging trips (N_{t}) and corresponding daily energy expenditure (DEE, kJ/d) in relation to N_{IDB} (while remaining in energy balance) is shown for $R_{\text{F}} = 35$ km (as in Látrabjarg, Iceland 1998), and for three different ingestion rates in Fig. 3. The examples in Fig. 3 illustrate the large influence N_{IDB} has on both N_{t} and DEE.

The combination of the highest N_{IDB} with the ‘lowest’ DEE (shown with arrows in Figures 3 and 4), reflected the observed N_{IDB} number well (mean N_{IDB} 6.6 trips/d, Table 6). This indicates that the N_{IDB} frequency is substantially higher than what would minimize energy expenditure and time investment, severely reducing the N_{t} . This better seen in Fig. 4 showing the change in energy cost per nest-foraging trip cycle as a function of N_{IDB} .

The factors determining diving bout duration in reality are unknown, but presumably include a mixture of digestive efficiency considerations, and the temporal availability of the prey. Changes in the time budget components with N_{IDB} (Fig. 5A), show increased swimming time (digestive time) with the N_{IDB} increase, and a corresponding nest time increase (Fig. 5B). This follows from the relationship that, in shorter digestive bouts, smaller maximal digesta volume is reached in the stomach, and lower egestion rate is therefore attained, requiring a longer IDB duration to evacuate the same amount of digesta. To a lesser degree, this is also due to the fact that less digesta is evacuated during the shorter ingestion phase, increasing the amount of digesta to be evacuated in the egestion phase. The bulk of the DEE increase is results from the combined increase in swimming and nest time (activities which have the same metabolic rate in Razorbills).

Time and energy balance. The time and energy budgets of the four razorbill parents are presented in Table 3. The bird's time budgets were 'approximately' in balance (balanced time budget being 50:50 partition between the nest and the sea), the individual values ranged between 41.6 and 68.0 % of the time at the nest. Energy balance was assumed when estimated net food energy intake (based on water influx), was 100% of DEE. The observed energy balance ranged from 88.5 to 140% of the estimate from water flux.

Individual feeding rates. – Estimated feeding rates (λ_{in}) ranged between 87 and 111 g/h, and the mean diving bout duration tended to shorten as λ_{in} increased (Table 4). The average time budgets of razorbill parents in the mega colony in Látrabjarg, Iceland (two seasons), and in the small Græsholmen colony in the Baltic Sea (Benvenuti et al.

2001, Dall'Antonia et al. 2001), are presented in Table 5, together with estimates of their corresponding energy budgets, based on the assumption that they were in energy balance. The observed foraging behavior, together with estimated digestive time utilization, is presented in Table 6.

The estimated average 'population' feeding rate in the 'bad' year in Látrabjarg was very low (62 g/h), and the 'good' year's estimate is presumably on the lower side (85 g/h, Table 6). The mean estimated population feeding rate by the Græsholmen birds was very high, or equal to the highest individual rate in Látrabjarg in the 'good' year (Table 4). It should be noted that Græsholmen razorbills are of the subspecies *A. t. torda*, individuals of which are 18% heavier than the Icelandic birds belonging to the subspecies *A. t. islandica*; in the DEE calculations, mass-specific activity-specific metabolic rates ($\text{kJ g}^{-1} \text{h}^{-1}$) were assumed to be 20% lower in the larger subspecies (Table 5).

Digestive volume. – The maximal stomach volume was 80 cm^3 , but this measurement refers to the maximum possible extent of expansion. A volume of 70 cm^3 is considered a more realistic estimate, and in better accordance with the stomach pumping observations (see 'Methods'). The gut volume was estimated to be 30 cm^3 . The empty gut was 1.05 m long, and had a mean outer radius of 3.1 mm ($n = 3$), producing an average cross-sectional area of 0.3 cm^2 .

Individual digestive time utilization. – N_t ranged between 0.5 and 1.6, the mean daily foraging bout number (N_{IDB}) was 6.1 ± 1.0 (SD). Mean one-way foraging distance (R_F) in Látrabjarg, Iceland (1998) was highly variable: $35 \pm 20.9 \text{ km}$ (\pm SD); range 11.2-64.1 km (see Table 4). The estimated average amount of ingested food and the mean diving bout duration were distinctively less in the two birds with high feeding rates (No.

13 and 14) than in the two with the lower feeding rates (No. 9 and 12). The estimated average amount of ingested food at any one time never exceeded the maximum stomach volume (70 cm^3), and was closest in bird No. 12 (63.5 g).

Digestive time utilization was examined with respect to two egestion phase durations (Table 4). (A) The egestion phase was assumed to correspond to the 'typical duration' inter-diving bouts (IDB's) only. (B) Egestion phase was assumed to correspond to total swimming time (i.e., including the 'long' IDB's). Comparison between the egestion phases revealed that the 'long' IDB's are also required for digestive purposes. It should be noted, however, that the model does not take into account elevated stomach content at the start of ingestion bouts, which would occur if feeding rate was truly constant, and thereby substantially increase the egestive rate. However, the feeding rate is likely quite variable between feeding bouts, which would invalidate such approach.

Parental energy supply (EPR) and the chick's energy demand (DME). – N_t as a function of the EPR, and the chick's body mass at nest departure (M_t) as a function of chick's daily metabolized energy (DME), are compared in Fig. 6. EPR_{\max} and EPR_{\min} , correspond to the minimum and maximum meal masses reported in the literature (see Table 2). The N_t required to raise a chick to the observed body mass is illustrated in Fig. 5, the 'maximal' range being between 1.8-4.3 trips d^{-1} parent $^{-1}$. $N_t > 4.3$ is needed to raise a chick to a greater body mass than maximally observed (214 g, Barrett 1984), the range being 5.0-7.1, and 7.1-10.2 trips d^{-1} parent $^{-1}$, corresponding to $M_m = 11.4$ and 8.0 g, respectively (i.e., EPR_{\min} and EPR_{\max}).

N_t of alternating foraging parents. – N_t is a negative hyperbolic function of the foraging distance (R_F), and changes most rapidly between 0-10 km (Fig. 7). As expected N_t was greatest when using allometrically predicted locomotor metabolic rates (Fig. 7A), intermediate when using the 140% estimate of the allometric predictions (Fig. 7B), and distinctively the lowest when the measured locomotor metabolic rates of instrumented birds were employed (Fig. 7C).

The difference in N_t between the three feeding rates (λ_{in}), followed the same pattern in all three scenarios (Fig. 7A-C), the difference being greatest at short foraging distances, but decreasing in absolute difference until $R_F = 30$ km, after which they remained similar. As expected N_t ranked with λ_{in} as: 110 > 90 > 70 g/h. When $\lambda_{in} = 70$ g/h and ‘instrumented’ locomotion metabolism was used, N_t reached only 0.6 trips/d when $R_F = 5$ km, and 0.3 trips/d when $R_F = 7.5$ km (not shown in Fig. 7C).

Of the AFP scenarios, only the combination of the highest feeding rate (110 g/h) and the ‘predicted’ locomotor metabolic rates (Fig. 7A) at $R_F = 35$ km attained the ‘minimal’ $N_t = 1.8$. Only the very shortest foraging trips (<10 km) surpassed the ‘maximal’ $N_t = 4.3$ limit, and foraging range (R_F) reduced with lower feeding rate.

N_t of simultaneously foraging parents. – The SFP N_t patterns followed the same general trends as described above for AFP, except being substantially higher (Fig 8).

The N_t of the two foraging strategies are compared in Table 7, at three selected foraging distances (R_F , 7.5, 20, and 35 km), roughly corresponding to the observed averages in the Græsholmen and Látrabjarg colonies. The average R_F from the small Græsholmen colony, Baltic Sea, was 6.8 at night and 18.7 km during the day, compared to 35.0 ± 20.9 km from Látrabjarg, Iceland (1998). The results were surprisingly diverse

and inconsistent between metabolic rates, foraging distance and feeding rates, and caused by the relatively large effects of slight changes in N_{IDB} between the scenarios. The changes between the ‘predicted’ and allometrically estimated metabolic rates were not parallel for the same reason. The instrumented birds had such a high metabolism that five out of the nine comparisons were unrealistically low ($N_t < 0.3$). Generally increase in feeding rate and foraging distance tended to reduce N_t , but both generalizations had contradictions. The N_t of the hypothetical SFP foraging-nest attendance strategy was potentially reduced by 26-42% by adopting the (observed) AFP strategy.

DISCUSSION

The ‘intermediate’ nest departure pattern of Razorbills and Murres is accompanied with very low parental energy supply rate, even when compared to other auks. Razorbills (Chapdelaine and Brousseau 1996), and Murres (e.g., Montevecchi and Piatt 1984, Hislop et al. 1991) do feed on high energy density prey, thus their low energy provisioning rates reflects a combination of small meal size, and in particular a low feeding frequency (De Santo and Nelson 1995). Foraging frequency is determined in concert by: time available after accounting for nest duties; foraging distance (flight time); how much food has to be gathered to balance the energy expenditure; the time required to obtain the given amount of food (feeding rate, diving time); and the food’s digestion time (swimming time).

Razorbill's (and presumably also the Murres) high metabolic output of both flying and diving (Chapter 1), elevates the daily energy expenditure and food requirements, and therefore the sensitivity of the time-energy budget to any changes in flight and diving duration (e.g., Houston et al. 1996). Razorbills however feed at 'moderate' one-way foraging distances (8.8-35 km), especially in comparison to Thick-billed Murres in Látrabjarg (168 km, Benvenuti et al. 1998). The range in Razorbill's feeding rates examined here (70-110 g/h), did not generate a particularly large variation in the foraging trip frequency for a given foraging distance, except when the distance is short ($R_F < 7.5$ km., Fig. 7).

Two main constraints of foraging trip frequency by Razorbill parents were identified: digestion time (swimming); and the alternate nest attendance and foraging organization. The alternate foraging behavior of Razorbill parents was estimated to reduce their potential feeding frequency by 26-42% from that if they foraged simultaneously (Table 7), as the other nidicolous species of the family. This was primarily because of the 'additional' nest time, and secondarily because of the 'additional' time investment associated with acquiring the energy to fuel the nest duties (Fig. 5).

The alternate foraging behavior is in common only among the three intermediate species (a synapomorphic, or shared derived trait), and which strongly suggests to be the single most important selective force responsible for the 'intermediate' nest departure pattern, thus generating most of the large EPR gap observed between the 'intermediate' and the semiprecocial nidicolous species.

Comparison of the parental energy supply to the estimated daily energy requirement of the chick (Fig. 6), strongly suggests that the EPR of razorbill parents is insufficient to

produce a greater chick mass at nest departure than observed (20-30% of adult body mass). This strong selection against chick growth rate in the safety of the nest poses the question if there is much leverage left in the parameter space concerned (growth rate and survival at sea) to produce alternative nest departure patterns? That is, the species in which the chick leaves the nest later and at larger proportional size (than 'intermediates'), does that occur because of a change in optimal nest departure time (Ydenberg 1989, Ydenberg et al. 1995), or because the EPR is higher in these species than in the 'intermediate' species. If the EPR is the dominant factor, the variation (both within and between) in the nidicolous nest departures patterns should to be highly positively correlated to the EPR. Given the preliminary data this seems to be the case, but to ideally test Ydenberg's optimal departure hypothesis, the daily mortality rates at both at sea and nest, and the growth rate at sea, need to be known (Ydenberg 1998), an information hard to come by (Gaston 1998). It is interesting in this context however, that the auk species with the highest chick nest mortality rate (*Cepphus* spp.), also have the highest chick growth rate in the family (and EPR), and their two chicks depart the nest fully grown (Ydenberg 1989). These two nest departure extremes (*Cepphus* and the 'intermediates') support the notion that the nest departure patterns are predominantly caused by species-specific differences in EPR, which effects (nest growth rate) is the dominant factor in the optimal nest departure 'dynamic equilibrium' (Byrd et al. 1991).

The parental time-energy model illustrates that the long observed swimming time of Razorbill parents (25-30% of the daily budget) is needed for digestive purposes, and that required digestive time for a given amount of food, is very sensitive to the duration of both diving and inter-diving bouts, and is greatly prolonged by more frequent and shorter

bouts (Fig. 3 and 4). It is perhaps misleading in a sense to portray digestion as a constraint to the feeding frequency, as that perception reflects digestion as an extracurricular activity rather than an essential part of living. However, this is partially a semantic issue, since digestion does take time and therefore effects the time allocation to other activities. The important aspect is that it can take quite different time to digest the same amount of food, depending on the duration of both diving bouts and swimming (inter-diving) bouts. The importance of digestion as constraint in relation to inter-specific nest departure patterns in auks is probably negligible, given that auk digestion features and foraging aspects don't differ greatly. As mentioned before the intermediate species differ from the simultaneously foraging species in that they require longer digestion, everything else being equal, since they need to consume more food to fuel their nest duties.

The realism of the digestive model and hence the results presented in this paper demand some discussion. The birds are only in 'full' control of the inter-diving bout duration (i.e., pending on prey availability to resume feeding), but the diving bout duration ultimately depends on prey availability (if not terminated before by a full stomach). The digestive time utilization reported in this paper is hard to interpret beyond the face value of the preliminary data provided, where the approximation of using the averages of variable feeding rates and diving bout durations can only provide general insights to the digestive dynamics. For example, on average it seems that diving bouts are terminated before reaching full stomach capacity. This might be the case, but it is more likely that feeding rates differ substantially between and even within diving bouts, sometimes leading to a 'premature' termination of feeding when the stomach is full. The

problem that this entails for predicting swimming time is the uncertainty in the V_i value, or the digesta volume at the start of the egestion phase.

Another aspect of uncertainty for swimming time predictions lies in the egestion phase termination criteria (V_R), also pending on the use of averages. In reality the birds might initiate feeding again with varying amount of residual stomach content. V_R also relates positively to swimming time by elevating the stomach evacuation rate in the subsequent diving bout, leading to more evacuated food during the subsequent ingestion phase, and thus shortening the egestion phase duration.

The use of the λ_{in} and T_{DB} averages here in the calculations and ignoring the effect of non-zero V_R in subsequent diving and inter-diving bouts, potentially introduces a bias in the swimming time estimation. However, aside from the fact that this variability is unknown, the calculation procedure used here, employing a fixed V_R , but starting the subsequent diving bout with zero stomach content, produces a conservative estimate of swimming time.

The digestive model presented does lend it self to be tested in laboratory experiments on stomach evacuation dynamics and their relation to digestive efficiency and time utilization. These experimental results need to be quantified to evaluate the role of digestive physiology and foraging ecology in relation to parental energy provisioning capacity and the determination of clutch size, and certainly will introduce a multidisciplinary framework for comparing the evolutionary forces behind the behavior, and eco-physiology of parental care.

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TABLE 1. List of parameters and variables.

| Symbol | Explanation | Value, units, reference |
|----------|--|--|
| AE | Energy assimilation efficiency | 75%, Brekke and Gabrielsen (1994) |
| C_F | Sandlance water production coefficient | 0.85 mL H ₂ O/g prey, Schmidt-Nielsen (1997); Gabrielsen (1996) |
| DEE | Daily energy expenditure | kJ/d, Eq. 3., Fig. 3B, 5B |
| $ADME$ | Chick's mean daily metabolized energy | kJ, $M_b 3.7M_b^{-0.23}$ Weathers (1992) |
| $PDME$ | Chick's peak daily metabolized energy | kJ, $5M_f^{0.78}$ Weathers (1992) |
| E_{in} | Food energy intake | kJ/d, Table 3, Eq. 4 |
| EPR | Parental energy provisioning rate | kJ/d, see text, Fig. 6 |
| E_M | Mean Sandeel energy density | 6.25 kJ/g, Gabrielsen (1996) |
| M_b | Adult body mass | g |
| M_f | Chick's body mass at nest departure | g, Table 2 and Fig. 6 |
| M_{in} | Daily adult food consumption | g/d, Tables 3 and 6 |
| M_m | Chick's mean meal mass | 8.0-11.4 g, Table 2 |
| MR_N | Nest metabolic rate | 45 J g ⁻¹ h ⁻¹ (Chapter 1) |
| MR_F | Flight metabolic rate | 231, 277, and 389 J g ⁻¹ h ⁻¹ (Chapter 1) |
| MR_D | Diving metabolic rate | 73, 88, and 259 J g ⁻¹ h ⁻¹ (Chapter 1) |
| MR_S | Swimming bout metabolic rate | 45 J g ⁻¹ h ⁻¹ (Chapter 1) |
| N_{DB} | Number of diving bouts per N_t | Table 4 and 6 |

| | | |
|-----------------|--|--|
| N_{IDB} | Number of inter-diving bouts per N_t | Tables 4 and 6, Fig. 3-5 |
| N_t | Daily foraging trip number, or chick's feeding frequency | Tables 4 and 6, Fig. 3B, 4, and 6-8 |
| T_D | Diving duration | h |
| T_{DB} | Diving bout duration | h |
| T_F | Flight duration | h |
| T_{IDB} | Inter-diving bout duration | h |
| T_N | Nest duration | h |
| T_S | Swimming duration | h |
| T_t | Foraging trip duration | h |
| R_F | Total one-way foraging distance | km |
| V_i | Residual digesta volume in stomach after ingestion phase | mL, see text |
| V_{in} | Accumulated ingested food | g |
| $V_{out}(t)$ | Accumulated egested digesta | g, see text, Eqq. 10 and 11, Fig. 1 and 2 |
| V_R | Residual digesta volume at the end of egestion phase | mL |
| V_S | Instantaneous digesta volume in stomach | 70 mL, see text |
| v | Flight speed | 58.3 km/h, Pennycuick (1987) |
| W_{in} | Total water influx | mL H ₂ O, Table 3 |
| λ_{in} | Adult feeding rate | 70-110 g/h, Table 4 |
| λ_{out} | Stomach egestion rate | $0.015 \text{ g min}^{-1} \text{ g}^{-1} V_S$, Fig. 2 |

TABLE 2. Data on geographic variation within the two subspecies of Razorbill, average chick's age and body mass at departure, in relation to daily net parental energy provisioning rate (EPR, kJ/d), EPR is the product of number of daily feedings $2N_t$ (by both parents), average meal mass M_m (g), food energy density $E_m = 6.25 \text{ kJ g}^{-1}$ (Hislop et al. 1991), and assimilation efficiency $AE = 0.75$ (Brekke and Gabrielsen 1994). The chick's average daily metabolizable energy (ADME) was estimated as $M_b(3.7M_b^{-0.23})$, and daily peak DME (PDME) as $5M_b^{0.78}$ (Weathers 1992). The values within the square brackets are estimates required to satisfy the ADME.

| Subspecies | Ad. M_b | Chick | | | Provisioning rate | | | ADME | PDME | Study |
|--------------------------|-----------|-----------|-----------|-------------|--------------------|------------------------|------------------|---------|---------|--------|
| | | Age | M_b | % Ad. M_b | $2N_t$ | M_m | EPR | | | |
| <i>Location</i> | (g) | (d) | (g) | (%) | (d ⁻¹) | (g) | (kJ/d) | (kJ/d) | (kJ/d) | |
| <i>A. t. torda</i> | | | | | | | | | | |
| White Sea, Russia | 701 | 15-20 | 170-190 | 24.2-27.1 | - | - | - | 193-210 | 275-300 | (1) |
| Hornoy, Norway | 714±49 | 21, 23 | 202, 214 | 28.3, 30.0 | - | - | - | 220-230 | 314-329 | (2) |
| St.-Mary Islands, Canada | 728±51 | 18.2±0.3 | 199.2±24 | 27.4 | 3.5±0.36 | 11.4±1.7 | 185.5 | 218 | 311 | (5, 6) |
| Graesholmen, Baltic Sea | 730.6 | 18-22 | 212±24 | 29.0 | 4.5±0.96 | [10.9] | [229] | 229 | 326 | (3, 4) |
| <i>A. t. islandica</i> | | | | | | | | | | |
| Látrabjarg, Iceland | 619 | - | [161-201] | [26.0-32.5] | 1.8 ^a | [21.1] ^a | [178] | 178 | 253 | (7, 8) |
| Skokholm, Wales | 630-637 | 17.2-18.5 | 165-186 | 26.0-29.5 | 4.7 | [8.6-9.5] ^b | [188-207] | 188-207 | 268-295 | (10) |
| Isle of May, Scotland | 637 | 19.1±0.2 | 195-207 | 30.6-32.5 | 2.8±0.12 | 8.0±1.0 ^c | 120 ^c | 215-225 | 306-320 | (9) |

Studies cited: (1) Bianki (1977), (2) Barrett (1984), (3) Bédard (1969), (4) Chapdelaine and Brousseau (1996), (5) Lyngs (1994), (6) Benvenuti et al. (2001), (7) this study, (8) Dall'Antonia et al. (2001), (9) Harris and Wanless (1986, 1989), (10) Lloyd (1977, 1979), (12) Plumb (1965).

