

RESEARCH ARTICLE

King penguins adjust their diving behaviour with age

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SUMMARY

Increasing experience in long-lived species is fundamental to improving breeding success and ultimately individual fitness. Diving efficiency of marine animals is primarily determined by their physiological and mechanical characteristics. This efficiency may be apparent *via* examination of biomechanical performance (e.g. stroke frequency and amplitude, change in buoyancy or body angle, etc.), which itself may be modulated according to resource availability, particularly as a function of depth. We investigated how foraging and diving abilities vary with age in a long-lived seabird. During two breeding seasons, small accelerometers were deployed on young (5 year old) and older (8/9 year old) brooding king penguins (*Aptenodytes patagonicus*) at the Crozet Archipelago, Indian Ocean. We used partial dynamic body acceleration (PDBA) to quantify body movement during dive and estimate diving cost. During the initial part of the descent, older birds exerted more effort for a given speed but younger penguins worked harder in relation to performance at greater depths. Younger birds also worked harder per unit speed for virtually the whole of the ascent. We interpret these differences using a model that takes into account the upthrust and drag to which the birds are subjected during the dive. From this, we suggest that older birds inhale more at the surface but that an increase in the drag coefficient is the factor leading to the increased effort to swim at a given speed by the younger birds at greater depths. We propose that this higher drag may be the result of young birds adopting less hydrodynamic postures or less direct trajectories when swimming or even having a plumage in poorer condition.

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INTRODUCTION

Breeders need to allocate energy to two conflicting activities; reproduction and self-maintenance (Stearns, 1989). Life history theory predicts that long-lived species should favour their own survival when young, as they have time to engage in future reproduction, but progressively favour reproduction as they age (Forslund and Pärt, 1995). This theory has received much support from experimental and field data as reproductive success often increases with age until senescence (McCleery et al., 2008). However, an alternative explanation of age-dependent reproductive performance could simply be an increasing capacity to find, capture and process prey with age, i.e. improvement in foraging efficiency (Daunt et al., 2007; Desrochers, 1992; Lemon, 1991; Greig et al., 1983). Indeed, individuals are expected to improve their foraging abilities with time as they learn how best to acquire resources. Accordingly, over time, this leads to the ability to gain energy fast enough to bear the costs of reproduction (e.g. Greig et al., 1983). In some seabird species, once individuals are able to sustain the reproductive costs, they regularly improve their parental investment with each successive reproductive attempt (Forslund and Pärt, 1995) *via* an improvement in both the quantity and quality of supplies to their young. Parental efficiency is thus expected to increase with

age through increased foraging abilities of the parents in the European shag, *Phalacrocorax aristotelis*, for instance (Daunt et al., 1999). However, evidence of improved foraging ability with age in free-ranging individuals is scarce [but see Brandt (Brandt, 1984) for the brown pelican, *Pelecanus occidentalis*], and the precise mechanisms by which such improvement may occur remain unclear. These mechanisms may be easier to highlight when individuals are subjected to strong environmental conditions (Daunt et al., 2007; Lescroël et al., 2009). A general suggestion is that physiological and anatomical changes over the course of ageing may affect foraging performance (e.g. Weddell seals, *Leptonychotes weddellii*) (Hindle and Horning, 2010).

Seabirds operate in two fundamentally different environments; on land, where they breed, and at sea, where they forage, which makes the characteristics that enhance foraging efficiency more difficult to study. The particular case of air-breathing divers, such as penguins, has been identified as one where major changes could occur in foraging capacity over time (Kooyman and Ponganis, 1998). These birds feed at great depth but have to return to the surface periodically to replenish oxygen stores. Individuals must then optimize air loading so as to minimize surface time and increase underwater time, while maximizing net energy gain which, itself,

involves pitting costs of transport (i.e. Ponganis and Kooyman, 2000; Sato et al., 2002) against the energy gains through prey capture (i.e. Butler, 2001; Davis and Weihs, 2007; Kooyman et al., 1992). We hypothesize that the growing experience of ageing individuals should enable diving birds to improve foraging performance by modulation of a suite of parameters, such as the swimming speed or the energy invested during a dive.