^a Instrumented and DLW treated birds which experienced large increase in diving and flight metabolism (Chapter 1), suggesting a possible reduction in feeding frequency by about one half.

^b Lloyd (1977, 1979) estimated the mean meal size = 3.9 g, which is almost certainly an underestimate. Daily feeding frequency ($2N_t$) increased from 4.7 to ~9.0 feedings per nest in a 'twinning' experiment (induced SFP, i.e., both parents feeding simultaneously, $n=4$).

^c Even when assuming food energy density as high as 7.2 kJ g^{-1} (as in 1986, Harris and Wanless 1989), the meal size is underestimated by one half in comparison to the requirement needed to satisfy the predicted ADME.

TABLE 3. Time and energy balances of four razorbill parents during the nestling period in Látrabjarg, Iceland, July 1998 (Chapter 1).

| Variables | Bird No. | | | |
|--|----------|-------|-------|-------|
| | 9 | 12 | 13 | 14 |
| <i>Time balance – At sea (% of T_T)</i> | 49.3 | 68.0 | 41.6 | 63.7 |
| Nest time, T_N (h/d) | 12.17 | 7.68 | 14.01 | 8.70 |
| Flight time, T_F (h/d) | 0.64 | 0.92 | 2.30 | 1.11 |
| Dive time, T_D (h/d) | 2.69 | 4.64 | 2.14 | 2.07 |
| Short swim time (A), T_{IDB} (h/d, see text) | 3.65 | 6.12 | 4.39 | 8.91 |
| ‘Long’ swim time (B), T_{IDB} (h/d, see text) | 4.99 | 4.64 | 1.17 | 3.21 |
| Total experimental time duration (d) | 1.27 | 1.93 | 2.03 | 1.98 |
| <i>Energy balance – E_{in}/DEE (%)</i> | 92.7 | 140.0 | 79.2 | 88.5 |
| DEE (kJ d^{-1}) | 1178 | 1428 | 1372 | 1212 |
| Water influx, W_{in} ($\text{g H}_2\text{O d}^{-1}$) | 198.1 | 363.3 | 197.4 | 195.0 |
| Food consumption, V_{in} (g d^{-1}) | 233 | 427 | 232 | 229 |
| Estimated food energy intake, E_{in} (kJ/d) | 1092 | 2001 | 1087 | 1073 |

TABLE 4. Average foraging behavior, and estimated average digestive time utilization by four instrumented razorbill parents during the nestling period in Látrabjarg, Iceland 1998.

| Variables | Bird No. | | | |
|---|----------|-------|-------|-------|
| | 9 | 12 | 13 | 14 |
| Mean one-way foraging distance, R_F (km) ^a | 11.2 | 52.0 | 45.3 | 64.1 |
| Daily number of foraging trips, N_t | 1.57 | 0.52 | 1.48 | 0.50 |
| Daily number of diving bouts, N_{DB} | 4.72 | 6.73 | 8.67 | 6.06 |
| Feeding rate, λ_{in} (g/h) | 87 | 92 | 109 | 111 |
| Ingestion phase | | | | |
| Mean diving bout duration, T_{DB} (h) | 0.571 | 0.690 | 0.241 | 0.343 |
| Food ingested per diving bout, V_{in} (g) | 49.5 | 63.5 | 26.2 | 38.1 |
| Egested digesta, V_{out} (g) | 10.9 | 16.2 | 2.7 | 5.4 |
| Residual digesta, V_i (g) | 38.8 | 47.2 | 23.7 | 32.7 |
| Egestion phase (A) | | | | |
| Mean 'short' inter-diving bout duration, T_{IDB} (h) | 0.763 | 0.910 | 0.488 | 1.475 |
| Egested digesta, V_{out} (g) | 19.4 | 26.5 | 8.5 | 24.1 |
| Residual digesta, V_R (g) | 19.4 | 20.7 | 15.2 | 8.6 |
| Egestion phase (B) | | | | |
| Mean total swimming time: long + short T_{IDB} (h) | 1.805 | 1.598 | 0.618 | 2.001 |
| Egested digesta, V_{out} (g) | 31.2 | 36.1 | 10.2 | 27.4 |
| Residual digesta, V_R (g) | 7.6 | 11.1 | 13.5 | 5.3 |

^aBird No. 9, R_F : 7.8 and 14.2 km. Bird No. 13, R_F : 34.0; 58.3; and 43.7 km.

TABLE 5. Comparison of daily activity-specific time (T) and energy (E) budgets of instrumented razorbill parents during the nestling period in two contrasting years in Látrabjarg, Iceland (65°30'N, 24°32'W), the world largest razorbill colony (230.000 pairs), and in a small colony (625 pairs) on Græsholmen, Baltic Sea (55°19'N, 15°11'E).

| | | Látrabjarg | | | | | |
|--------|--------------------------------------|------------|-------|-------------|------|-------------------|------|
| | | 'Bad' year | | 'Good' year | | Græsholmen | |
| | AASMR ^a | T | E^a | T | E | T | E |
| | (J h ⁻¹ g ⁻¹) | (h) | (kJ) | (h) | (kJ) | (h) | (kJ) |
| Nest | 45 | 9.1 | 242 | 12.8 | 357 | 13.4 | 353 |
| Flight | 389 | 2.3 | 529 | 1.2 | 289 | 1.0 | 227 |
| Dive | 259 | 6.7 | 1026 | 3.5 | 561 | 2.1 | 318 |
| Swim | 45 | 5.9 | 157 | 6.5 | 181 | 7.5 | 197 |
| At sea | - | 14.9 | 1712 | 11.2 | 1031 | 10.6 ^b | 742 |
| DEE | - | - | 1954 | - | 1388 | - | 1095 |

^a Values from instrumented birds which experienced inflated cost of locomotion (Chapter 1). The average activity-specific metabolic rates of Græsholmen razorbills (*A. t. torda*), (body mass: 731 g, Benvenuti et al. 2001), were assumed to be 20% lower than the Icelandic razorbills (*A. t. islandica*), (body mass: 'bad year' 591 g, 'good year' 619 g, Dall'Antonia et al. 2001), i.e., compensating for the 20% mass difference.

^b Assuming to be in the nest for the remainder of the day: 13.4 = 24 - 10.6 h.

TABLE 6. Average foraging behavior, and estimated digestive time utilization of instrumented razorbill parents during the nestling period in two contrasting years in Látrabjarg, Iceland (65°30'N, 24°32'W), the world largest razorbill colony (230.000 pairs), and in a small colony (625 pairs) on Græsholmen, Baltic Sea (55°19'N, 15°11'E).

| Variables | Látrabjarg | | Græsholmen |
|--|------------|--------|------------------|
| | 'Bad' | 'Good' | |
| One-way foraging distance, R_F (km) | 67 | 35 | 8.8 ^a |
| Number of daily foraging trips, N_t | <1 | 1 | 2.25 |
| Foraging trip duration, T_t (h) | 14.9 | 11.2 | 3.3 |
| Food consumption, V_{in} (g) | 417 | 296 | 234 |
| Feeding rate, λ_{in} (g/h) | 62 | 85 | 111 |
| Diving bouts per trip, N_{DB} | 11.4 | 6.6 | 2.9 |
| Ingestion phase | | | |
| Mean diving bout duration, T_{DB} (h) | 0.59 | 0.53 | 0.32 |
| Food ingested per diving bout (g) | 36.6 | 45.0 | 35.5 |
| Egested digesta, V_{out} (g) | 9.5 | 10.2 | 4.8 |
| Residual digesta, V_i (g) | 27.1 | 34.8 | 30.7 |
| Egestion phase | | | |
| Mean inter-diving bout duration, T_{IDB} (h) | 0.52 | 0.98 | 1.15 |
| Egested digesta per IDB, V_{out} (g) | 16.9 | 20.6 | 19.9 |
| Residual digesta, V_R (g) | 10.2 | 14.4 | 10.8 |

^aWeighted average of: diurnal (6.8 km, n=31); and nocturnal foraging trips (18.7 km, n=8).

TABLE 7. Potential reduction in daily number of foraging trips per parent (N_t) by alternate foraging parents (AFP), from hypothetical simultaneous foraging (SFP), at three foraging distances (R_F , km), three feeding rates (λ_{in} , g/h), and three combinations of locomotion metabolic rates (diving and flying, see text).

| R_F km | λ_{in} g/h | <i>Predicted MR</i> | | | <i>Estimated MR</i> | | | <i>'Instrumented' MR</i> | | |
|-------------|-----------------------|---------------------|-------|----|---------------------|------|----|--------------------------|------|----|
| | | AFP | SFP | % | AFP | SFP | % | AFP | SFP | % |
| 7.5 | 70 | 5.89 | 9.69 | 39 | 3.90 | 6.22 | 37 | - | - | - |
| 7.5 | 90 | 6.71 | 11.52 | 42 | 5.13 | 7.63 | 33 | 1.51 | 2.11 | 28 |
| 7.5 | 110 | 7.35 | 12.32 | 40 | 5.94 | 7.99 | 26 | 2.4 | 3.39 | 29 |
| 20 | 70 | 2.52 | 4.08 | 38 | 1.74 | 2.77 | 37 | - | - | - |
| 20 | 90 | 2.92 | 4.42 | 34 | 2.05 | 3.08 | 33 | 0.56 | - | - |
| 20 | 110 | 3.28 | 4.68 | 30 | 2.31 | 3.49 | 34 | 0.96 | 1.45 | 34 |
| 35 | 70 | 1.60 | 2.42 | 34 | 1.02 | 1.69 | 40 | - | - | - |
| 35 | 90 | 1.73 | 2.74 | 37 | 1.28 | 1.96 | 35 | 0.34 | - | - |
| 35 | 110 | 1.91 | 2.97 | 36 | 1.38 | 2.04 | 36 | 0.58 | 0.94 | 38 |

Figure legends:

FIG. 1. Schematic of the digestion model. The model is temporally divided into ingestion phase (0-30 min) when both food ingestion and stomach egestion occur, and egestion phase (30-118.7 min) when only stomach egestion occurs (the phases illustrated with vertical broken lines). This example illustrates a Razorbill ingesting 45 g of prey over a 30 min period (feeding rate $\lambda_{in} = 1.5$ g/min), the accumulated food ingested shown by V_{in} . The stomach fills during the ingestion phase at a decelerating rate, as portrayed by the instantaneous stomach's digesta volume (V_S). The deceleration in the stomach's food volume (V_S) is caused by a negative feedback by acceleration in the egestion rate ($\lambda_{out} \text{ g min}^{-1} \text{ g}^{-1} V_S$) associated with increased digesta volume in the stomach ($\lambda_{out} = 0.015 \text{ g min}^{-1} \text{ g}^{-1} V_S$, see Fig. 2), and can be observed by comparison to the V_{out} curve, the accumulated digesta volume egested. The residual digesta volume residing in the stomach at the end of the ingestion phase is termed V_i , and V_R at the end of the egestion phase. This example is terminated at an empirically chosen $V_R = 10$ g, 118.7 min from the start of feeding.

FIG. 2. Stomach egestion rate (λ_{out} , $\text{g min}^{-1} \text{ g}^{-1} M_m$) in relation to ingested meal mass (M_m , g). Regression (through the origin): $\lambda_{out} = 0.015 (\pm 0.0004 \text{ SE}) M_m$. ANOVA: $F_{1,16}=1338.5$; $P<0.00001$; $R^2=98.9\%$; $\text{SEE}=0.600$. *Open circles*: Group 1 (non-absorptive, small meal); *open squares*: Group 2 (absorptive, small meal); *filled circles*: Group 3 (non-absorptive, large meal); and *filled squares*: Group 4 (absorptive, large meal).

FIG. 3. (A) Daily number of foraging trips per parent (N_t), and corresponding (B) daily energy expenditure (DEE, kJ/d), in relation to the number of inter-diving bouts per foraging trip (N_{IDB}), while remaining in energy balance. This example illustrates the effect of N_{IDB} on time-energy budgets (see also Fig. 4), through change in the egestion rate (λ_{out}). The foraging distance (R_F) is 35 km (as in Látrabjarg, Iceland 1998), using ‘estimated’ flight and diving metabolic rates (140% of allometrically predicted, see text), and the results are evaluated for three feeding rates (λ_{in} : 70; 90; 110 g/h). The highest N_{IDB} possible while remaining in energy balance, and without incurring a large increase in DEE (shown by arrows, see text), was used in all subsequent foraging trip frequency analysis (see also Fig. 4). The mean observed number of inter-diving bouts per trip by instrumented razorbill parents in Látrabjarg, Iceland 1998, was 6.6 (Table 6). The potential maximal energy expenditure ceiling (4xBMR, 1308 kJ/d) is presented with a horizontal broken line.

FIG. 4. Energy acquisition per foraging trip (DEE/ N_t) as a function of inter-diving bout number (N_{IDB}) per foraging trip. The conditions are otherwise identical to as in Fig. 3. The mean observed N_{IDB} per trip, by instrumented razorbill parents in Látrabjarg, Iceland 1998, was 6.6 (Table 6).

FIG. 5. The change in the daily: (A) time budget; and (B) energy budget; in response to number of inter-diving bouts per foraging trip (N_{IDB}). In this example the foraging distance (R_F) is 35 km (the mean R_F in Látrabjarg, Iceland 1998), using ‘estimated’ flight and diving metabolic rates (140% of allometric prediction, see text), and feeding rate λ_{in}

= 90 g/h. The bars illustrate the activity-specific composition of one foraging trip-nest cycle. The trip-nest cycle duration initially (N_{IDB} : 1-4) lengthens rapidly with N_{IDB} , then (N_{IDB} : 5-7) the increase diminishes, and starts reducing when $N_{IDB} = 8$ (A). The energy budget (B) shows a parallel pattern, demonstrating that the change in swimming time, induced by N_{IDB} , accounts for almost all of the change in both time and energy budgets. This is because as the number of inter-diving and diving bouts increase, the stomach evacuation rate (λ_{out}) is reduced since less food is ingested per bout with shortening ingestion/diving bout duration.... This lengthens the time at sea, and correspondingly the nest time.

FIG. 6. Correspondence between the parental energy supply (EPR) and the chick's energy demand. Comparison of Razorbill daily foraging trip number (N_t , note that it is illustrated per parent), as a function of energy provisioning rate (EPR), and corresponding chick's body mass at nest departure (M_f) as a function of chick's daily metabolized energy (DME). EPR is the product of: $2N_t$; average meal mass (M_m); and average net food energy density (E_m , 4.69 kJ/g). M_m was assumed 8.0 g (EPR_{min}) or 11.4 g (EPR_{max}), see Table 2. Average DME and peak DME are calculated as functions of M_f , following Weathers (1996). The apparent minimum N_t needed to produce $M_f = 165$ g is 1.8 trips d^{-1} parent $^{-1}$ ($M_m = 11.4$ g, AFP). The apparent maximum is 4.3 trips d^{-1} parent $^{-1}$ (AFP) corresponding to $M_f = 214$ g ($M_m = 8.0$ g, see Table 2). Above this limit the parents can supply a larger chick. The N_t needed to raise a chick to adult mass (619 g) by an alternately foraging parent, bringing back 8.0 g M_m is 10.2 trips d^{-1} parent $^{-1}$ (PDME = 752.5 kJ/d), or 7.1 trips d^{-1} parent $^{-1}$ (ADME = 522.2 kJ/d). When the parents bring back

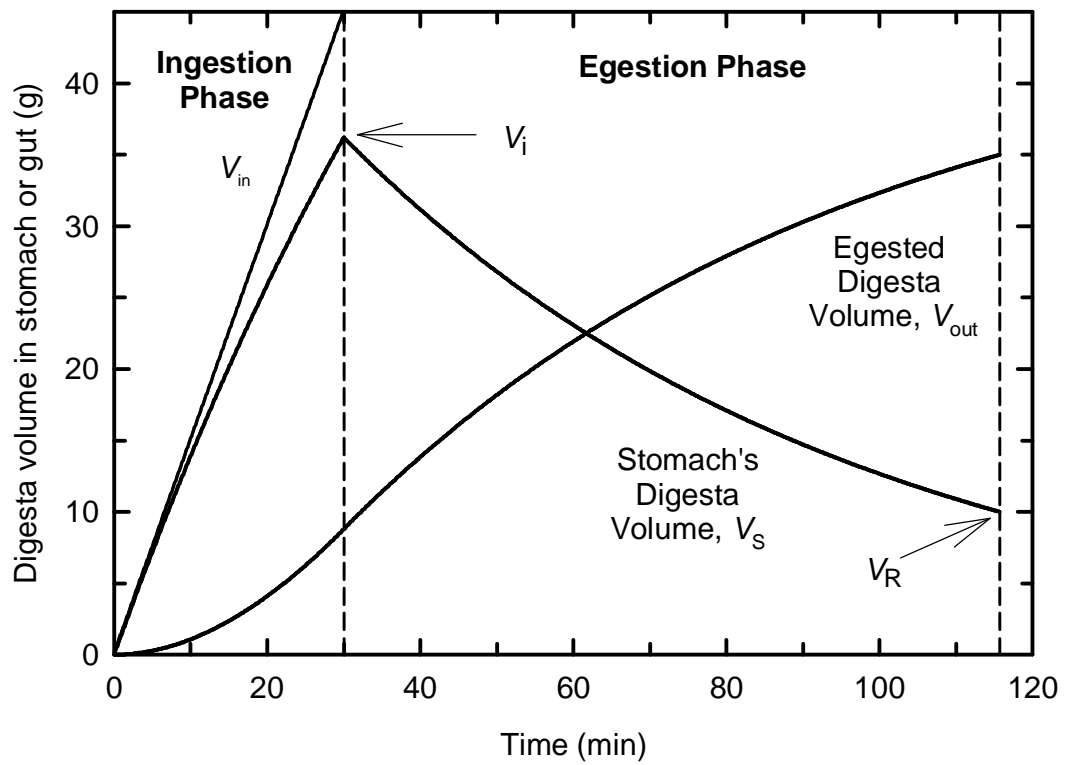
11.4 g M_m , the corresponding N_t is 7.1 trips d^{-1} parent $^{-1}$ (PDME), or 5.0 trips d^{-1} parent $^{-1}$ (ADME).

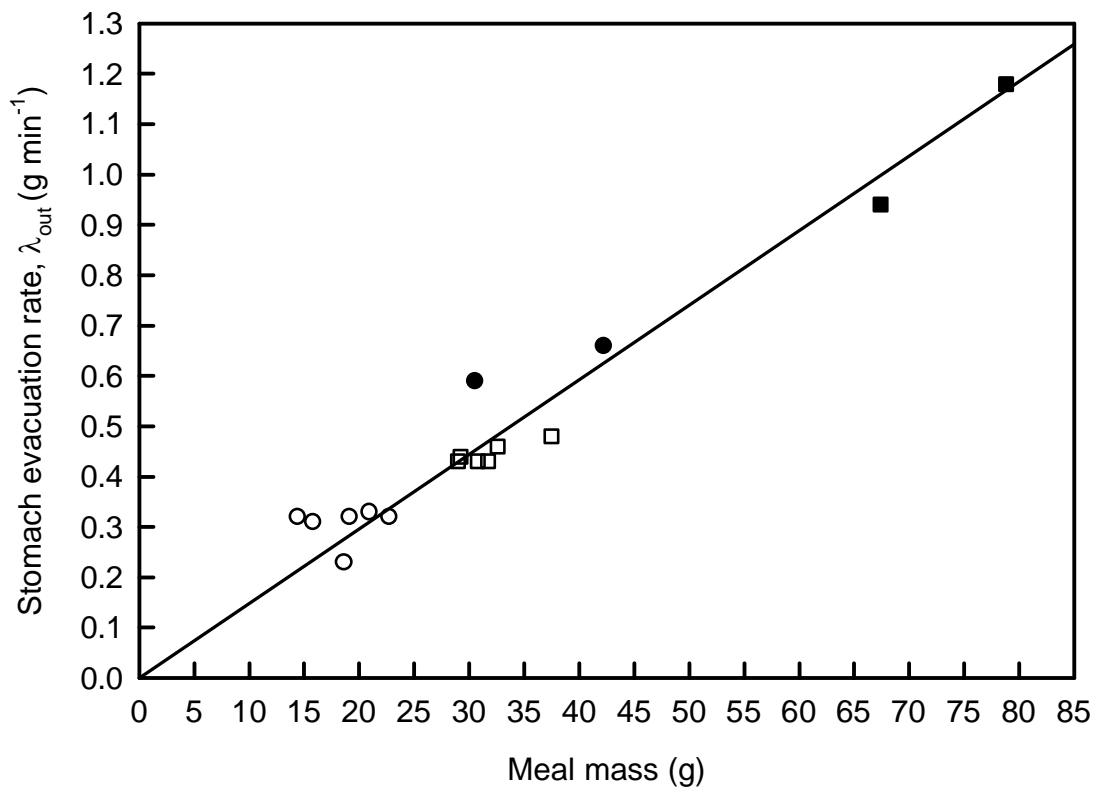
FIG. 7. Daily number of feeding trips per parent (N_t) of *alternate foraging parents* (AFP) in energy balance with respect to foraging range (R_F). Three feeding rates λ_{in} : 70; 90; and 110 g/h, are examined, and with respect to three combinations (A-C) of diving- (MR_D) and flight- (MR_F) metabolic rates. (A) $MR_D = 45.1$, $MR_F = 141.4$ kJ/h. (B) $MR_D = 63.1$, $MR_F = 197.5$ kJ/h. (C) $MR_D = 160.2$, $MR_F = 240.7$ kJ/h. The average R_F from Látrabjarg, Iceland (1998) was 35.0 ± 20.9 km, but 6.8 (day) and 18.7 km (night), in the small Græsholmen colony, Baltic Sea. Apparent minimal (1.8) and maximal (4.3) N_t are shown with horizontal broken lines (see Fig. 5).

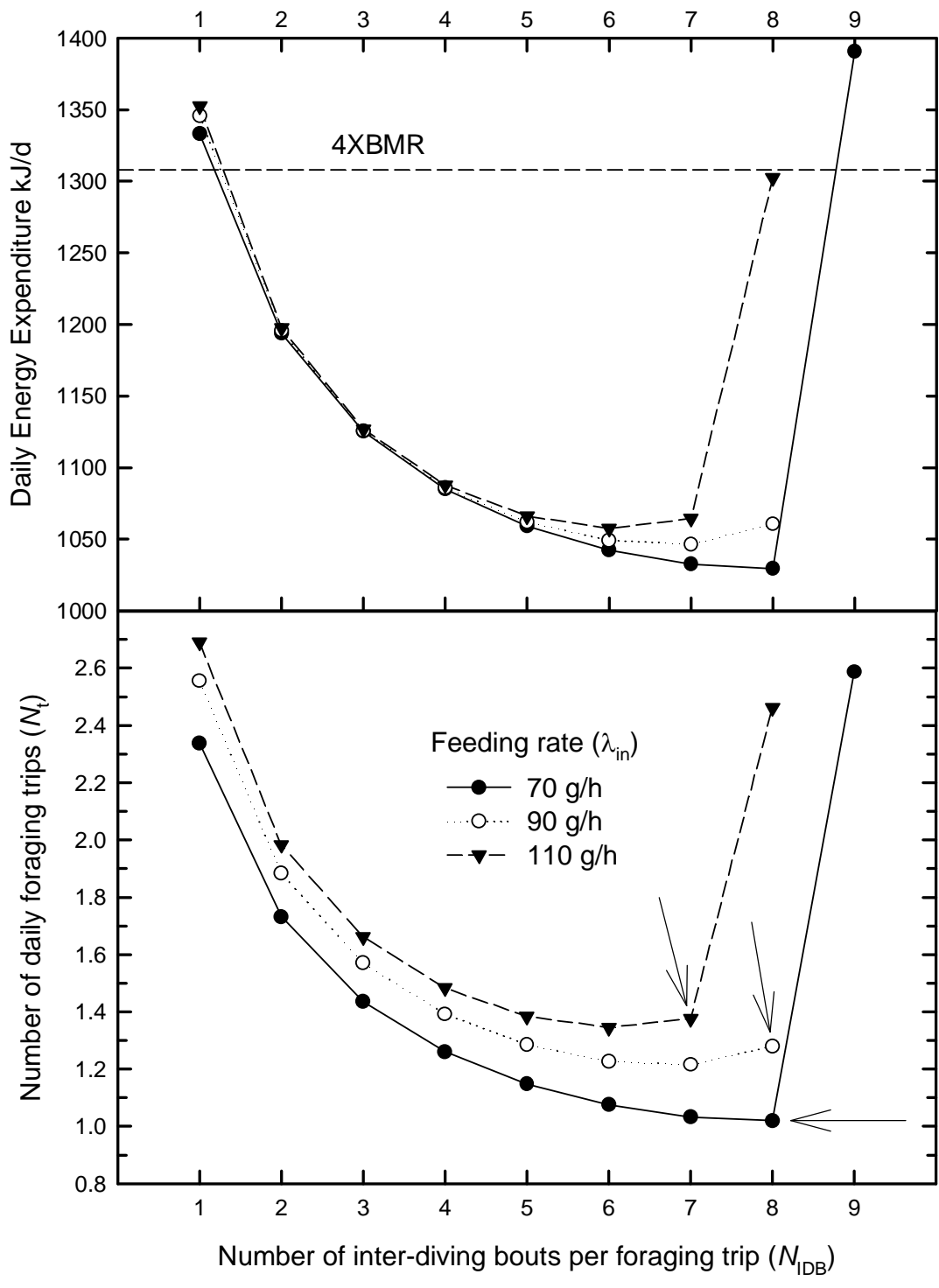
FIG. 8. Daily number of feeding trips per parent (N_t) of *simultaneously foraging parents* (SFP) in energy balance with respect to maximum foraging range (R_F). Three feeding rates (λ_{in} : 70; 90; and 110 g/h), are examined, with respect to three combinations (A-C) of diving- (MR_D) and flight- (MR_F) metabolic rates. (A) $MR_D = 45.1$, $MR_F = 141.4$ kJ/h. (B) $MR_D = 63.1$, $MR_F = 197.5$ kJ/h. (C) $MR_D = 160.2$, $MR_F = 240.7$ kJ/h. The average R_F from Látrabjarg, Iceland (1998) was 35.0 ± 20.9 km, but 6.8 (day) and 18.7 km (night), in the small Græsholmen colony, Baltic Sea. Apparent minimal (1.8) and maximal (4.3) N_t are shown with horizontal broken lines (see Fig. 5).

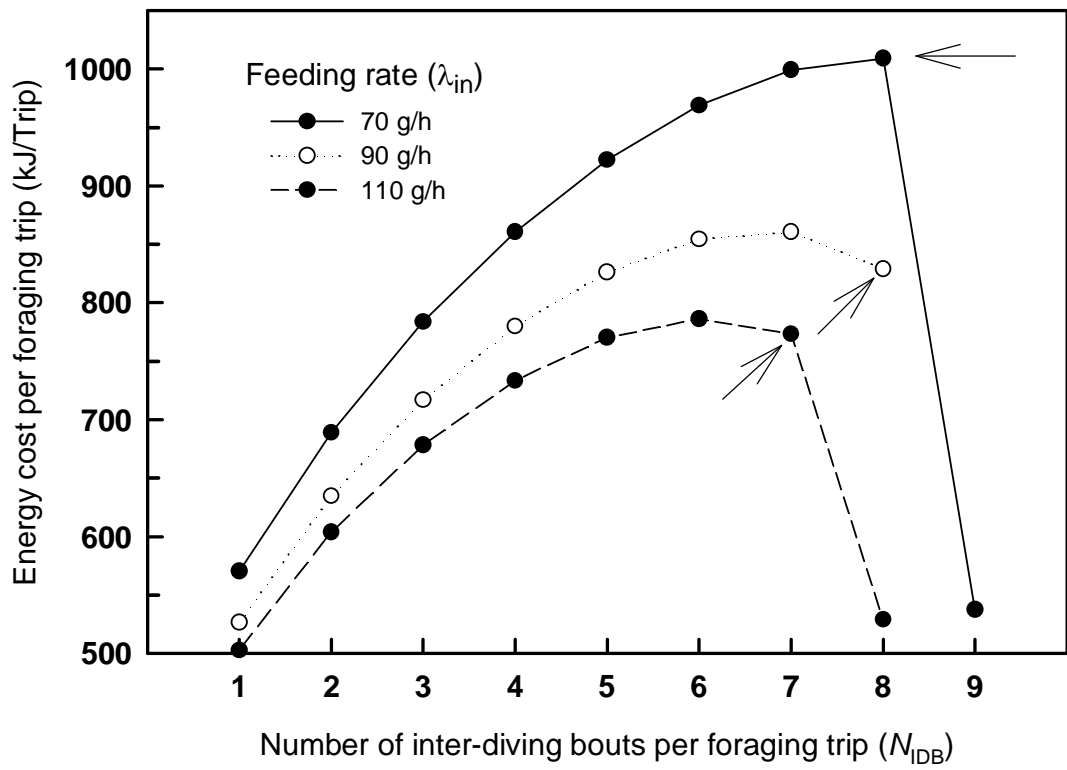
FIG. 9. Change in parental body mass (A) during incubation, and (B) during the nestling period in Látrabjarg, Iceland 1998. Each record represents one bird (no replicates), prior

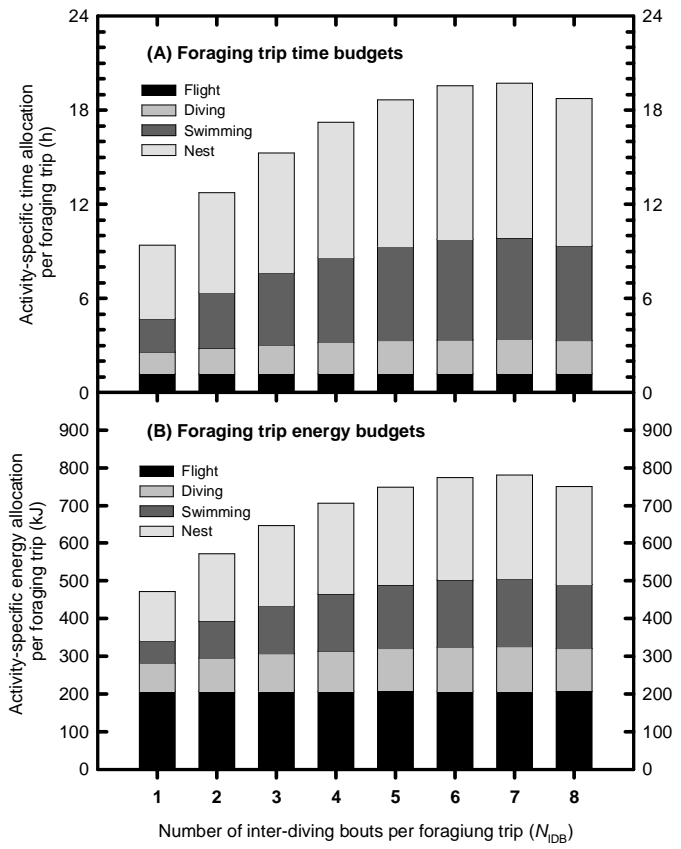
to any manipulations. (A) The average daily body mass gain (g/d), regression: $M_b = 612.7 (\pm 32.7 \text{ SE}) + 5.0 (\pm 4.1 \text{ SE}) \text{ date}$; $F_{1,10} = 1.463$; $P = 0.25$. (B) The average daily body mass loss (-g/d, physiological stress rate) as a function of chick age (d), regression: $M_b = 649.9 (\pm 10.6 \text{ SE}) - 5.94 (1.81 \text{ SE}) \text{ chick age}$. ANOVA: $F_{1,36} = 10.778$; $P < 0.0023$; $R^2 = 23\%$; SEE = 32.86.