King penguins, *Aptenodytes patagonicus* (J. F. Miller 1778), have an extensive parental investment. They forage in remote areas up to 650 km distant from their breeding site during the Austral summer (Charrassin and Bost, 2001), diving to depths of up to 340 m (Pütz and Chérel, 2005) for a breeding period that takes in excess of a year (Barrat, 1976). We would expect these performances to be subject to extreme selection pressures for judicious time and energy management and, given that in other penguin species young breeders are markedly less successful at breeding than older individuals before senescence (Nisbet and Dann, 2009), that experience may play a substantial role in this. We therefore used loggers on free-ranging king penguins to examine how their foraging behaviour (i.e. diving behaviour) changes with age. This was made possible because the study colony in the Crozet Archipelago has been monitored since 1998 (Gendner et al., 2005) and because we could use accelerometry as a proxy for energy expenditure during diving (Gleiss et al., 2010). Specifically, we monitored partial dynamic body acceleration (PDBA) (see Green et al., 2009; Gleiss et al., 2010), a measure of overall body motion, in relation to performance during diving in 5 and 8/9 year old chick-rearing breeders. We hypothesized that young breeders should be less efficient divers than older ones, especially in those strategies that might relate to changes in buoyancy, known to be a major force in modulating energy expenditure in diving birds (Lovvorn and Jones, 1991; Sato et al., 2002).

MATERIALS AND METHODS

Study area and data collection

The study was carried out in the king penguin (*A. patagonicus*) colony of La Grande Manchotière, at Possession Island, Crozet Archipelago (46°25'S, 51°45'E) during the early chick-rearing phase (i.e. chicks less than a month old) of the 2009 and 2010 breeding seasons. Breeding king penguins of known age were equipped with data loggers to monitor their foraging activities. Two age classes were studied: 8 young breeders (5 years old; 1 female and 1 male in 2009, and 5 females and 1 male in 2010) and 15 older breeders (8/9 years old; 3 females and 2 males in 2009, and 4 females and 6 males in 2010). According to Weimerskirch and colleagues, the average age at first breeding of this species is 6 years and almost 90% of birds have attempted to breed by the time they are 8 years old (Weimerskirch et al., 1992). Studied birds had been implanted with passive transponder tags when they were 10 month old chicks, i.e. just before fledging [for more methodological details, see Gendner et al. (Gendner et al., 2005)]. Microtagged birds were monitored from this time using an automatic monitoring system, their transponders being detected by antennae buried under the access pathways between the colony and the sea. The durations of the penguins' sojourns at sea and on land allowed us to determine their reproductive status, breeding success and the different stages of their life cycle (Descamps et al., 2002). To initiate the present study, birds were captured outside the colony, when they departed for the sea, in order to avoid disturbing the chick and neighbouring breeders. Before logger deployment, birds were weighed and measured (flipper and bill lengths) to produce an index of body condition (residuals of a linear regression between body mass and

flipper and bill lengths) (Green, 2001; Schulte-Hostedde et al., 2005), and blood was sampled for subsequent sex determination (Griffiths et al., 1998). Penguins were also weighed after the trip.

We attached black, cylindrical data loggers (W380-D2GT, Little Leonardo, Tokyo, Japan; 80×19 mm length×diameter, 32 g) to the feathers on the centre of the penguins' lower back to minimize the effect of drag (Bannasch et al., 1994) using waterproof Tesa tape (Wilson and Wilson, 1989). Animal handling did not last more than 15 min. Devices had a flash memory of 128 Mbit in which data were stored at 12 bit resolution. Depth was measured every second between 0 and 380 m, with a relative resolution of 0.1 m and an absolute accuracy of ±1 m. Acceleration was recorded along the longitudinal (surge) and dorso-ventral (heaving) axes between ±3 g at 16 or 32 Hz. The recordings lasted between 82 and 132 h (depending on the recording frequency). All equipped birds were recaptured after one foraging trip, before they entered the colony, and the data loggers were retrieved. After being released, all individuals continued to breed normally and their breeding success was monitored until the end of the season. This study was approved by the ethics committee of the French Polar Institute Paul Emile Victor (Arrêtés 2008-71, 2009-57, 2009-59).