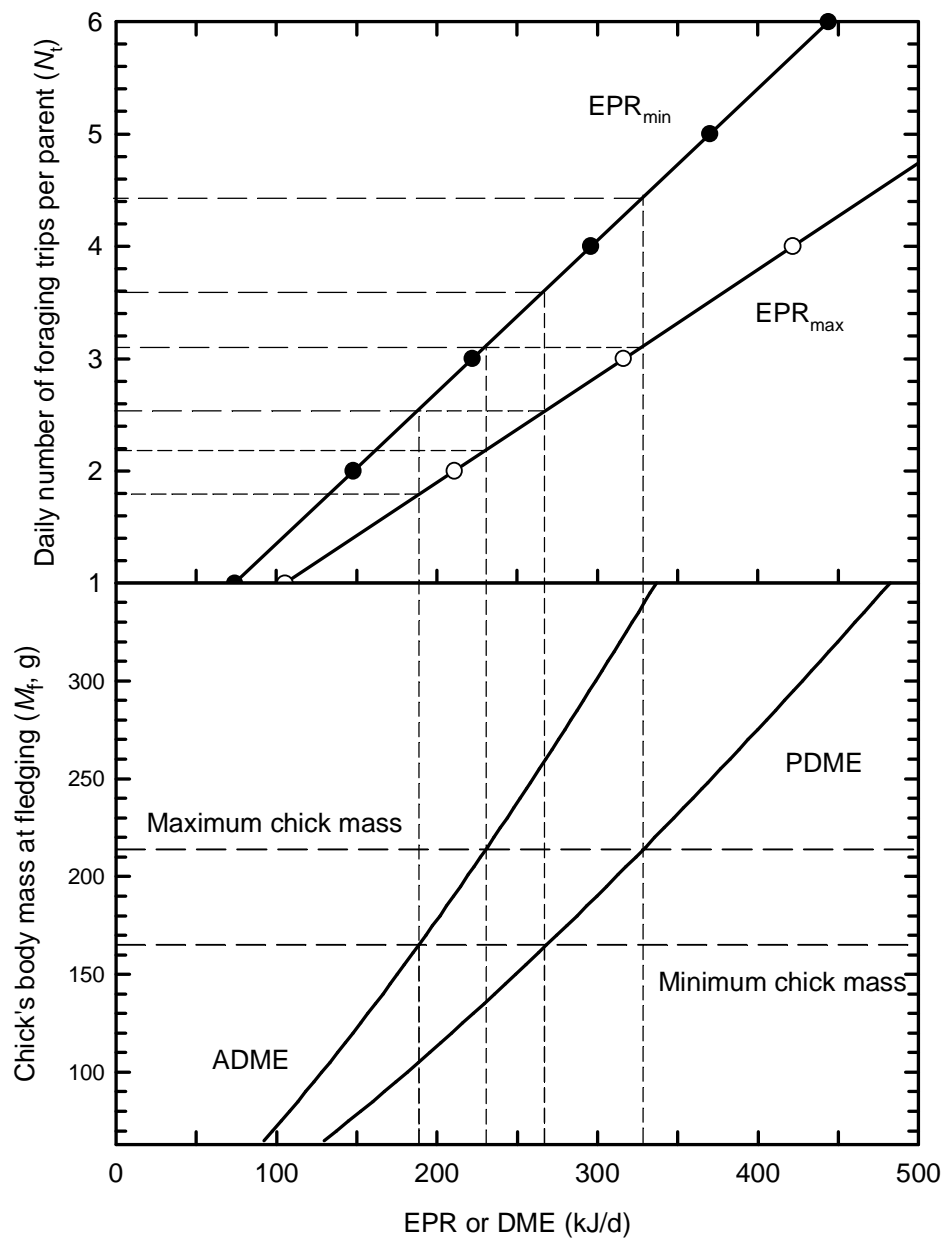


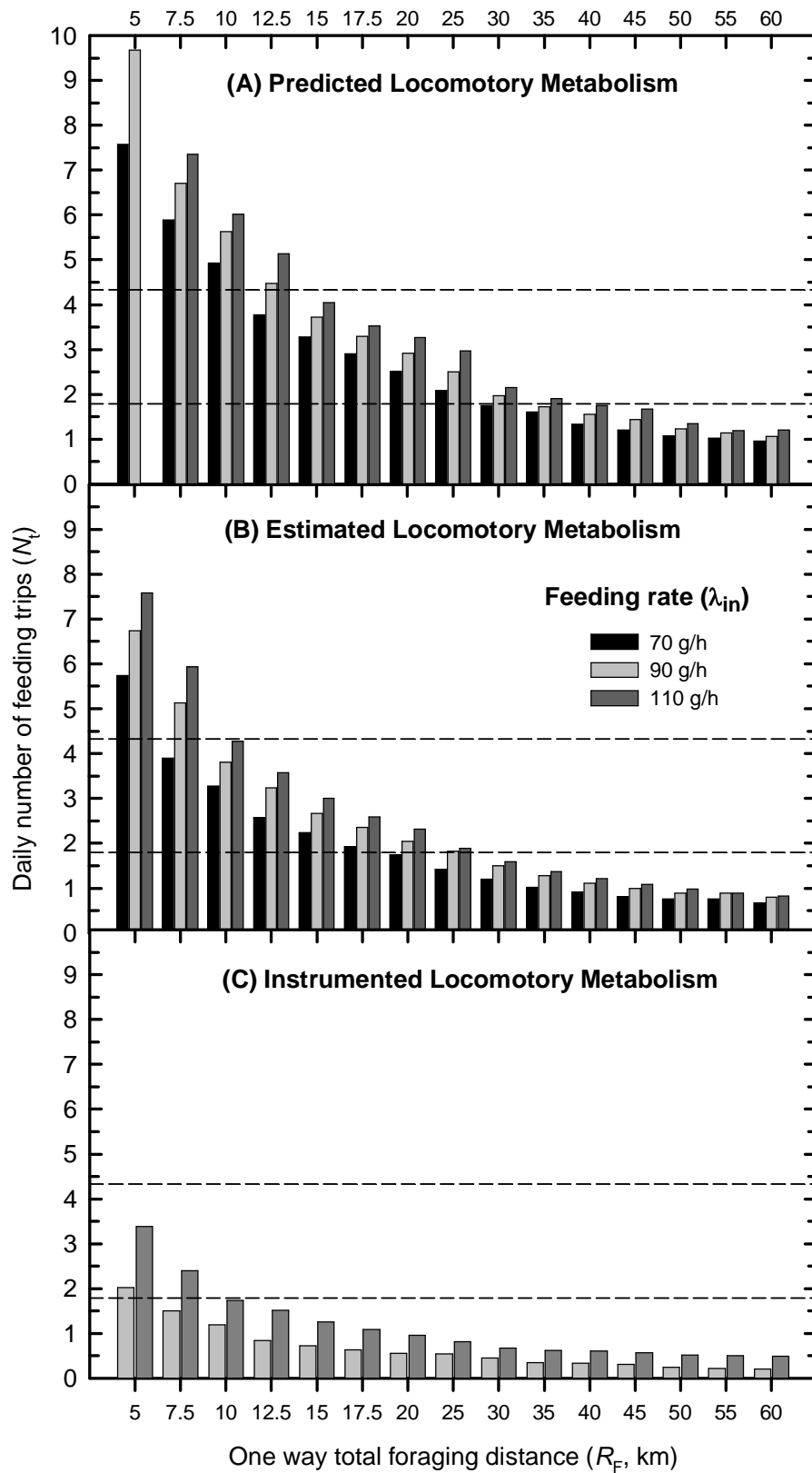


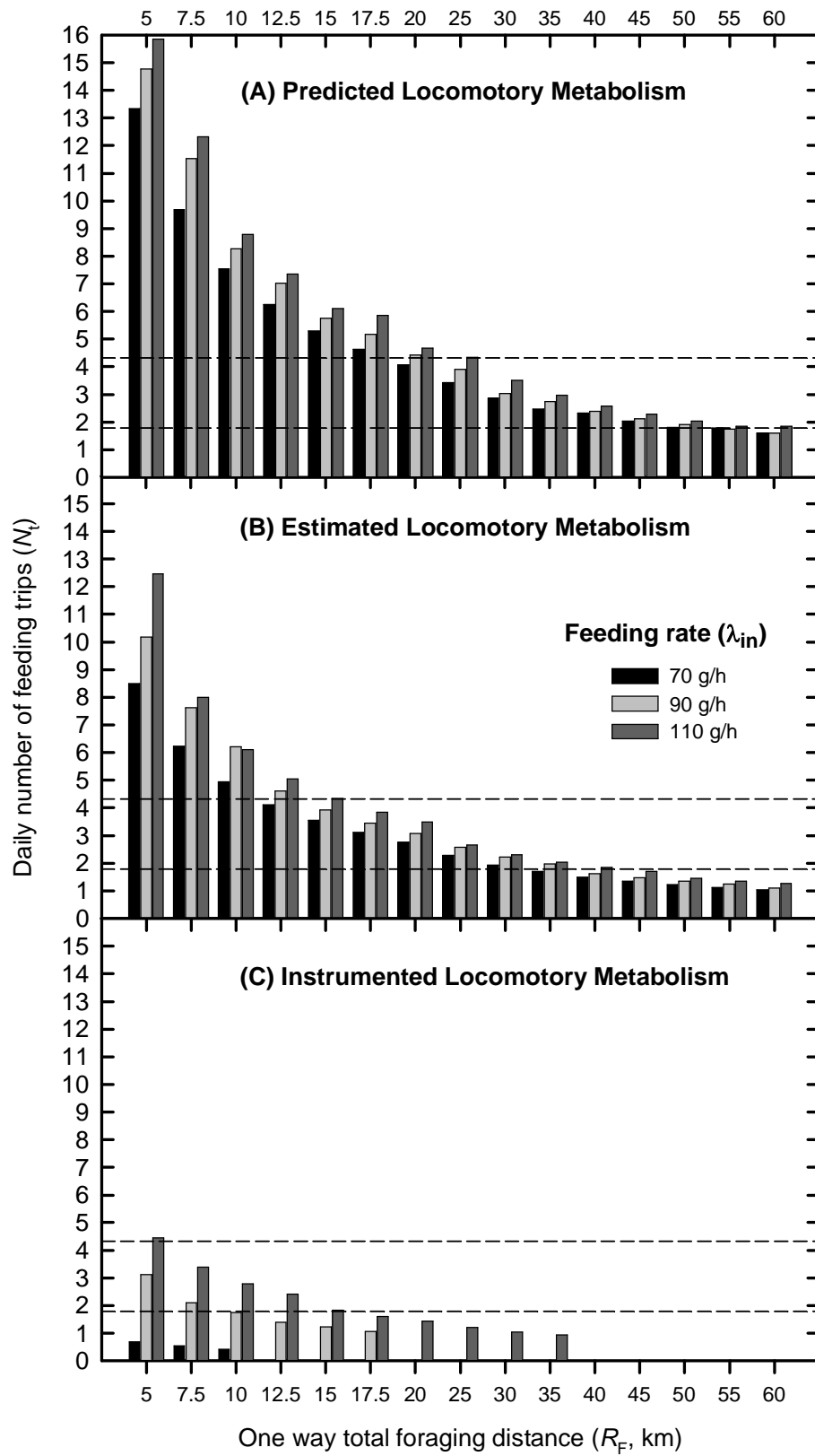


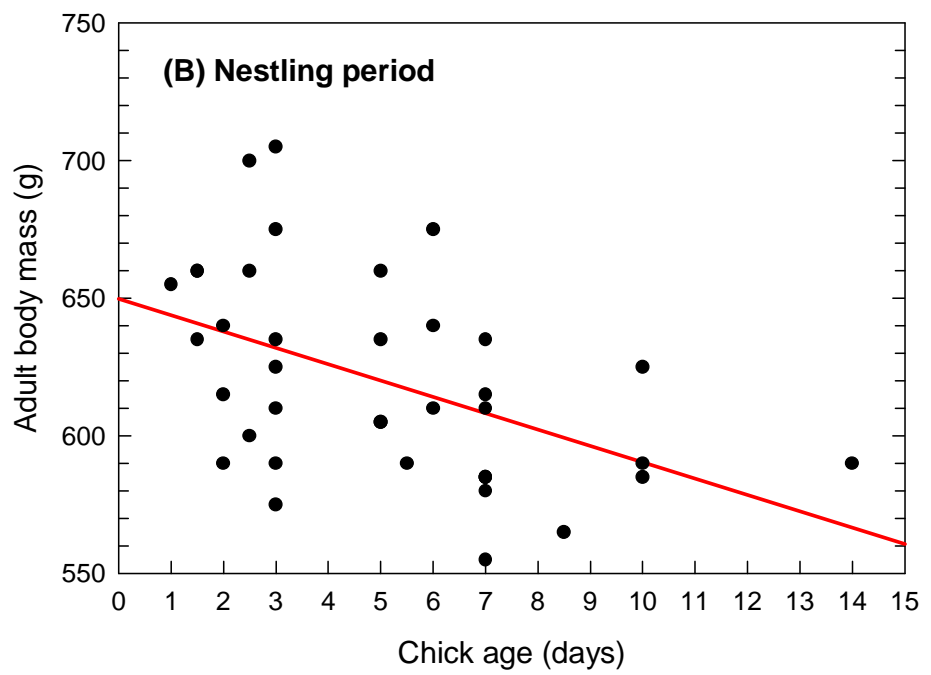
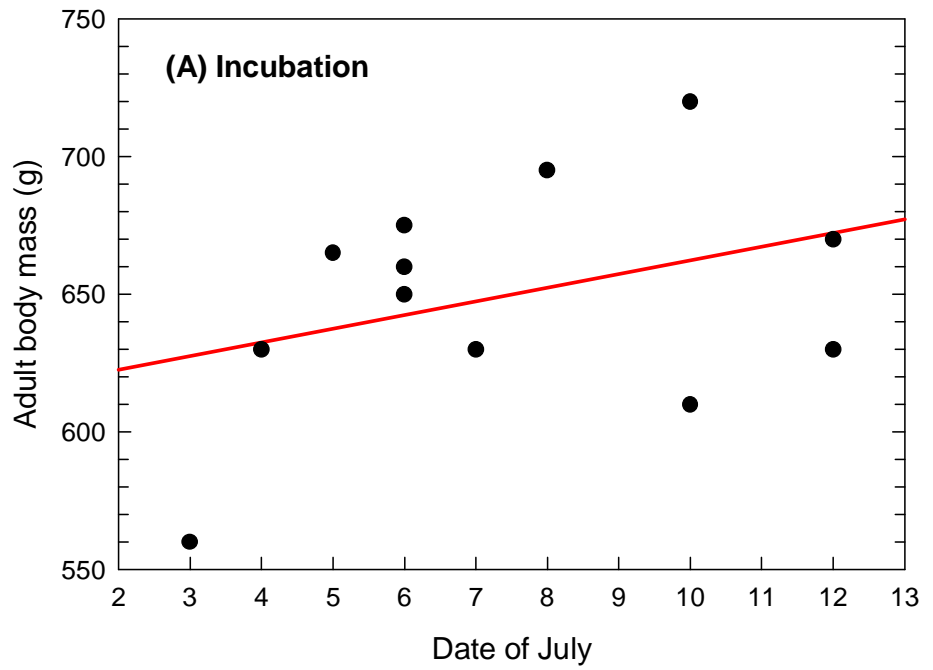












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**FORAGING BY DEEP DIVING BIRDS IS NOT CONSTRAINED
BY AN AEROBIC DIVING LIMIT: A MODEL OF
DEPTH-DEPENDENT DIVING METABOLIC RATE**

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foraging constraints, penguins.

RUNNING HEAD: Avian depth-dependent diving metabolic rate

ABSTRACT: The theoretical aerobic diving limit (tADL) specifies the duration of a dive after which oxygen reserves available for diving are depleted. tADL has been calculated by dividing the available oxygen stores by the diving metabolic rate (DMR). Contrary to diving mammals, most diving birds examined to date exceed the tADL by a large margin. This discrepancy between observation and theory has engendered two alternative explanations suggesting that dive duration is extended either (1) anaerobically or (2) by depressing aerobic metabolism. Current formulations of tADL uncritically assume that DMR is independent of depth. However, diving birds differ from other vertebrate divers by having a larger respiratory system volume and by retaining air in their plumage while diving, thereby elevating buoyancy. Because air compresses with depth, diving power requirement decreases with depth. Following this principle, we modeled DMR to depth for Adelie and little penguins and reformulated the tADL accordingly. The model's results suggest that fewer than ~5% of natural dives by Adelie penguins exceed the reformulated tADL(d), or maximal aerobic depth, and none in the more buoyant little penguin. These data suggest that, for both small and large species, deep diving birds rarely if ever exceed tADL(d).

The most important aspects of the physiological and metabolic processes dictating diving in air-breathing, homeothermic endotherms are the oxygen storage capacity and the rate of oxygen consumption. The combination of these two factors is summarized descriptively by the aerobic diving limit (ADL). The ADL is defined as the maximum period of breath-holding that does not result in an increase in blood lactic acid concentration during or after a dive (Kooyman et al. 1983). If dives consistently exceeded ADL, the accumulation of lactic acid would result in progressive, exponential lengthening of the post-dive pauses or, depending on the extent, a suspension of diving until normal lactate levels were reestablished (Kooyman 1989).

Post-diving plasma lactate levels of birds have only been measured twice, in both instances in the laboratory (Ponganis et al. 1997; Stephenson et al. 1992), and because of the practical difficulty of measurement, especially in relatively small-bodied animals like birds, the situation is not likely to improve much. This has led to the substitution in diving studies of a 'calculated' ADL or cADL, also termed 'theoretical' or tADL in the literature (Kooyman and Kooyman 1995), the latter notation being followed here. tADL is the time when the available oxygen reserves are depleted, and it is calculated by dividing the available oxygen stores (mL O₂) by the diving metabolic rate (DMR, mL O₂ s⁻¹). In many studies, observed dive times exceed the tADL, sometimes by a considerable amount. Most notable is the ability of Weddell seals to dive three times longer than their measured ADL determined by post-dive lactate levels. The heart and central nervous system, which are sensitive to low oxygen levels, must therefore be supplied for longer than other tissues, implying that ADL is not really an abrupt phenomenon (as simplistically implied in the tADL definition), but a transitional process. A critical

assumption in the calculation of tADL is that DMR is constant and independent of depth. This paper demonstrates for positively buoyant birds that DMR decreases with depth, because of reduced buoyancy resulting from compression of the air in the respiratory system and feathers, and that depth-dependent DMR largely explains the discrepancy between observed (bADL) and expected tADL.

Most species of avian divers that have been examined, penguins in particular, consistently surpass the tADL, commonly by a wide margin (Boyd and Croxall 1996; Chappell et al. 1993a; Chappell et al. 1993b; Croll 1990; Croll et al. 1992; Croll and McLaren 1993; Kooyman 1975; Kooyman 1989; Kooyman et al. 1992; Kooyman and Kooyman 1995; Wilson 1995). However, in most of these studies, the post-dive pauses that follow dives surpassing the tADL in duration do not exceed those following “aerobic” dives ($<tADL$) and do not lengthen over a series of dives, as expected for dives surpassing the ADL. Exceptions occur only after rare dives exceeding the tADL by a large margin (e.g., Croll and McLaren 1993; Ydenberg and Guillemette 1991). This discrepancy between observation and tADL has generated a behavioral definition of the ADL (bADL), which assumes that only those dives followed by extended post-dive pauses exceed the ADL (Kooyman and Kooyman 1995).

The common absence of extended pauses after dives that greatly exceed tADL, and the large discrepancy between the tADL and bADL when post-dive pauses do lengthen (e.g., Culik et al. 1998; Luna-Jorquera and Culik 2000), has engendered two currently competing explanations (Boyd 1997). The first explanation states that dive duration is anaerobically extended. The second states that dive duration is extended by depressing aerobic metabolism (Boyd 1997; Kooyman 1989) by reducing blood flow to peripheral

tissues (Stephenson and Jones 1992), possibly supplemented by localized hypothermia (Bevan et al. 1997; Handrich et al. 1997; Wilson and Grémillet 1996). This hypometabolism hypothesis is generally considered better supported by a diverse body of evidence (Boyd 1997; Butler and Jones 1997; Davis and Guderley 1987; Davis and Guderley 1990; Kovacs and Meyers 2000; Mill and Baldwin 1983).