Data analysis

Data downloaded from the loggers were analysed using IGOR Pro (version 6.04, WaveMetrics, Portland, OR, USA). A dive was considered to have started when the depth exceeded 1 m and was divided into three phases: the descent, bottom and ascent phases (Wilson, 1995). The beginning and end of the bottom phase were defined as the combination of two conditions: (i) the depth was >85% of the maximum depth of the dive, and (ii) the absolute value of the vertical transit rate became <0.25 ms⁻¹. A bimodal distribution of maximum depth frequencies has been classically observed in king penguins, and has been used to separate shallow from deep dives (Kooyman et al., 1992). We only analysed deep dives, i.e. those >50 m, as these dives should show potential differences between groups more obviously. The following parameters were calculated for each dive: total dive duration, descent, bottom and ascent durations, maximum depth and post-dive duration (i.e. time spent at the surface until the next dive). The number of vertical undulations during the bottom phase, i.e. the point of inflexion in the dive profile (termed 'wiggles' hereafter), was calculated and used as a proxy for prey encounters (Bost et al., 2007; Hanuise et al., 2010).

As a proxy of the whole-body activity during a dive, we calculated the PDBA (in ms⁻² or g) (Wilson et al., 2006; Green et al., 2009; Halsey et al., 2009; Gleiss et al., 2010). Changes in PDBA proceed essentially from a change in the flipper beat frequency and/or amplitude. An increase in one of these parameters can be the result of (i) a stronger propulsive force to overcome a greater buoyancy in the first metres of a dive, and/or (ii) an acceleration to pursue a prey (or eventually escape from a predator). In the following analysis, as we were only interested in the biomechanical aspects of the dives (i.e. PDBA and speed analysis), we concentrated on the descent and ascent phases of the dive, excluding the bottom phase where most prey are encountered by king penguins (Ropert-Coudert et al., 2000), i.e. where acceleration could be influenced by prey pursuit/predator avoidance. We derived the mean PDBA using the dynamic accelerations along the two axes measured. To do this, the specific (propulsive activities) and gravity-related accelerations were first separated by a two-band, low-pass filter (IFDL, version 4.02, WaveMetrics). Derived values of specific acceleration were then converted into absolute positive values [abs(x) and abs(y)] and the resultant values from two channels added to

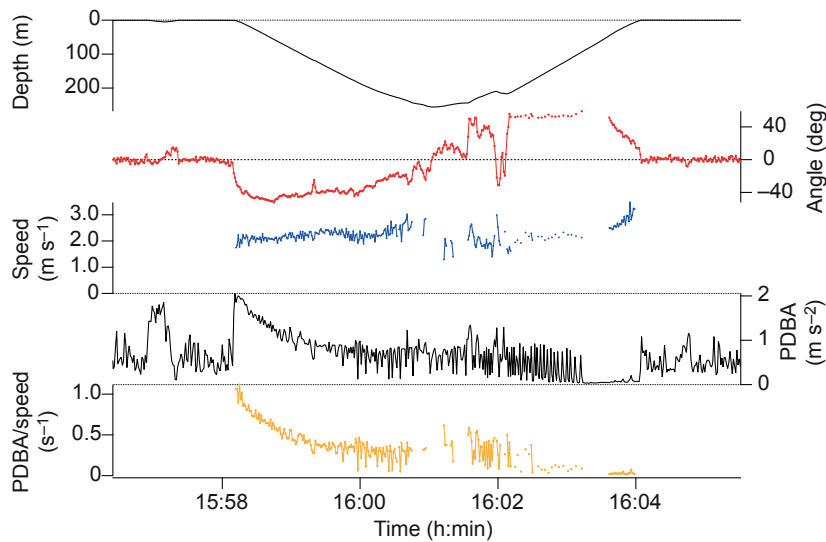


Fig. 1. Example of a diving profile with the depth (black), body angle (red), swimming speed (blue), mean partial dynamic body acceleration (PDBA, black) and the ratio PDBA/speed (orange) plotted against time.

give the PDBA. The PDBA was calculated at 16 or 32 Hz (according to acceleration sampling) and was averaged over 1 s.