A neglected third possibility is that the tADL assumptions are incorrect (Boyd and Croxall 1996), because oxygen reserves are underestimated, diving metabolic rate is overestimated, or both. Although all components of oxygen storage capacity have been evaluated for only a few avian species, the measurements and assumptions involved are nevertheless considered fairly robust (Kooyman 1989; but see Ponganis et al. 1993). In contrast, DMR has never been measured directly in free-ranging birds. The DMR values used in tADL calculations come from laboratory measurements (Baudinette and Gill 1985; Butler and Woakes 1984; Croll and McLaren 1993; Culik et al. 1996; Culik et al. 1994b; Hui 1988; Luna-Jorquera and Culik 2000) and from time-partitioned field metabolic rates (FMR) (Chappell et al. 1993a; Kooyman et al. 1992; Nagy et al. 1984). Excluding an outlier from Nagy et al. (1984) these DMR values lie within the range of 2-4 times the SMR (Kooyman 1989). No laboratory study to date has measured the oxygen consumption of a diving bird at a depth greater than a few meters. Furthermore, the time-partitioned FMR studies cited above equate 'FMR at sea' with DMR. The 'FMR at sea' results from time allocations to various activities (diving, swimming, resting, and flying) that differ in their average metabolic costs, and therefore cannot represent DMR by definition, a point also made by Bevan et al. (1995).

The assumption that DMR is constant and independent of depth has received relatively little discussion in the literature (but see Clowater and Burger 1994; Wilson et al. 1992). It is well known, however, that birds differ from mammals in having an approximately three times larger respiratory system air volume (at one kg) (Calder 1984), in addition to the plumage air, and that buoyancy is far more important than drag in determining the energy cost of diving in shallow divers (Lovvorn 1991; Stephenson et al. 1989a). The theoretical consequences of this ‘air cargo’ on diving metabolic rate at depth are examined in this paper to determine whether they explain why birds systematically exceed conventionally calculated tADL. This approach is based on evaluating the reduction in air volume with depth, which follows Boyle’s Law (Davis et al. 2001; Nowacek et al. 2001; Skrovan et al. 1999; Webb et al. 1998; Williams et al. 2000; Wilson et al. 1992). Reduced air volume decreases both buoyancy and body surface area at depth, the latter determining parasite body drag. Depth-dependent body volume (and surface) are used here to calculate depth-dependent DMR: $DMR(d)$, which in turn is used to calculate a depth-dependent ADL: $tADL(d)$. Variables and parameters are compiled from the literature for the best-known avian diver in this context, the Adelie Penguin (*Pygoscelis adeliae*). The model’s results show that the magnitude of $DMR(d)$ reduction is sufficient alone, i.e., without taking hypometabolism into account, to reconcile observed dive times with the tADL. Accordingly, fewer than ~4% of dives by Adelie Penguins (field data from Chappell et al. 1993a) are likely to be anaerobic. To expand the scope of the model with respect to body size, an identical model of the more buoyant little penguin (*Eudyptula minor*) was constructed and compared to field data (Bethge et al. 1997; Gales et al. 1990). No dives by little penguins are likely to be anaerobic.

Basic Assumptions and Parameters

Body Volume. The air volume of diving birds is composed of plumage air (V_P) and respiratory system volume (V_R) (Calder 1984). It is assumed that V_R is augmented from the anecdotally observed habit of deep-diving birds to dive after inspiration (Croll et al. 1992; Kooyman et al. 1971; Stephenson et al. 1989b), but see the “*Discussion*” for the case of shallow divers/diving.

The total volume of an Adelie Penguin at the surface: $V_O = V_b + V_R + V_P$ (see eq. 6), where V_b is solid body volume. $V_b = M_b/\tau$, where τ is solid body density, 1065 kg m^{-3} (Stephenson 1993). Thus, $V_b = 3.756 \times 10^{-3} \text{ m}^3$. V_R is calculated by eq. 1 (Calder 1984), where M_b is body mass.

$$V_R = 1.55 \times 10^{-4} M_b^{0.92} = 5.55 \times 10^{-4} \text{ m}^3, \quad (1)$$

V_P at the surface was calculated by an ‘ellipsoid volume subtraction.’ The method assumes that the bird’s ‘inner core’ volume (V_I) is roughly ellipsoid shaped, the volume of which is,

$$V = (4/3)\pi \mathbf{a} \mathbf{b}^2, \quad (2)$$

where \mathbf{a} is the semimajor axis (m), and \mathbf{b} is the semiminor axis (m). The ‘inner core’ constitutes the solid body volume and the total respiratory volume (m^3),

$$V_I = V_b + V_R = 4.324 \times 10^{-3} \text{ m}^3 \quad (3)$$

The outer core’s semiminor axis (\mathbf{b}_O) at the sea surface is the radius of the bird’s thickest cross sectional area, called ‘frontal body area’ A_f (0.02083 m^2) (Bannasch 1995),

$$\mathbf{b}_O = \sqrt{A_f / \pi} = 0.0814 \text{ m} \quad (4)$$

Ptilosuppression and water pressure were taken into account by assuming that the plumage layer thickness (f) is 5×10^{-3} m when just submerged as found by Kooyman et al. (1973). The outer core's semiminor axis less the plumage layer thickness gives the inner core semiminor axis (\mathbf{b}_I), $\mathbf{b}_I = \mathbf{b}_O - f$, or 0.0765 m. The inner core's semimajor axis at the surface, \mathbf{a}_I ,

$$\mathbf{a}_I = (3/4)(V_I / \pi \mathbf{b}_I^2) = 0.1765\text{m} \quad (5)$$

The outer core's semimajor axis (\mathbf{a}_O), $\mathbf{a}_O = \mathbf{a}_I + f$, or 0.1812 m. The outer core, or total volume (V_O), which incorporates both the inner core and the plumage volume,

$$V_O = V_I + V_P. \quad (6)$$

V_O was calculated using the outer core semi-axes in eq. 2: $V_O = 5.034 \times 10^{-3} \text{ m}^3$. The V_P was found by subtraction of the 'inner' ellipsoid from the 'outer' ellipsoid,

$$V_P = V_O - V_I = 7.23 \times 10^{-4} \text{ m}^3. \quad (7)$$

Because V_P has proven difficult to measure accurately (Stephenson 1993), the calculated V_P was compared to an empirical regression equation (Lovvorn and Jones 1991) derived from duck (Anatidae) V_P measurements (Dehner 1946; Lovvorn and Jones 1991). The equation $V_P = 0.2478 + 0.123 M_b$ for ducks, gives $7.40 \times 10^{-4} \text{ m}^3$ for the Adélie penguin, which is only 2.3% higher than the value of V_P estimated above. It should be noted that largest body mass used to produce the equation for ducks was 1.2 kg, and so the Adélie penguin data point represents roughly a three-fold extrapolation.

In the only measurement to date of the loss of air trapped in plumage arises from an ingenious experiment by Stephenson (1995), in which approximately half the air escaped the plumage of lesser scaup (*Aythya affinis*) during diving. Assuming no loss of air is

therefore conservative because any reduction in air volume (including underwater exhalation) will lower buoyancy, parasite drag, and correspondingly the DMR(d).

Body Volume at Depth. The change in V_b resulting from hydrostatic compression with depth follows Archimedes Principle and Boyle's Law (the product of gas volume and pressure is a constant). Assuming that no gas is lost during a dive, the gas volume decreases as an inverse hyperbolic function of depth, affecting the total body volume,

$$V(d) = \frac{P_s(V_R + V_P)}{P_s + P_s \left(d / \left(\frac{10329.561}{\rho} \right) \right)} + V_b, \quad (8)$$

where P_s is atmospheric pressure at the surface (101.3 kPa), ρ is seawater density (kg m^{-3}), the constant is one standard atmosphere (ATM, kg m^{-2}), and d is depth (m).

Net Buoyancy at Depth. Net buoyant force at depth is the difference between the buoyant force (first term in eq. 9) and the gravitational force (the second term),

$$B_{\text{net}}(d) = \rho g V(d) - g M_b. \quad (9)$$

Frontal Body Area at Depth. A_f is the 'area of reference' to which parasite drag was compared by Bannasch (1995). Parasite drag will be scaled later with respect to change in A_f with depth, but the change in the reference area with depth is dealt with here first.

Total body volume at depth $V(d)$ can be written as the outer core ellipsoid volume at depth, $4/3 \pi \mathbf{a}_O(d) \mathbf{b}_O(d)^2$, where $\mathbf{a}_O(d)$ is the outer core's ellipsoid semimajor axis length at depth and $\mathbf{b}_O(d)$ is the corresponding semiminor axis length at depth. The change in $V(d)$ with pressure is assumed to be uniform in all three dimensions. Thus, the ratio between

$\mathbf{b}_O(d)$ and $\mathbf{a}_O(d)$ is constant at all depths and equal to the ratio in a just-submerged bird, $\mathbf{a}_O = 2.226\mathbf{b}_O$ (0.1812/0.0814). Body length is likely to change less than diameter with compression. Again, equal compression is a conservative assumption because if most of the change were in the minor axis, then the cross sectional area would decrease even faster with depth and reduce the buoyancy even more rapidly. The change in A_f as a function of depth,

$$A_f(d) = \pi \left(\sqrt[3]{\frac{V(d)}{(4/3)\pi 2.226}} \right)^2. \quad (10)$$

Basal Metabolic Rate (BMR). ‘On land’ was chosen to represent ‘baseline’ metabolism during diving: 3.6 W kg⁻¹ (Culik and Wilson 1991), or 14.4 W for a four kg Adelie Penguin. Metabolism in the peripheral tissues decreases during the dive, due to vasoconstriction and possibly cooling (Bevan et al. 1997; Boyd 1997; Handrich et al. 1997; Stephenson and Jones 1992). Thermal insulation is bound to decrease with depth as the body’s insulative airspaces are compressed, and heat loss by forced convection increases with swimming speed (Grémillet et al. 1998; Hind and Gurney 1997; Luna-Jorquera et al. 1997). Choosing BMR ‘on land,’ over the higher RMR ‘on water’ (see Bethge et al. 1997; Culik and Wilson 1991) is closer to the expected baseline metabolic rate while diving. We conservatively assumed no decrease in BMR with depth or dive duration.

Oxygen Reserves. Adelie penguin’s total O₂ reserves available for diving are 217 ml (Table 1), and for the little penguin they are 56.7 mL (Table 2). The calculation of the O₂ reserves follows Stephenson et al. (1989b), except when otherwise noted, and is given in

detail for Adelie penguin in Table 1. Differences in calculations for little penguin are itemized in ‘*Little Penguin Model.*’

Types of Diving Profiles. Diving birds exhibit a range of diving profiles, from square shaped ‘U’ (U) dives to ‘V’ shaped dives (V) (for diving profile definitions see Schreer et al. 2001). Four parameters describe all ‘simple’ dive profiles: maximum depth (d_{\max}), angle of descent, angle of ascent, and distance covered in the bottom phase.

The DMR(d) values of both V and U dive profiles are modeled here for Adelie penguin (but only the U profile for little penguin due to lack of information), since they represent the extremes in the diving profile spectrum. The U profile, characterized by vertical ascent and descent is the shortest distance to depth, and the least costly diving profile, to a given depth. The V profile is the opposite in terms of distance and cost to depth, the extent depending on the actual angles of descent and ascent. The angle of descent and ascent in V profiles are assumed identical here (Wilson 1995) and are referred to as the diving angle (α , °). The α exhibited by instrumented free diving Adelie Penguins is a linear positive function of the maximum depth attained in a dive (d_{\max} , Eq. 11) and is derived from fig. 6.8 in Wilson (1995).

$$\alpha(d_{\max}) = 6.667 + 0.782d_{\max}, \quad d_{\max} < 106\text{m}, \alpha > 0^\circ, d_{\max} > 106\text{m}, \alpha = 90^\circ. \quad (11)$$

When α is less than vertical, the bird travels a longer distance than the change in depth (Δd). The actual diving distance is the product of the depth change and the ratio of the diving speed (v) to the vertical speed $\Delta d v/v_v(\alpha(d_{\max}), v)$. Vertical velocity is a function of $\alpha(d_{\max}, v)$ and v ,

$$v_v(\alpha(d_{\max}), v) = d_{\max} / \left(d_{\max} / (\sin(\alpha(d_{\max}))) / v \right). \quad (12)$$

Because our goal is to model the ADL(d), the duration of the bottom phase is maximized for both diving profiles, the maximum duration limit being set by the available oxygen reserves. Except when diving to the maximum aerobic depth (d_{amax} , in which case the bottom time is zero), both profile types are configured to have a bottom phase.

The observed average diving speed (i.e., not horizontal ‘traveling’ speed) by Adelie Penguins is 1.5 m s^{-1} (Wilson 1995; Wilson et al. 2002). After this speed is reached at the end of the acceleration phase, we assume that it remains constant with depth for the sake of computational simplicity. This is true for non-feeding dives of Adelie penguins, but feeding dives are characterized by bursts of faster speeds (Wilson et al. 2002).

Little Penguin Model

In order to examine the applicability of the ADL to a broader range of body size, we evaluated a model for the 1.2 kg little penguin. The little penguin is an ideal candidate, since it is the smallest penguin species, but especially because it has been characterized to have the lowest biochemical and histochemical ‘anaerobic capacity’ of penguins (Baldwin 1988; Baldwin et al. 1984; Mill and Baldwin 1983).

The little penguin’s metabolic input, and all metabolic output parameters are compiled as in the Adelie penguin model, and multiplied by the net power efficiency (E_{net}) estimated from identical canal-respirometry data for the little penguin by Bethge et al. (1997), provided in Table 3 (see ‘*Net Power Efficiency*’). The general methodological outline for derived parameters follows the ‘*Basic Parameters and Assumptions*,’ and

references therein. Any differences in calculation procedures for basic parameters in the little-penguin model are explained below and are itemized in Table 2.

We extrapolated the relationship between frontal area and parasite drag in Adelie and Gentoo penguins (see '*Parasite Power*'), to that of the little penguin. For example at 2.3 m s⁻¹ speed this extrapolation gives 0.53 N drag for the little penguin.

Since little penguin plumage thickness (f) is unknown, plumage volume was estimated with Lovvorn's and Jones' (1991) regression equation: $V_P = 2.478 \times 10^{-4} + 1.232 \times 10^{-4}$ kg body mass, giving $V_P = 3.956 \times 10^{-4}$ m³ for a body mass of 1.2 kg.

Coincidentally, the estimated f (0.005 m) was the same as that found for the Adelie penguin by Kooyman et al. (1973). f was estimated by subtracting the lengths of 'inner core' and 'outer core' semiminor axes (eq. 4), each calculated from the frontal area and volume relationship (eq. 10): one based on the inner body core volume ($A_{f, \text{inner}} = 8.492 \times 10^{-2}$ m², $\mathbf{b}_I = 0.052$ m); and the other based on the outer body core volume ($\mathbf{b}_O = 0.057$ m).

A_f at the surface was estimated with eq. 10, using the total volume, and assuming that the little penguin has the same shape, that is, the ratio between the known \mathbf{b}_O and estimated \mathbf{a}_O axes, as in the Adelie penguin model ($\mathbf{a}_O/\mathbf{b}_O = 2.226$), $A_f = 1.0124 \times 10^{-2}$ m².

Quantitative data on little penguin diving profiles are unavailable, thus the modeled dives were assumed to be U-shaped, ($d_v = S_a$, and $v_v = v$, see later). The acceleration distance (S_a) was assumed to be 2.5 m (Wilson and Wilson 1995).

Average little penguin flipper length is 0.118 m (Williams 1995). Back width was estimated to be 0.068 m by assuming that the 'middle back' section has the same proportion of the wingspan (w) as in the Adelie penguin (28.9%), $w \sim 0.304$ m.

The results of five BMR studies on little penguins vary considerably, between 3.12-4.93 W kg⁻¹ (Nicol et al. 1989). Four of these studies were done by C. D. Stahel and S. C. Nicol and coworkers, who suggested that seasonal variation might contribute to this variability. Their lowest BMR measurement (3.3±0.70 W kg⁻¹) is indistinguishable from 3.12±0.1 W kg⁻¹ obtained by Baudinette et al. (1986). This BMR measurement was chosen to represent the little penguin baseline metabolism during diving.

The blood oxygen reserve calculation followed the outline in Table 1. Blood volume was assumed to be the same fraction of body mass as in the Adelie penguin (10.15%, Table 1). Little penguin mean hemoglobin blood concentration is 0.138 g Hb mL⁻¹ (Nicol et al. 1988), which is 73.8% of that of the Adelie penguin (Table 1), and myoglobin percentage of wet muscle mass is 2.8% (Baldwin et al. 1984), which is 77.8% of the value obtained for Adelie penguins (Table 1). Total blood oxygen is 18.8 mL, total muscle oxygen is 13.7 mL, and total pigment-bound oxygen 32.5 mL. Respiratory oxygen volume was estimated to be 24.2 mL, and the total oxygen volume available for diving was, $VO_{2T} = 56.7$ ml, or 87.1% of the Adelie penguin's mass-specific total oxygen reserve.

Components of the Depth-Dependent Diving Metabolic Rate Model

The approach taken here combines classical aeronautical theory (Pennycuick 1975; 1989), and direct laboratory measurements of parasite drag (Bannasch 1995), or extrapolations of the latter, to evaluate the components of mechanical power output.

Metabolic power input from both species was obtained by using diving respirometry data and estimated net aerobic power efficiencies (E_{net}) obtained in artificial canals (Bethge et al. 1997; Culik et al. 1994b). E_{net} is commonly calculated as the product of muscular (or aerobic, η_a) and mechanical (or propulsion, η_m) efficiencies (Blake 1991; Oehme and Bannasch 1989; Stephenson et al. 1989a). Muscular efficiency is the conversion rate of chemical energy to kinetic energy, and mechanic efficiency is the translation of muscle work to propulsive work. The product of the total mechanical power output and the inverse of E_{net} gives the metabolic power input needed to meet the required mechanical power output to depth, or DMR(d).

When diving horizontally at constant speed, thrust equals drag, and ‘negative lift’ equals positive buoyancy. Drag is composed of five components. First, profile drag (D_{pro}) is the ‘backward’ drag of the wings and is described here using the theory of Pennycuick (1975). Second, induced drag (D_{ind}) is a ‘negative lift’ force in both Adelie and little penguins’ cases, since they are both positively buoyant at depths less than the maximum aerobic depth attainable (d_{amax} , see Appendix B in the Internet version of this paper). Hence during descent, they have to produce ‘negative lift’ equal to the positive buoyancy. This is achieved by movement of water upward, the reverse of an airborne bird in flight forcing air downward, implementing Lanchester’s jet momentum theory of lift generation (Pennycuick 1989). Simply put, one can think of induced power as the power needed to sufficiently move water upwards to equal the buoyancy, in order to *remain* at depth. Third, parasite drag (D_{par}) is the frictional drag of the fuselage body. Direct measurements of parasite drag of wingless Adelie penguin (and other species) models from Bannasch (1995) are used here, after extrapolating them with regard to

species-specific, and depth-specific differences in frontal area, and correcting them for the difference in kinematic viscosity of fresh and salt water. Fourth, inertial drag is the ‘vertical’ resistance to flapping the wings, however in practice this drag cancels out and is not dealt with further (Pennycuick 1975; 1989). Fifth, the penguin has to produce metabolic power against buoyancy when descending, but when ascending this (then ‘negative’) power aids the ascent by reducing the metabolic power input required.

Mechanical power output to depth is the sum of the power components, for example while descending,

$$P_O(d, v) = P_{\text{pro}}(d) + P_{\text{ind}}(d, v) + kvP_{\text{par}}(d, v) + P_B(d) \quad (13)$$

The specifics of mechanical power output calculation depends on the phase of the dive, which are portrayed in ‘*DMR(d) Calculation Procedures.*’

Metabolic power input to depth at speed $P_I(d, v)$ equals the sum of BMR and the product of inverse net power efficiency (E_{net}) and mechanical power output to depth at speed $P_O(d, v)$,

$$P_I(d, v) = \frac{1}{K} \left(\left(\frac{1}{E_{\text{net}}} P_O(d, v) \right) + \text{BMR} \frac{\Delta d}{v_v(\alpha(d_{\text{max}}), v)} \right), \quad (14)$$

where the metabolic power input to depth (W) is converted into oxygen consumption (ml O₂) by multiplication with the inverse of K , the energy equivalent of one mL of oxygen ($K = 20.0832 \text{ J mL O}_2^{-1}$) (Schmidt-Nielsen 1997).

Net aerobic power efficiency (E_{net}), is calculated as the ratio of total mechanical power output (P_O) to metabolic power input (P_I) less BMR (Blake 1991),

$$E_{\text{net}} = \frac{P_o}{(P_1 - \text{BMR})}. \quad (15)$$

E_{net} was evaluated from average power input in a still-water canal (at assumed depth of 0.5 m), as measured by Culik et al. (1994b) for Adelie penguin (see also Culik et al. 1994a; Culik and Wilson 1991; Culik et al. 1991), and by Bethge et al. (1997) for little penguin (see also Nicol et al. 1989). The calculations are summarized in Table 3.

The bird both accelerates and decelerates during the measurement trial in the canal, and the average power requirements for the speed changes (including accelerational reaction) need to be subtracted from P_1 to obtain the net average power consumption of steady locomotion. We assume here that the E_{net} during speed change is the same as at a constant speed.

The cost of acceleration consists of two components, P_a (eq. 32) {check the numbers of these equations} the power needed to accelerate the body forward, and $P_1(d_v)$ (eq. 31), which is the cost of accelerating entrained water (Daniel 1984; Vogel 1994). The cost of deceleration likewise is composed of two components, the accelerational reaction of entrained water, and the body deceleration, which is assumed to be predominantly metabolically passive by ‘breaking,’ guessed to be one fourth of the acceleration power $P_q = 0.25P_a$ (eq. 16). E_{net} is relatively insensitive to this factor, it was reduced by 4.18% and 5.2% for Adelie and little penguins respectively, when P_q was reduced by 75% (the value used here). The other components, parasite power $P_{\text{par}}(0.5, v)$, induced power $P_{\text{ind}}(0.5)$, and profile power $P_{\text{pro}}(0.5, v)$, are calculated with eqq. 25, 21, 18 respectively.

E_{net} was calculated by iteration, since it occurs on both sides of the equal sign,

$$E_{\text{net}} = \frac{P_{\text{par}}(0.5, v) + P_{\text{ind}}(0.5) + P_{\text{pro}}(0.5, v)}{P_1 - \left(\frac{1}{E_{\text{net}}} \frac{P_a + 2P_r + P_q}{T_r} \right)} - \text{BMR}, \quad (17)$$

where T_r is the time a penguin takes to swim the canal length. For Adelie penguins the canal length was 21 m, speed 1.5 m s^{-1} , and for little penguins the canal length was 18 m, and assumed speed 1.8 m s^{-1} (extrapolated). E_{net} for Adelie and little penguins were 0.137 and 0.147, respectively (Table 3).

E_{net} is, by definition, sensitive to changes in the components of mechanical power output. For example, when plumage volume is reduced by one half of the conservative maximum assumed here (Stephenson 1995), E_{net} becomes 0.108 for both species (implying 0.54 in mechanical efficiency, given 0.2 muscle efficiency, see Table 3). Thus, the apparent lowered costs of diving, by reduction in the mechanical power output, are more than counterbalanced by the resulting lesser E_{net} .

Profile power (P_{pro}) is the rate of work against wing drag, and decreases with depth as net buoyancy decreases (the effect of the depth-dependent decrease in A , the ‘equivalent flat plate area’ of the body (eq. 19), is conservatively ignored here). This basically reflects the reduction in wing flapping frequency and or stroke amplitude, as $B_{\text{net}}(d)$ decreases with hydrostatic compression, but diving speed is kept constant. Profile power was estimated using eq. 11 from Pennycuick (1975), by replacing body mass with net buoyancy at depth. Hence during acceleration, ascent, and descent,

$$P_{\text{pro}}(d) = \frac{v}{v_v(\alpha(d_{\text{max}}), v)} \int_{d_i}^{d_j} \left(\frac{X 0.877 k^{0.75} B_{\text{net}}(d)^{1.5} A^{0.25}}{\rho^{0.5} S_d^{0.75}} \right) dd, \quad (18a)$$

where X is the profile power ratio (2, dimensionless), k is the induced drag factor (1.2, dimensionless), S_d is the disk area (eq. 20). d_i and d_j define the depth range (Δd) of the integral corresponding to d_0 and d_v during acceleration, d_v and d_{\max} during descent' and d_{\max} and d_0 during ascent (this notation is followed hereafter). P_{pro} rate in the bottom phase of the dive,

$$P_{\text{pro}}(d_{\max}) = \frac{X 0.877 k^{0.75} B_{\text{net}}(d_{\max})^{1.5} A^{0.25}}{\rho^{0.25} S_d^{0.75}}, \quad (18b)$$

$$A = 2.85 \times 10^{-3} M_b^{0.667}. \quad (19)$$

$$S_d = (\pi w^2) / 4, \quad (20)$$

where w is the wingspan (m). The wingspan of the Adelie penguin was calculated by adding the length of each flipper (Williams 1995), to the distance between them (0.112 m), measured from fig. 1b in Bannasch (1986), $w \approx 0.49$ m.

Induced Power. When descending and swimming at the bottom at positive buoyancy, the bird has to produce a balancing 'negative lift.' This is induced power (P_{ind}) and is assumed here to be independent of diving orientation, although when the angle of descent surpasses some stalling angle, the negative lift generation as formulated in eqq. 21a, b is lost. However, one can consider that P_{ind} is the cost of necessary 'tension maintenance' against the positive buoyancy, which is independent of orientation, and that eqq. 21a, b and 22 estimate this cost for any descent angle. A simple explanation of P_{ind} while diving is that when the bird maintains a vertical position in the water column, it is the power needed to produce the upward movement of water in order to remain stationary (at positive buoyancy). After the lift is 'lost,' a bird is assumed to either increase its wing

flapping frequency and/or stroke amplitude to balance the induced drag, and thereby to increase the speed of trailing water behind the bird by $v_i(d)$ (eq. 22) while the maintaining the same diving speed. Positive buoyancy aids the ascent (see ‘*Buoyant Power*’), analogously to an airborne bird descending to earth under gravitational pull. P_{ind} in this case is opposite to the upward movement of the bird, and it is the cost of displacing water to the rear of the bird. Because the calculation of P_{ind} at low speeds is unreliable (Pennycuick 1989), particularly during acceleration, it is simplistically assumed here that P_{ind} during acceleration is the same as at constant diving speed. P_{ind} in acceleration, descent, and ascent,

$$P_{\text{ind}}(d, v) = \frac{v}{v_v(\alpha(d_{\text{max}}), v)} \int_{d_i}^{d_j} v_i(d, v) k B_{\text{net}}(d) dd, \quad (21a)$$

where $v_i(d, v)$ is the upward velocity of the water at depth (eq. 22). P_{ind} in the bottom phase of the dive,

$$P_{\text{ind}}(d_{\text{max}}, v) = v_i(d_{\text{max}}, v) k B_{\text{net}}(d_{\text{max}}). \quad (21b)$$

$$v_i(d, v) = B_{\text{net}}(d) / (2S_d v \rho), \quad (22)$$

where d becomes d_{max} in the bottom phase calculation.

Parasite Power. The power exponents in Bannasch’s (1995) regression equations for parasite drag for Adelie Penguin, $D_{\text{par}}(v) = 0.5844 v^{1.5278}$, and Gentoo Penguin (*P. papua*), $D_{\text{par}}(v) = 0.8171 v^{1.5321}$ ($R^2 = 99.9\%$, $P < 0.001$ for both species), are virtually identical, reflecting near identical geometric shape of the two species. The difference in the intercepts, x , therefore reflects the size difference in the reference area between the species.

By assuming a linear relationship between the intercepts of the $D_{\text{par}}(v)$ equations above (x , 0.5844 and 0.8171) and the corresponding frontal body reference areas (A_f , 0.02083 and 0.02706 m²) for Adelie and Gentoo Penguins, respectively, and by using the average power exponent of the speed (1.53), one can extrapolate x with respect to the hydrostatically reduced reference area at depth $A_f(d)$. Accordingly, one may use the changes in body volume of Adelie penguins and the corresponding surface area with depth, derived from Boyle's Law and elementary geometry, to extrapolate drag at any depth and speed, $D_{\text{par}}(d, v)$. It is assumed that the drag of little penguins behaves in the same fashion, (i.e., solving x , using $A_f = 0.010124$ m² at the surface as a starting point). For either species, x is scaled as a function of frontal body area (m²) at depth,

$$x(A_f(d)) = -0.1936 + 37.3515A_f(d). \quad (23)$$

Parasite drag at any given speed and depth is found by substituting eq. 10 for $A_f(d)$ in eq. 23 and inserting the resulting $x(A_f(d))$ into eq. 24,

$$D_{\text{par}}(d, v) = x(A_f(d))v^{1.53}. \quad (24)$$

Bannasch's (1995) parasite drag measurements were performed in a freshwater flume at 17.6°C. To use these measurements to calculate the parasite drag in the respiratory canals, and in sea conditions, one must account for the increase in kinematic viscosity (m² s⁻¹) for the more viscous salt-water conditions. This is done by multiplying the measured parasite drag by the appropriate kinematic viscosity conversion factor (kv , dimensionless). The kv is the ratio of the two relevant kinematic viscosities. The kinematic viscosity for each situation was linearly interpolated (table 2.1 in Vogel 1994): 17.6°C freshwater 1.0772x10⁻⁶ m² s⁻¹ (flume); 4°C seawater 1.6798x10⁻⁶ m² s⁻¹ (Adelie penguin's respiratory canal and sea conditions); and 10°C freshwater 1.2843 x10⁻⁶ (little

penguin respiratory canal); 14°C $1.2843 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$ seawater (little penguin at sea). For Adelie penguins, $kv = 1.559$. For little penguins, $kv = 1.192$ at sea and 1.216 in the respiratory canal (for the E_{net} calculation).

Parasite power to depth $P_{\text{par}}(d, v)$, in ascent and descent phases,

$$P_{\text{par}}(d, v) = kv \frac{v}{v_v(\alpha(d_{\text{max}}), v)} \int_{d_i}^{d_j} D_{\text{par}}(d, v) dd. \quad (25a)$$

Parasite power rate in bottom phase, $P_{\text{par}}(d_{\text{max}}, v)$,

$$P_{\text{par}}(d_{\text{max}}, v) = v D_{\text{par}}(d_{\text{max}}, v) kv. \quad (25b)$$

Parasite power in acceleration phase $P_{\text{par}}(d_v, v)$,

$$P_{\text{par}}(d_v, v) = kv \frac{v}{v_v(\alpha(d_{\text{max}}), v)} \int_{d_0}^{d_v} x(A_f(d)) \left(a \sqrt{\frac{d}{0.5a}} \right)^{1.53} dd, \quad (25c)$$

where the first term in the integral is the parasite drag, and the second term gives speed at depth. During constant acceleration (as assumed), instantaneous speed is equal to the product of acceleration (eq. 28) and the time elapsed.

Buoyant Power. Boyle's Law dictates an inverse hyperbolic decrease of air volume with hydrostatic pressure, and the net buoyant force concurrently changes as an inverse hyperbolic function of depth according to eq. 9. Power exerted is obtained by integrating net buoyancy: when moving against buoyancy, as in descent, $d_i = d_v$, and $d_j = d_{\text{max}}$; when supplemented by ('negative') buoyancy as in ascent, $d_i = d_{\text{max}}$, and $d_j = d_0$,

$$P_B(d) = \int_{d_i}^{d_j} B_{\text{net}}(d) dd. \quad (26)$$

DMR(*d*) Model Calculation Procedures

It is computationally convenient to split the calculation of total oxygen consumption into four phases: (1) acceleration (denoted by the subscript I), (2) decent (subscript D), (3) bottom (subscript B), and finally (4) ascent (subscript A). In what follows, the calculation procedures are formulated for each phase.

Acceleration Phase. The total oxygen consumption (mL) during the acceleration phase, from the surface (d_0) to the depth when constant speed is attained (d_v , see eq. 30),

$$VO_{2I} = \frac{1}{K} \left(\frac{1}{E_{\text{net}}} (P_a + P_r(d_v) + P_B(d_v) + P_{\text{ind}}(d_v, v) + P_{\text{pro}}(d_v) + P_{\text{par}}(d_v, v)) + T_v \text{BMR} \right), \quad (27)$$

It is assumed that acceleration is constant from zero to the target speed, $v = 1.5 \text{ m s}^{-1}$ in the Adelie penguin and 1.8 m s^{-1} in the little penguin, over the distance $S_a = 2.5 \text{ m}$, as measured in African penguins (*Spheniscus demersus*) (Wilson and Wilson 1995). Acceleration (m s^{-2}) is,

$$a = v^2 / (2S_a). \quad (28)$$

The time (T_v , s) it takes to attain the target speed is the duration of the acceleration phase,

$$T_v = v/a. \quad (29)$$

The depth when constant target speed is attained (d_v , m),

$$d_v = \sin(\alpha(d_{\text{max}})) S_a \quad (30)$$

Acceleration reaction power was calculated using the total body volume at depth halfway down to d_v ,

$$P_r(d_v) = \rho S_a V(d_v/2) C_a a, \quad (31)$$

where C_a is the added mass coefficient (Daniel 1984; Vogel 1994), $C_a = 0.082$ when entrained water is moving parallel to the body axis (Lamb 1932). In determining C_a , we assumed that the penguin's body shape resembles an ellipsoid where length is four times the maximal diameter (fineness ratio). Indeed, Adelie and Gentoo Penguins have fineness ratios of 4.00 and 4.35 respectively (Bannasch 1995). The actual fineness ratio of a normal little penguin is unknown, but based on body length of 0.404 (Lovvorn et al. 2001) and the body diameter estimate (0.108 m) it is 3.74,. Acceleration power,

$$P_a = a M_b S_a. \quad (32)$$

Descent Phase. The total oxygen consumption during the descent phase, from the depth when constant speed is attained ($d_i = d_v$) to maximum depth ($d_j = d_{\max}$),

$$\dot{V}O_{2D} = \frac{1}{K} \left(\left(\frac{1}{E_{\text{net}}} (P_B(d) + P_{\text{par}}(d, v) + P_{\text{ind}}(d) + P_{\text{pro}}(d, v)) \right) + \text{BMR} \frac{\Delta d}{v_v(\alpha(d_{\max}), v)} \right), \quad (33)$$

Decent time (s),

$$T_D = (d_{\max} - d_v) / v_v(\alpha(d_{\max}), v). \quad (34)$$

Bottom Phase. Rate of oxygen consumption ($\text{mL O}_2 \text{ s}^{-1}$) at maximum depth,

$$\dot{V}O_{2B}(d_{\max}) = \frac{1}{K} \left(\frac{1}{E_{\text{net}}} (P_{\text{par}}(d_{\max}, v) + P_{\text{ind}}(d_{\max}) + P_{\text{pro}}(d_{\max}, v)) + \text{BMR} \right). \quad (35)$$

Total oxygen consumption during the bottom phase,

$$VO_{2B} = T_B \dot{V}O_{2B}(d_{\max}) \quad (36)$$

where T_B is the maximum aerobic bottom time,

$$T_B = \frac{VO_{2T} - (VO_{2I} + VO_{2D} + VO_{2A})}{\dot{V}O_{2B}(d_{\max})}. \quad (37)$$

Ascent Phase. The total oxygen consumption during the ascent phase, from maximum depth (d_{\max}) to the surface (d_0),

$$VO_{2A} = \frac{1}{K} \left(P_B(d) + \left(\frac{1}{E_{\text{net}}} (P_{\text{par}}(d, v) + P_{\text{ind}}(d) + P_{\text{pro}}(d, v)) \right) + \text{BMR} \frac{\Delta d}{v_v} \right), \quad (38)$$

Ascent phase duration,

$$T_A = d_{\max} / v_v (\alpha(d_{\max}), v). \quad (39)$$

All the calculations above assume positively buoyant diving, since the maximal aerobic depth attainable d_{amax} , is less than depth at neutral buoyancy d_{NB} (see eq. A1 in Appendix A in the Internet version of this paper). For Adelie Penguin, $d_{\text{NB}} = 82$ m, and 126 m for little penguin. If the plumage volume (V_P) is reduced by one half d_{NB} becomes 56 and 80 m respectively. When $d_{\text{amax}} > d_{\text{NB}}$, the changes in eqq. 33 and 38 are given in Appendix B in the Internet version of this paper.