All analyses were conducted following correction for the attachment angle of the logger: body angle was considered to be 0 deg when the bird rested on the water surface between two dives (Ropert-Coudert et al., 2006). Swim speed was determined from the dive angle and the rate of change of depth [rate of change of depth/sin(body angle)] (Cook et al., 2010). Because swim speed was calculated using rate of change of depth and body angle, speed data were excluded when the rate of change of depth was too small ($<1 \text{ m s}^{-1}$) (see Fig. 1).

We used PDBA divided by swimming speed as a proxy of efficiency; specifically, large PDBA/speed values would indicate that the birds had higher costs of transport. Given the large data size, we classified maximum dive depth and current depth into 5 m categories. We averaged PDBA, swim speed and PDBA/speed for each maximum depth class (5 m) and current depth class (5 m). Current depth refers to any specific depth within the range of depths passed through by birds on their way from the surface to the maximum depth. Then we calculated the difference between young and old birds for each maximum depth class and current depth class for graphic representation (Fig. 2).

Statistical analyses

Statistical analyses were computed using the R statistical environment (version 2.11, R Development Core Team). PDBA, swim speed and PDBA/speed were analysed using a likelihood mixed regression approach (nlme package) (Pinheiro et al., 2010). Linear mixed models (LMMs) were fitted with normal distributions. Normality of residuals was asserted using a Shapiro–Wilk normality test. Individuals were included as a random effect to account for repeated measurements. All models included the following parameters as fixed effects: age class (older birds being the reference category), sex (females being the reference category), year of equipment and body condition. We included the maximum dive depth and current depth as covariates in the models. Non-significant fixed effects were then removed one by one from the model. Model selection was based on the lowest Akaike's Information Criterion (AIC) value. The breeding success was analysed using generalized linear models (GLMs) fitted with binomial distribution. Trip duration and mass gain were analysed using a non-parametric Wilcoxon rank sum test. Results are presented as means \pm s.e.m., unless stated otherwise. The threshold for significance was set at 0.05.

RESULTS

During the two seasons, none of the 8 young birds bred successfully, whereas 4 out of the 15 older birds reared a chick until fledging; none of these successes occurring in 2010. The difference in breeding success between age classes was not significant (GLM, $P=0.997$).

We found no difference in the dive depth and duration between the two age classes, or in the durations of the different dive phases, the percentage of time spent in each phase relative to total dive duration and the number of wiggles (Table 1). We also did not find any differences between the two age classes in body mass (Wilcoxon rank sum test, $W=68$, $P=0.640$; 10.53 ± 1.12 and 10.20 ± 0.75 kg for older and young birds, respectively; means \pm s.d.) and body condition (Wilcoxon rank sum test, $W=80$, $P=0.210$; 0.25 ± 1.00 and -0.26 ± 0.77 for older and young birds, respectively; means \pm s.d.) before the feeding trip, or in mass gain during the feeding trip (Wilcoxon rank sum test, $W=57$, $P=0.970$; 2.90 ± 0.85 and 2.89 ± 1.06 kg for older and young birds, respectively).

Descent phase

Maximum depth, current depth and age (supplementary material Table S1A) were retained in the best model based on AIC selection (AIC = $-29,345.59$, $\Delta\text{AIC}=4.20$ with the closest model, i.e. model with body condition). The PDBA increased with maximum depth and decreased with current depth (supplementary material Table S1A, $P<0.001$ and $P<0.001$, respectively). The PDBA was positively affected by the age class of individuals; younger birds had higher PDBA values (Fig. 2A; supplementary material Table S1A, $P=0.008$). Moreover, the difference between age classes increased with increasing current depth ($P<0.001$) although the difference decreased during deeper dives ($P<0.001$).

Maximum depth, current depth, sex, age class and year of equipment (supplementary material Table S1B) were retained in the best model explaining differences in the swim speed based on AIC selection (AIC = $-14,154.89$, $\Delta\text{AIC}=5.10$ with the closest model, i.e. model with body condition). The swim speed during descent decreased as birds performed deeper dives (supplementary material Table S1B, $P<0.001$). The current depth affected the swim speed positively during the descent phase ($P<0.001$), and this increase was affected by age ($P<0.001$) so that young breeders increased their speed at a faster pace during the descent (Fig. 2C).

Maximum depth, current depth, age class, year of equipment and body condition (supplementary material Table S1C) were retained

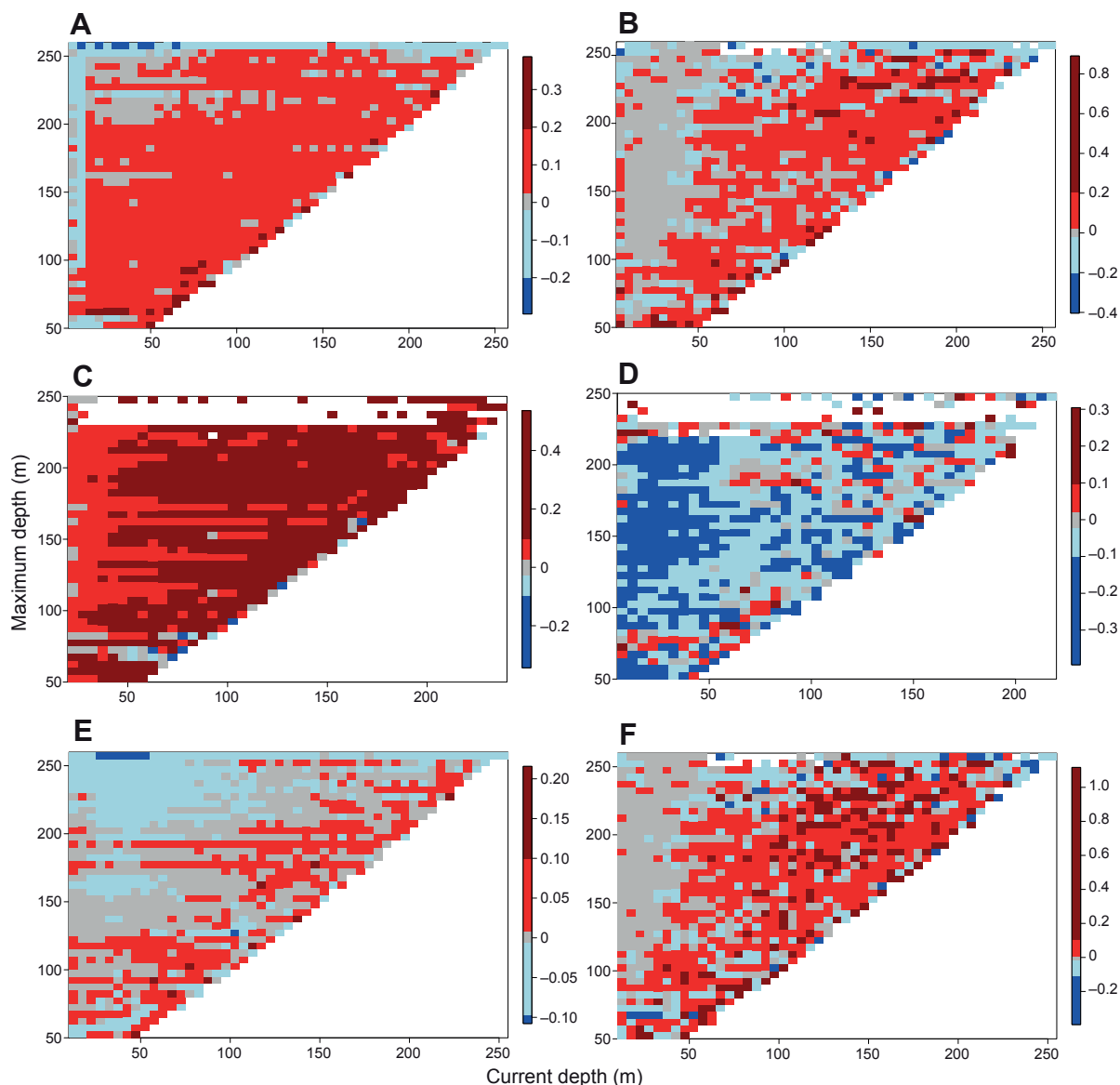


Fig. 2. Mean differences between young and older breeders in (A,B) PDBA (m s^{-2}), (C,D) swimming speed (m s^{-1}) and (E,F) the ratio PDBA/speed (s^{-1}) according to the maximum dive depth (y-axes) and the current depth (x-axes). Results for the descent phase are on the left (A,C,E), while results for the ascent phase are on the right (B,D,F). Red indicates that young breeders display greater values than older birds; blue indicates the opposite.