Model of Depth-Dependent Aerobic Diving Limit

The aerobic diving limit $\text{ADL}(d)$ is defined here as the maximum diving time (s) to any given depth (d), at which the residual oxygen reserves (if any) will be used in the bottom phase, but still allowing an aerobic return to the surface. That is, the $\text{ADL}(d)$ estimates

how long an bird can dive to any particular depth as the sum of oxygen consumption in all four phases of the dive,

$$VO_{2T} - (VO_{2I} + VO_{2D} + (T_b \dot{V}O_{2B}(d_{\max})) + VO_{2A}) = 0, \quad (40)$$

where the sum of the oxygen consumption in each phase of the dive equals the total oxygen reserves (VO_{2T}). The maximum aerobic depth (d_{\max}) that is reachable occurs when there is no oxygen left for a bottom phase (i.e., when $T_B = 0$). The ADL as a function of depth: tADL(d);

$$\text{tADL}(d) = T_D + T_A + T_v + T_B. \quad (41)$$

Results

The components of mechanical power output (and the BMR) as functions of depth in an exemplary U-shaped diving profile of Adelie penguin to an arbitrarily chosen 60 m depth, are shown in fig. 1. The largest component is buoyant power, which affects the depth-specific power output the most. Parasite power increases rapidly during acceleration, but remains relatively constant with depth after that. Induced power increases slightly at high buoyancy, but is a small component overall. As formulated, profile power is strongly dependent on buoyancy, but reaches relatively low values at depths greater than 20 m.

The instantaneous oxygen consumption at depth by an Adelie penguin, or depth-specific diving metabolic rate for the same exemplary dive as in fig. 1., is given in fig. 2. Including the cost of acceleration and accelerational reaction, positive buoyancy is the predominant factor of the ‘costly’ descent. Negative buoyancy aids the ascent, as

illustrated by the ‘down-step’ at the end of bottom phase in fig. 2, and more importantly by the overall suppression of power output during ascent. It costs ~ 6.8 (or $1/E_{\text{net}}$) times as much energy to offset one unit of buoyant power during descent as the buoyancy supplements during ascent (at the same respective depth).

Adelie Penguin Model

$t\text{ADL}(d)$ for both **V** and **U** diving profiles are given in fig. 3, together with the corresponding bottom times. For the **U**-shaped profile, the maximum $t\text{ADL}(d)_{\text{U}}$ is 104.7 s (at 18 m depth), where the $t\text{ADL}(d)_{\text{U}}$ curve peaks. After their peaks, both the $t\text{ADL}(d)_{\text{U}}$, and the bottom time curves decline linearly. The maximum aerobic depth ($d_{\text{amax, U}}$) is 72 m (for a total of 98.1 s).

For the **V**-shaped profile, the maximum $t\text{ADL}(d)_{\text{V}}$ was 101.1 s (at 14.5 m depth), $d_{\text{amax, V}}$ was at 54 m. Bottom time decreases exponentially with depth, reflecting the increase in proportional time at depth, largely masking the opposite effect of the increase in the diving angle with depth.

The model results were compared to the most extensive data set ($n=14048$ dives) available on free-diving Adelie penguins (Chappell et al. 1993a): the average dive time was 73.2 ± 18.6 s ($\pm\text{SD}$); and the average dive depth 26 ± 13 m. Using the area of the normal curve, fewer than 6.68% of all dives exceeded the model’s maximum $t\text{ADL}(d)_{\text{V}}$. It is unknown which diving profile—deep and/or long dives—pertains in nature. However if we assume that Adelie penguins avoid surpassing $\text{ADL}(d)$, less than 4.25% of all dives exceed the model’s maximum $t\text{ADL}(d)_{\text{U}}$, in duration, and those which do exceed the limit

only slightly (see fig. 5 in Chappell et al. 1993a). Less than 1.58% of all dives exceed the model's $d_{\text{amax, v}}$, and less than 0.02% exceed the model's $d_{\text{amax, U}}$ (Chappell et al. 1993a). $d_{\text{amax, U}} = 72.3$ m is 0.61 standard deviations less the mean maximum depth of 84 ± 19 m ($n=20$, Whitehead 1989).

Little Penguin Model

$t\text{ADL}(d)_{\text{U}}$ is provided in fig. 4, together with the corresponding bottom time, the maximum $t\text{ADL}(d)_{\text{U}}$ is 74.9 s (at 15 m depth), and the maximum aerobic depth attainable ($d_{\text{amax, U}}$) is 51 m (for a total of 57.9 s).

The model's results were compared to the most extensive data set available ($n = 6025$) of instrumented little penguins in Marion Bay, Tasmania (Bethge et al. 1997): average diving duration was 21 ± 8.4 s ($\pm\text{SD}$); and average diving depth 3.4 ± 3.94 m. Based on the area of the normal curve, no little penguin's dives exceeded either the maximum duration or the maximum depth predicted by the model. Average maximum depth of little penguins near Phillip Island, Australia was 30 m (Montague 1984).

Discussion

The results of this exercise strongly suggest that Adelie Penguins perform little anaerobic diving, and that little penguins perform none whatsoever. This result is likely to apply generally to highly positive buoyant avian deep-divers, and certainly not only penguins.

The assumption of depth-independent (linear) DMR is not tenable for positively buoyant birds, in which case DMR is a nonlinear function of depth. It is therefore fundamentally inappropriate to calculate their ADL by linearly extrapolating measured average DMR to greater depths, which can easily produce a bias of similar magnitude as the observation (bADL) and prediction (cADL) gap. This also applies to ADL calculated by using the swimming speed at which cost of transport (COT, J m^{-1}) is minimal (e.g., Bethge et al. 1997; Culik et al. 1994b; Luna-Jorquera and Culik 1999), since COT is also depth-dependent.

The model's realism depends largely on how precisely and accurately the changes with depth can be described for the depth-dependent variables, and, of course, the estimates of initial values. Although this will probably never be achieved to everybody's satisfaction (including ours), the conservative choice of the model's parameters strengthens the interpretation of the model's results. On that basis, we are confident in the main conclusion that diving is predominantly aerobic, and primarily attributable to reduction in high buoyancy while diving to depths shallower than the point of neutral buoyancy. Hypometabolism offers too small a scope of metabolism reduction to explain the large gap between observation (bADL) and prediction tADL (compare BMR to DMR in fig. 2).

Given the observed range in the values here, reducing respiratory air volume always decreases maximum dive duration in our model, because the metabolic fuel (O_2) content of a volume of air is greater than its highest buoyant carrying cost. This explains anecdotal observations that deep-diving (an arbitrary criteria of say >20 m) birds submerge after inspiration (Croll et al. 1992; Kooyman et al. 1971; Stephenson et al.

1989b). It is well known fact, however, that many shallow divers submerge after expiration (Livesey and Humphrey 1984; Lovvorn 1991; Ross 1976; Tome and Wrubleski 1988). Although aerobic dives following expiration must be of shorter overall duration, they are energetically cheaper due to the reduced buoyancy, thus one would expect that highly buoyant shallow divers, i.e., experiencing proportionally the greatest costs of buoyancy, would benefit the most by diving after expiration. However, for this strategy to remain advantageous, any increase in diving frequency accompanied with the shorter dives, cannot override the energetic savings of shorter dives. As diving depth increases, so do the benefits of lowering the transport (buoyancy) costs of the air cargo. Indeed birds which are not maximizing dive duration, but rather minimizing the DMR, by anticipating depth and dive duration, should calibrate the respiratory air cargo accordingly (see Keijer and Butler 1982). The aspect of optimal diving air supply is beyond the scope of this paper, but for the interested, see an excellent study by Sato et al. (2002), combining both biomechanical and experimental approaches to this problem.

There are reports where the length of diving pause on the surface between dives does increase at an accelerating rate with the length of the preceding dive (e.g., Benvenuti et al. 2001; Croll et al. 1992; Culik et al. 1996; Kooyman and Kooyman 1995; Schreer et al. 2001; Ydenberg and Guillemette 1991). But instead of invoking surpassed ADL as an explanation, one possible 'alternative' is that digesta accumulation (Guillemette 1994; Guillemette 1998) compresses the air sacs, reducing the air volume available for diving. This idea is amenable to experimentation by measuring changes in respiratory volume after incremental feedings.

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APPENDIX A

Depth of Neutral Buoyancy

Depth at neutral buoyancy is calculated by finding at which depth the hydrostatic pressure compresses a bird's air compartments to the volume required to make the bird's density exactly equal to that of the water's,

$$d_{\text{NB}} = \left(\frac{10329.561}{\rho} \left(1 / \left(\left(\frac{M_b}{\rho} - \frac{M_b}{\tau} \right) / (V_R + V_P) \right) \right) \right) - \frac{10329.561}{\rho}. \quad (\text{A1})$$

Eq. A1 calculates the difference between solid body volume and volume of displaced water; when the total body airspace ($V_R + V_P$) equals this volume, neutral buoyancy is attained. To convert this equality to depth, the ratio of the volume difference and total airspace (at one ATM) is the compression ratio, and taking the inverse gives the depth in multiples of ATM's. Lastly the standard ATM is converted to kg m^2 (the constant 10329.561) and divided by the water density (in kg m^3) in order to get water density-dependent depth (in m) equivalent to one ATM. The subtraction of one ATM density-dependent depth equivalent corrects the depth for the atmospheric air mass.

Note that that the apparently small density difference (and temperature effect on density) between fresh and seawater makes a large difference to d_{NB} . For example Lovvorn et al. (2001; 1999) calculated $d_{\text{NB}} = 62$ m, for thick-billed murre ($M_b = 1.087$ kg, $V_b = 1.021$ L, $V_P = 0.382$ L, $V_R = 0.174$ L), by assuming a fresh-water density of 999 kg m^3 at 14.5°C (note that eq. A1 gives $d_{\text{NB}} = 75$ m in this case because of differences in calculation). However, correcting the oversight that murrens actually dive in seawater, using seawater density of 1026.1 kg m^3 (at 10°C) in eq. A1 gives $d_{\text{NB}} = 138$ m. The d_{NB}

value plays an important role in Lovvorn's et al. subsequent biomechanical modeling, because thick-billed murre frequently dive deeper than d_{NB} (Croll et al. 1992).

Given the parameter values used here for the Adelie Penguin (seawater at 4°C, density 1025.8 kg m³), $d_{NB} = 82$ m, which is greater than d_{amax} for either dive profile type modeled here. For Little Penguin in seawater at 20°C (density 1024 kg m³), $d_{NB} = 126$ m.

If a bird can dive aerobically beyond the depth of neutral buoyancy $d_{amax} > d_{NB}$ (e.g., Thick-billed murre, Croll et al. 1992; Falk et al. 2000), the calculation of DMR(d) during the ascent and descent phases needs to be further divided into positively and negatively buoyant subcomponents, i.e., above and below, respectively, the d_{NB} . This situation is dealt with in Appendix B.

APPENDIX B

DMR Calculation at Negative Buoyancy

A bird may sometimes surpass aerobically the depth of neutral buoyancy ($d_{\max} > d_{\text{NB}}$, eq. A1), e.g., when diving deep in freshwater, when solid body density is sufficiently high, or when plumage volume is sufficiently small or becomes small enough, e.g., by plumage wetting (Mahoney 1984; Stephenson and Andrews 1997). In this case, the calculation of oxygen consumption in descent and ascent phases are each split into two parts describing positive and negative buoyancy respectively. The positively buoyant part of the descent is calculated using eq. 33, but integrating from d_v to d_{NB} instead of d_{\max} . The negatively buoyant part of the descent phase is,

$$\text{VO}_{2\text{D}, > d_{\text{NB}}} = \frac{1}{K} \left(P_{\text{B}}(d) + \left(\frac{1}{E_{\text{net}}} (P_{\text{par}}(d, v) + P_{\text{ind}}(d) + P_{\text{pro}}(d, v)) \right) + \text{BMR} \frac{\Delta d}{v_v(\alpha(d_{\max}), v)} \right) \quad (\text{B1})$$

where Δd is the difference in depth ($d_{\max} - d_{\text{NB}}$). eq. B1 differs from eq. 33, by the addition of the negative buoyant power to the metabolic drag power, i.e., the metabolic power is reduced by the ‘external’ sinking force.

Similarly the positively buoyant part of the ascent is calculated using eq. 38, (but integrating from d_v to d_{NB}). The negatively buoyant part of the ascent phase ($d_{\max} > d_{\text{NB}}$) is

$$\text{VO}_{2\text{A}, > d_{\text{NB}}} = \frac{1}{K} \left(\left(\frac{1}{E_{\text{net}}} (P_{\text{B}}(d) + P_{\text{par}}(d, v) + P_{\text{ind}}(d) + P_{\text{pro}}(d, v)) \right) + \text{BMR} \frac{\Delta d}{v_v(d_{\max}, v)} \right) \quad (\text{B2})$$

APPENDIX C

List of Symbols

| Symbol | Explanation |
|---------------------|--|
| A | Equivalent flat plate area (m^2), eq. 19 (Pennycuick 1975) |
| ADL | Aerobic diving limit (s) |
| A_f | Frontal body reference area (m^2) on the sea surface |
| $A_f(d)$ | Frontal body reference area at depth, eq. 10 |
| a | Acceleration (m s^{-2}), eq. 28 |
| a | Length of ellipsoid body semimajor axis (m, see ' <i>Body Volume</i> ') |
| a_I | 'Inner core' ellipsoid body semimajor axis length on the sea surface (m), eq. 5 |
| a_O | 'Outer core' ellipsoid semimajor axis length on the sea surface (0.1812 m) |
| BMR | Basal metabolic rate (W) (Culik and Wilson 1991) |
| $B_{\text{net}}(d)$ | Net buoyant force at depth (N), eq. 9 |
| b | Length of ellipsoid semiminor axis (cm, see ' <i>Body Volume</i> ') |
| bADL | 'Behaviorally' defined ADL (s) (Kooyman and Kooyman 1995) |
| b_I | Length of 'inner core' ellipsoid body semiminor axis on sea surface (m) |
| b_O | Length of 'outer core' ellipsoid body semiminor axis (m), eq. 4 |
| COT | Cost of transport (J m^{-1}) |
| C_a | Added virtual mass coefficient (0.082, dimensionless) (Lamb 1932) |
| cADL | 'Calculated' aerobic diving limit (s) (Kooyman and Kooyman 1995) |
| DMR | Diving metabolic rate (W) |
| DMR(d) | Diving metabolic rate at depth (W) |

| | |
|------------------------|--|
| D_{ind} | Induced drag (N) |
| $D_{\text{par}}(d, v)$ | Parasite drag at depth and speed (N), eq. 24 |
| D_{pro} | Profile drag (N) |
| d | Depth (m) |
| $d_{\text{amax, U}}$ | Maximum aerobic depth in a ‘U-shaped’ dive profile (m) |
| $d_{\text{amax, V}}$ | Maximum aerobic depth in a ‘V-shaped’ dive profile (m) |
| d_i | ‘Initial depth,’ range definition symbol (m) |
| d_j | ‘Final depth,’ range definition symbol (m) |
| d_{max} | Maximum depth of a dive (m) |
| d_{NB} | Depth at neutral buoyancy (m), eq. A1, Appendix A |
| d_v | Depth at which constant diving speed is reached (m), eq. 30 |
| E_{net} | Net power efficiency (dimensionless), eq. 15 and 17, Table 3 |
| f | Plumage thickness when just submerged (0.005 m) (Kooyman et al. 1973) |
| g | Gravitational acceleration (9.807 m s^{-2}) |
| K | Energy equivalent of oxygen ($20.0832 \text{ J mL O}_2^{-1}$) (Schmidt-Nielsen 1997) |
| k | Induced power factor (1.2, dimensionless) (Pennycuick 1989) |
| kv | Kinematic viscosity conversion factor (dimensionless) |
| M_b | Body mass (4 kg) (Bannasch 1995) |
| $P_B(d)$ | Buoyant power to depth (W), eq. 26 |
| $P_I(d, v)$ | Metabolic power input to depth at speed (W), eq. 14 |
| $P_O(d, v)$ | Sum of mechanical power output to depth at speed (W), eq. 13 |
| P_S | Atmospheric pressure (ATA) at the sea surface (101.3 kPa) |
| P_a | Accelerational power (W), eq. 32 |

| | |
|------------------------|--|
| $P_{\text{ind}}(d, v)$ | Induced power to depth, at speed v (W), eqq. 21a, b |
| $P_{\text{par}}(d, v)$ | Parasite power to depth (W), eqq. 25a, b, c |
| $P_{\text{pro}}(d)$ | Profile power (W), eqq. 18a, b |
| P_q | Deceleration power (1.12 W), eq. 16, |
| $P_r(d, v)$ | Accelerational reaction power (W), eq. 31 |
| Re | Reynolds number (dimensionless) |
| RMR | Resting metabolic rate (W) (IUPS-Thermal-Commission 1987) |
| SMR | Standard metabolic rate (W) (IUPS-Thermal-Commission 1987) |
| S_a | Acceleration distance (2.5 m) (Wilson 1995) |
| S_d | Disk area (m^2), eq. 20 (Pennycuick 1989) |
| T | Time (s) |
| T_A | Duration of ascent phase (s), eq. 39 |
| T_D | Duration of descent phase (s), eq. 34 |
| T_B | Maximum aerobic bottom time (s, bottom phase duration), eq. 37 |
| T_r | Time taken (14 s) to swim one trip in a respiratory canal (Culik et al. 1994b) |
| T_v | Time until diving speed is constant (s, acceleration phase duration), eq. 29 |
| tADL | Theoretical aerobic diving limit (s) (Kooyman and Kooyman 1995), eq. 38 |
| tADL(d) | Theoretical aerobic diving limit to depth (s), eq. 41 |
| U | ‘U-shaped’ diving profile (see ‘ <i>Dive Profile Types</i> ’) |
| V | ‘V-shaped’ diving profile (see ‘ <i>Dive Profile Types</i> ’) |
| V | Volume |
| V_I | Ellipsoid inner body core volume (m^3), eq. 3 |
| V_O | Ellipsoid outer core (total) body volume (m^3), eq. 6 |

| | |
|---------------------------|--|
| V_P | Plumage volume on the sea surface (m^3), eq. 7 |
| V_R | Respiratory system volume on sea surface (m^3), eq. 1 (Calder 1984) |
| VO_{2A} | Total O_2 consumption in ascent phase (mL O_2), eq. 38 |
| VO_{2B} | Total O_2 consumption in bottom phase (mL O_2), eqq. 36, B2 |
| VO_{2D} | Total O_2 consumption in decent phase (mL O_2), eqq. 33, B1 |
| VO_{2I} | Total O_2 consumption in acceleration phase (mL O_2), eq. 27 |
| VO_{2P} | Pigment bounded oxygen volume (mL) |
| VO_{2R} | Respiratory oxygen volume (mL) |
| VO_{2T} | Total oxygen volume available for diving (mL), see eq. 40 |
| $V(d)$ | Total body volume at depth (m^3), eq. 8 |
| V_b | Solid body volume (m^3) |
| $\dot{V}O_{2B}(d_{max})$ | Oxygen consumption rate in bottom phase (mL $O_2 s^{-1}$), eq. 35 |
| v | Diving speed, relative to body ($m s^{-1}$) (Culik et al. 1994b) |
| $v_i(d, v)$ | Induced velocity as a function of depth and diving speed ($m s^{-1}$), eq. 22 |
| $v_v(\alpha(d_{max}), v)$ | Vertical diving velocity as a function of maximum depth and relative diving speed ($m s^{-1}$), eq. 12 |
| w | Wingspan (m, see ' <i>Profile Power</i> ') |
| X | Profile power ratio (2, dimensionless) (Pennycuick 1989) |
| x | Multiplicative regression coefficient of parasite drag ($kg s^{-1}$), eq. 23 |
| $\alpha(d_{max})$ | Diving angle as a function of maximum depth ($^\circ$) (Wilson 1995), eq. 11 |
| Δd | Change in depth (m) |
| η_a | Aerobic efficiency (0.2, dimensionless) (Blake 1991) |
| η_m | Mechanic efficiency (0.57, dimensionless, Table 3) |

| | |
|--------|--|
| ρ | Seawater density with 35‰ salinity (at 4° C and 1 ATM, 1026.7 kg m ³) (UNESCO 1987) |
| τ | Average body tissue density (1065 kg m ³) (Stephenson 1993) |