in the best model explaining differences in PDBA/speed based on AIC selection ($\text{AIC}=-63,586.28$, $\Delta\text{AIC}=7.94$ with the closest model, i.e. model with sex). PDBA/speed increased with maximum depth and decreased with current depth ($P<0.001$ and $P<0.001$, respectively), but was not affected by age class (Fig. 2E; supplementary material Table S1C, $P=0.754$). Nevertheless, the positive effect of the interaction between current depth and age class indicates that with increasing current depth, younger breeders increased their PDBA/speed values at a faster pace than older breeders (Fig. 2E; supplementary material Table S1C, $P<0.001$).

Ascent phase

Maximum depth, current depth, sex and age class were retained in the best model explaining differences in PDBA value during the ascent phase (supplementary material Table S2A) based on AIC selection ($\text{AIC}=-18,396.40$, $\Delta\text{AIC}=6.58$ with the closest model, i.e. model with year of equipment). The PDBA decreased with

maximum depth and increased with current depth (supplementary material Table S2A, $P<0.001$ and $P<0.001$, respectively). The positive effect of the interaction between current depth and age class indicates that the decrease in PDBA with decreasing current depth (i.e. when ascending) was faster for younger breeders (Fig. 2B; supplementary material Table S2A, $P<0.001$). The negative interaction between maximum depth and age class means that the decrease in PDBA with increasing maximum depth is greater for younger breeders than for older breeders ($P<0.001$).

Maximum depth, current depth, sex and age class were retained in the best model to explain differences in swim speed (supplementary material Table S2B) based on AIC selection ($\text{AIC}=2241.66$, $\Delta\text{AIC}=4.57$ with the closest model, i.e. model with year of equipment). The swim speed increased with increasing maximum dive depth (supplementary material Table S2B, $P<0.001$) but current depth affected the swim speed negatively ($P<0.001$), so that speed increased over the ascent. This interacted with age (Fig. 2D; supplementary

Table 1. Dive characteristics according to age class and sex of individuals

	Older breeders		Young breeders		Age	Sex
	Females (N=7)	Males (N=8)	Females (N=6)	Males (N=2)		
Mean maximum dive depth (m)	154.79±52.85	143.49±45.41	154.49±48.18	168.91±51.12	<i>P</i> =0.670	<i>P</i> =0.423
Mean dive duration (s)	269.43±62.38	261.64±57.37	261.40±53.98	281.86±64.47	<i>P</i> =0.403	<i>P</i> =0.025
Mean proportion of bottom phase in relation to the dive	0.31±0.12	0.33±0.12	0.31±0.12	0.32±0.12	<i>P</i> =0.996	<i>P</i> =0.198
Mean descent duration (s)	91.67±30.38	83.95±26.87	86.63±26.60	91.55±30.61	<i>P</i> =0.815	<i>P</i> =0.375
Mean ascent duration (s)	95.30±32.38	91.07±29.94	94.45±29.40	100.52±32.33	<i>P</i> =0.070	<i>P</i> =0.910
Mean post-dive duration (s)	56.26±26.74	60.95±24.60	59.54±24.05	59.41±24.46	<i>P</i> =0.176	<i>P</i> =0.125
Mean number of wiggles during a dive	5.98±4.01	6.75±4.11	6.43±3.86	6.72±4.03	<i>P</i> =0.573	<i>P</i> =0.534

Data are means ± s.d.

material Table S2B, *P*<0.001), meaning that the decrease in speed with current depth (i.e. the increase in speed along the ascent) was steeper for older breeders than for younger ones.

Maximum depth, current depth and age class were retained in the best model explaining differences in PDBA/speed (supplementary material Table S2C) based on AIC selection (AIC=−17,986.41, ΔAIC=4.82 with the closest model, i.e. model with year of equipment). PDBA/speed decreased with maximum depth and increased with current depth (supplementary material Table S2C, *P*<0.001 and *P*<0.001, respectively), but was not affected by age class (Fig. 2F; supplementary material Table S2C, *P*=0.154). Nevertheless, the positive effect of the interaction between current depth and age class indicates that the increase in PDBA/speed values with increasing current depth was faster for younger breeders than for older breeders (*P*<0.001). The negative interaction between maximum depth and age class means that the decrease in PDBA/speed values with increasing maximum depth was faster for younger breeders than for older breeders (*P*<0.001).

DISCUSSION

As experience accumulates, individuals should progressively acquire skills that improve their efficiency in food acquisition (Jansen, 1990). While foraging behaviour is one of the main factors contributing to survival and breeding success, few studies have investigated the relationship between foraging – in this case diving – strategies and age in breeding in long-lived seabirds.

Inter-age differences in descent and ascent speeds (Fig. 2C,D), as well as inter-age differences in effort, as reflected by PDBA (Fig. 2A,B), are ecologically interesting but do not allow us to examine the inter-age allocation of effective effort unless PDBA is considered with respect to performance. Division of PDBA values by speed does, at least, attempt this because the general premise is that higher PDBA values should relate to higher performances, here speed. In this, our results indicate two major differences between young and older birds: the effort in relation to performance in the descent and ascent phase.

In a general sense, if overall a greater effort was allocated to performance by younger birds, we might propose that their propulsive mechanism was less efficient. Penguins primarily use the pectoral muscles for propulsion (see Bannasch, 1995; Alexander, 1992); thus, theoretically muscle development could influence swimming capacity (Hindle et al., 2009). Muscle efficiency is obviously a difficult parameter to estimate in free-ranging animals, and this hypothesis cannot be verified. Nonetheless, even if true, this could not explain the full extent of the observed patterns. First, during the initial part of the descent, older birds exerted more effort for a given speed (Fig. 2E) although the process seemed to reverse during the final part of the descent. So, as depth increased, the

younger penguins tended to work harder in relation to performance. Second, younger birds worked harder per unit speed for virtually the whole of the ascent except for the final metres within 50 m of the surface, where the two groups exerted similar effort (Fig. 2F).

There are primarily two forces with which penguins swimming underwater have to deal, drag and upthrust, and thus we also propose that the variation observed in effort-related performance in our young and old birds can be explained in these terms.

Drag is a function of speed and, as speed varies little during the descent and ascent phases of the dive (for instance, for a dive of 100 m, the mean speed during the descent was 2.29, 2.43 and 2.56 m s^{−1} for depths of 25, 50 and 75 m, respectively) (see also Ropert-Coudert et al., 2001; Wilson et al., 2002), drag presumably cannot account for depth-dependent changes in effort-related speed during the descent (Fig. 2E; supplementary material Tables S1C, S2C). The second force, the upthrust of a submerged penguin, can be divided into two fractions; the whole-body upthrust excluding the air space, and the air-dependent upthrust. As body tissues are essentially incompressible, there can be no change in whole-body upthrust with depth (if air is excluded) so no depth-dependent changes in effort-related speed are to be expected from our birds. We note that even differences in body composition between older and younger birds, such as having different proportions of fat, which can affect buoyancy substantially (e.g. Biuw et al., 2003), could not produce a depth-dependent effect in effort-related performance. Air is, however, compressed by pressure so that air in the respiratory spaces and feathers of penguins will be compressed with depth according to Boyle's Law, which will affect upthrust and therefore how hard the penguins have to work to counteract it (see Wilson et al., 2011).