Table 1: Oxygen reserves for diving in Adelie Penguin. The calculation follows Stephenson et al. (1989b) and references therein, except where noted

| Oxygen reserves | Value | Study |
|--|--|--------|
| Grand total oxygen reserve (VO_{2T}): | 217 mL (100%) | |
| Total blood oxygen: | 85 mL (39%) | |
| Arterial blood volume | 124 mL | (1) |
| Venous blood volume | 322 mL | (1) |
| Mean hemoglobin concentration | 0.187 g mL ⁻¹ | (1, 2) |
| O ₂ binding capacity of hemoglobin ^a | 1.356 mL O ₂ g ⁻¹ Hb | (2) |
| O ₂ saturation of arterial blood | 100% | (3, 4) |
| O ₂ saturation of venous blood | 70% | (3, 4) |
| Useable proportion of blood O ₂ | 96% | (5) |
| Total muscle oxygen: | 59 mL (27%) | |
| Body mass | 4 kg | (6) |
| Muscle fraction of body mass ^b | 35% | (1) |
| Myoglobin fraction of wet muscle mass | 3.6 % g ⁻¹ | (7) |
| O ₂ binding capacity of myoglobin | 1.24 mL O ₂ g ⁻¹ Mb | (4) |
| Myoglobin saturation | 95% | (4) |
| Useable proportion of muscle O ₂ | 99% | (4) |

| | | |
|---|-------------|---------|
| Total respiratory oxygen volume (VO_{2R}) | 73 mL (34%) | |
| Total respiratory volume (V_R) | 555 mL | (8) |
| Mean fractional O_2 concentration | 17.6% | (9, 10) |
| Proportion of useable respiratory O_2 | 75% | (5) |

Notes: The studies referred above are: (1) Chappell et al. (1993a); (2) Lenfant et al. (1969); (3) Rothe (1983); (4) Stephenson et al. (1989b); (5) Hudson and Jones (1986); (6) Bannasch (1995); (7) Mill and Baldwin (1983); (8) Calder (1984) ; (9) Scheid et al. (1974); (10) Torre-Bueno (1978).

^aOxygen binding capacity $1.2 \text{ mL } O_2 \text{ g}^{-1}$ in Viscor et al. (1984).

^b0.25 in Stephenson et al. (1989b).

Table 2: Variables and parameters specific of Adélie penguin and the little penguin

| Symbol | Explanation | Little Penguin | Adelie Penguin |
|----------------------|---|-------------------------|-----------------------|
| A | Equivalent flat plate area (m ²), eq. 19 (Pennycuick 1975) | 3.2185×10^{-3} | 0.00718 |
| A_f | Frontal body reference area (m ²) on the sea surface, see text | 1.0124×10^{-2} | 0.02083 |
| a | Acceleration (m s ⁻²), eq. 28 | 0.648 | 0.45 |
| a_I | ‘Inner core’ ellipsoid semimajor axis length on the sea surface (m), eq. 5 | - | 0.1765 |
| a_O | ‘Outer core’ ellipsoid semimajor axis length on the sea surface (m), see text | - | 0.1812 |
| b_I | Length of ‘inner core’ ellipsoid body semiminor axis (m), see text | 0.052 | 0.0765 |
| b_O | Length of ‘outer core’ ellipsoid body semiminor axis (m), eq. 4 | 0.057 | 0.0814 |
| $d_{\text{amax, U}}$ | Maximum aerobic depth of ‘U-shaped’ dive profile (m) | 51 | 72 |
| $d_{\text{amax, V}}$ | Maximum aerobic depth in a ‘V-shaped’ dive profile (m) | - | 54 |
| d_{NB} | Depth at neutral buoyancy (m), eq. A1, Appendix A | 126 | 82 |
| kv | Kinematic viscosity conversion factor, from 17.6°C fresh water to 10°C seawater (dimensionless) | 1.246 | - |
| kv | - , from 17.6°C fresh water to 4°C seawater (dimensionless) | - | 1.559 |

| | | | |
|-----------|---|------------------------|------------------------|
| M_b | Body mass (kg), see text | 1.2 | 4 |
| S_d | Disk area (m ²), eq. 20 (Pennycuick 1989) | 0.0726 | 0.1886 |
| T_v | Time until constant v , acceleration phase duration (s), eq. 29 | 2.8 | 3.3 |
| V_I | Ellipsoid inner body core volume (m ³), eq. 3 | 1.31×10^{-3} | 4.324×10^{-3} |
| V_O | Total body volume (m ³), eq. 6 | 1.705×10^{-3} | 5.034×10^{-3} |
| V_P | Plumage volume (m ³), see text | 3.954×10^{-4} | 7.23×10^{-4} |
| V_R | Respiratory system volume (m ³), eq. 1 (Calder 1984) | 1.83×10^{-4} | 5.55×10^{-4} |
| VO_{2P} | Pigment bounded oxygen volume (mL), see text and Table 1 | 32.5 | 144 |
| VO_{2R} | Respiratory oxygen volume (mL), see text and Table 1 | 24.2 | 73 |
| VO_{2T} | Total oxygen volume available for diving (mL), see eq. 40 | 56.7 | 217 |
| V_b | Solid body volume (m ³), see text | 1.127×10^{-3} | 3.756×10^{-3} |
| w | Wingspan (m), see text | 0.304 | 0.49 |

Table 3: calculation of net power efficiency (E_{net}), which is the ratio of average metabolic input (P_I) to average net power output (P_O)

| Variable | Adelie Penguin | Little Penguin |
|--|--------------------------|--------------------------|
| Net metabolic power input (W, P_I - BMR) | 40.35 | 18.04 |
| P_I , W at speed: ($m s^{-1}$) | 54.75 (1.5) ^a | 21.34 (1.8) ^b |
| BMR (W) | 14.4 ^c | 3.3 ^d |
| Mechanical power output P_O (W) | 5.06 | 2.37 |
| $P_{par}(0.5, v) kv$ (W, eq. 22) | 2.52 | 0.99 |
| $P_{ind}(0.5, v)$ (W, eq. 18) | 0.25 | 0.12 |
| $P_{pro}(0.5)$ (W, eq. 15) | 2.30 | 1.25 |
| Average mechanical power costs of speed | | |
| change ($P_a + 2P_r + P_q$)/ T_r | 0.47 | 0.29 |
| P_a (W, eq. 25) | 4.50 | 1.94 |
| $2P_r$ (W, eq. 28) | 0.94 | 0.45 |
| P_q (W, eq. A3) | 1.12 | 0.49 |
| T_r (s) | 14 | 10 |
| Net power efficiency (E_{net} , eqq. 15 and 17) | 0.137 | 0.147 |
| Mechanical efficiency ^e | 0.68 | 0.74 |

^a(Culik et al. 1994b)

^b(Bethge et al. 1997)

^c(Culik and Wilson 1991)

^d(Nicol et al. 1989)

^eAssuming muscle (aerobic) efficiency of 0.2 (Blake 1991; Hill 1950).

Figure legends:

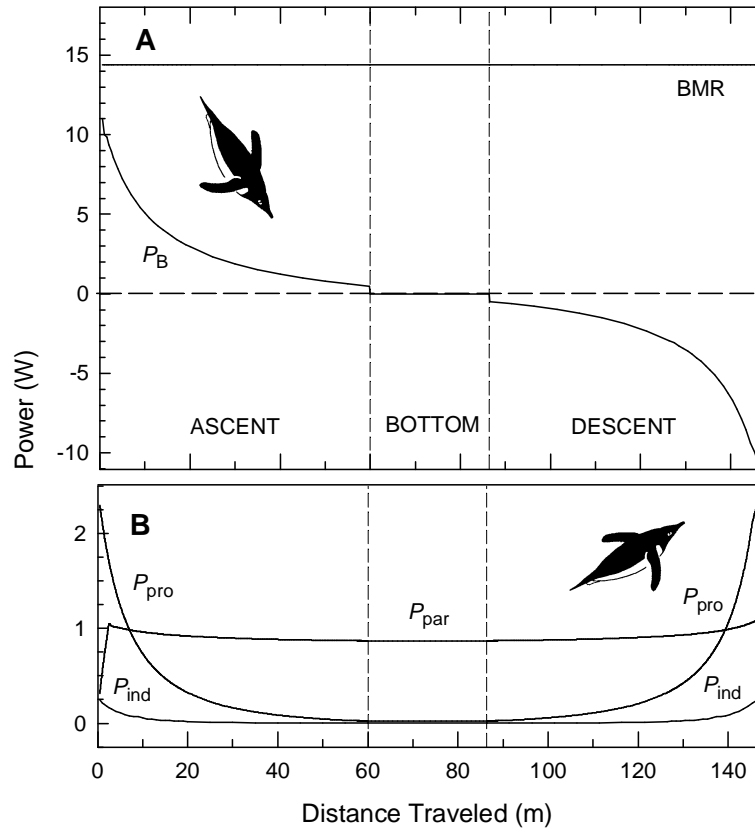
Figure 1: Instantaneous power (W) components of an exemplary U-shaped dive by Adelie penguin, as functions of depth, to maximum depth of 60 m, at diving speed of 1.5 m s⁻¹. A, Power exerted against buoyancy (positive values), and supplemented by buoyancy (negative values), and basal metabolic rate. B, Profile, parasite and induced powers. The Adelie Penguin ascends and descends vertically, and swims horizontally in the bottom phase of the dive. Note that the x -axis gives the total distance traveled, and the vertical broken lines denote the beginning and end of the bottom phase (17.1 s).

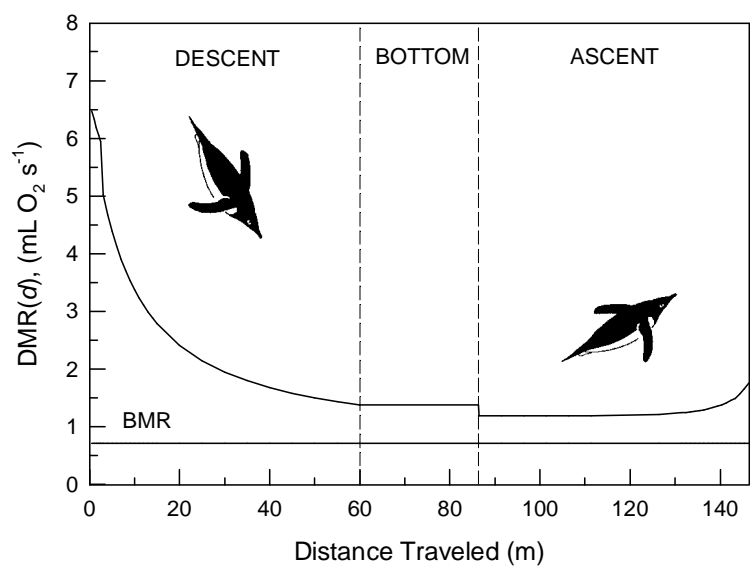
Figure 2: Adelie penguin's instantaneous diving metabolic rate (mL O₂ s⁻¹) at depth, $DMR(d)_U$, in a exemplary U-shaped dive to 60 m (as in fig. 1). Note that the x -axis gives the total distance traveled, and the vertical broken lines denote the beginning and end of the bottom phase (17.1 s).

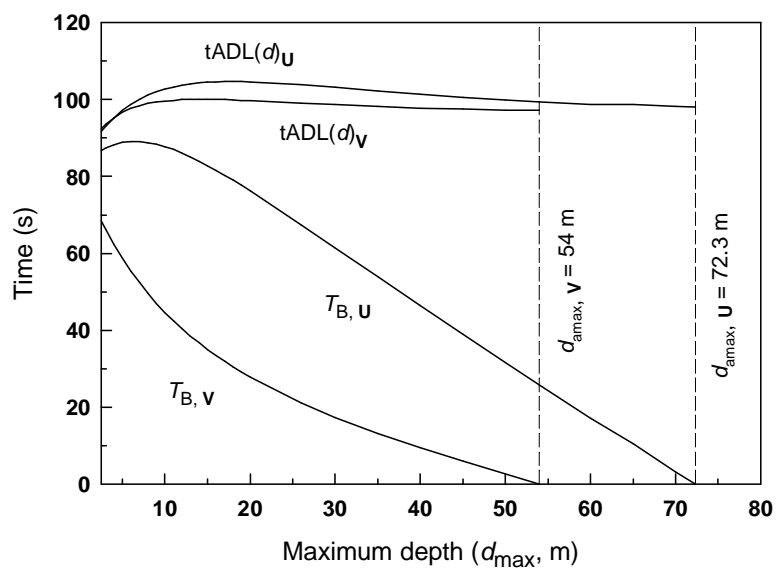
Figure 3: Depth-dependent aerobic diving limit $ADL(d)$, of Adelie Penguin diving at a relative speed of 1.5 m s⁻¹. The results of two types of diving profiles are shown (denoted by the 'U' and 'V' subscripts). The U-shape dives are characterized by vertical descent and ascent, and a horizontal 'bottom phase,' and the maximum $tADL(d)_U$, is 104.7 s (at 18 m depth). The V-shape dives are characterized by an increasing angle (from the horizontal) of descent and ascent, as a function of the maximal depth attained (see text), and the maximum $tADL(d)_V$, is 101.1 s (at 14.5 m depth). Also shown, is the maximal aerobic time available for the bottom phase (T_B) of a dive to a given maximum depth

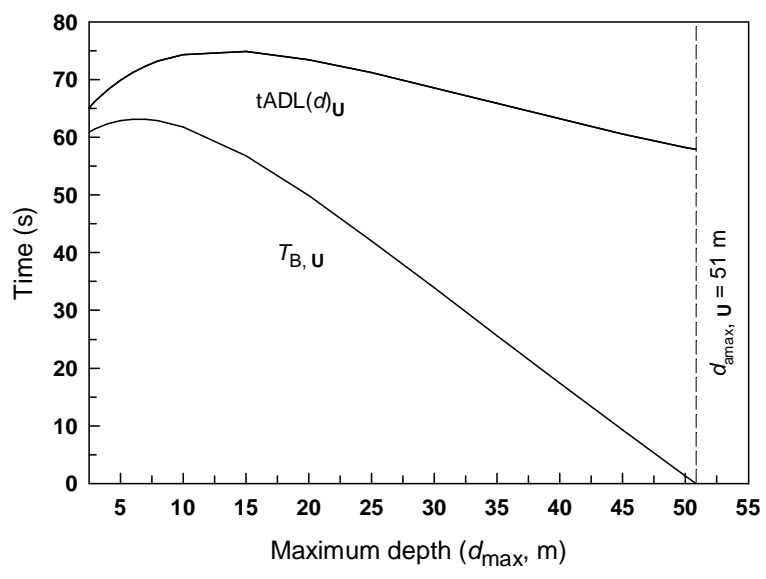
d_{\max} , allowing for an ascent without oxygen debt. $d_{\max, \text{U}} = 72.3$ m (which takes 98.1 s to reach), and $d_{\max, \text{V}} = 54$ m, are the maximum aerobic depths attainable, of the respective dive profiles. In comparison the average dive time of instrumented Adelie penguins was 73.2 ± 18.6 s (mean \pm SD), and the average dive depth 26 ± 13 m (Chappell et al. 1993a), of 14048 dives.

Figure 4: Depth-dependent aerobic diving limit $\text{ADL}(d)_{\text{U}}$, of little penguin diving at a relative speed of 1.8 m s^{-1} , in a U-shape diving profile, characterized by vertical descent and ascent, and a horizontal ‘bottom phase.’ Also shown, is the maximal aerobic time available for the bottom phase (T_{B}) of a dive to a given maximum depth d_{\max} , but allowing an ascent without inducing an oxygen debt. The maximum $t\text{ADL}(d)_{\text{U}}$, is 74.9 s (at 15 m depth), and $d_{\max} = 51$ m is the maximum aerobic depth attainable (for a total of 57.9 s). In comparison the average dive time of instrumented little penguins was 21 ± 8.4 s (mean \pm SD, $n=6025$), and average diving depth 3.4 ± 3.94 m ($n=6025$) (Bethge et al. 1997).









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