We can use Newtonian physics to approximate the forces of drag and upthrust to which swimming king penguins are subject as a function of depth to see what can be altered to account for the patterns that we observed. If we assume that the body density of king penguins (excluding air spaces) is about the same as seawater (see Wilson et al., 1992), then the upthrust to which diving birds are subject (*U_p*; N), is given by:

$$U_p = gV\rho / (1 + 100D), \quad (1)$$

where *V* is the volume of air in both the feathers and respiratory space (l), *D* is the depth (m), *ρ* is the density of the water (taken to be 1030 kg m^{−3}) and *g* is the gravity. A bird swimming down against this upthrust has to expend energy for the work done, which depends on the sin of the dive angle. In addition, swimming king penguins have to use energy to counteract the drag force (*F_d*; N), which is given by:

$$F_d = 0.5U^2\rho C_d A, \quad (2)$$

where *U* is the speed (taken to be ~2.0 m s^{−1}) (Ropert-Coudert et al., 2001), *ρ* is the density of seawater (taken to be 1030 kg m^{−3}),

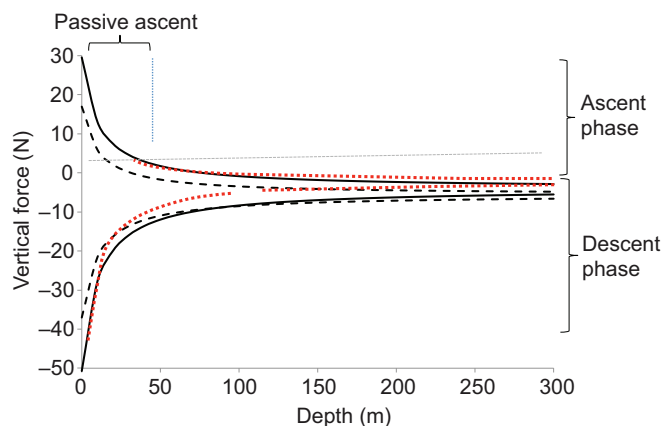


Fig. 3. Proposed vertical forces experienced by young (dashed black lines) and older (continuous black lines) king penguins during the descent and ascent phases of the dives as a function of current depth. The higher the negative force, the more work must be invested by the birds to maintain progression. The dashed red lines superimposed on the older and young bird lines show which of the two groups should experience the greater effort with respect to performance (PDBA/speed). In the scenario shown, the mass, air volume in the feathers, speed and cross-sectional area were equal for the two groups (12 kg , 0.251 kg^{-1} , 2.0 m s^{-1} and 0.0435 m^2 , respectively). In addition, descent and ascent angles are 54 and 36 deg, respectively (Hanuise, 2011). In order to make the patterns of effort-related performance concur with those observed (see Fig. 2E,F), the older bird respiratory space volume was considered to be 50% higher (0.211 kg^{-1}) than that assumed to be the mean (Kooyman, 1975), and the young bird respiratory space volume was considered to be 50% lower (0.081 kg^{-1}). In addition, the drag coefficient (nominally 0.0368) (Culik et al., 1994) was considered to be 40% higher in the younger birds (see Discussion).

C_d is the drag coefficient of a penguin (taken to be 0.0368) (Culik et al., 1994) and A is the cross-sectional area of the penguin at the point of its greatest girth (0.0435 m^2) (Viblanco et al., 2012). Depending on whether the penguins are swimming down or up and the depth at which they are swimming, the upthrust may help, or hinder, progress. With a few assumptions, we can calculate the vertical forces to which diving king penguins are subject using this approach. Using a mean body mass of 12 kg (our own data) and assuming that the birds contain 0.251 air kg^{-1} body mass (see Wilson et al., 1992) in addition to respiratory air amounting to 0.161 kg^{-1} body mass (Kooyman, 1975) there can only be a diminishing upthrust with increasing depth but obviously no differences between young and old birds. In order to account for the observation that older birds exert more effort on descent for a given vertical speed, but that this effort changes with depth (without any change in descent angle or speed), the only solution is for them to be diving with greater air volumes. Therefore, we assume this to be the case. However, because of Boyle's Law (see above), with increasing depth, the value of the air-mediated upthrust diminishes for both young and old birds, with drag becoming the major force with which the birds have to contend. This being the case, the only explanation for the increased effort by the younger birds to swim at a given speed at greater depths (see Fig. 2E,F) is that some term in the equation for deriving the drag (Eqn 2) is higher in the younger than in the older birds. Given their morphological similarity (no significant differences were observed in morphological measurements; flipper lengths were 316.3 ± 13.7 and $323.6 \pm 8.2\text{ mm}$, and beak lengths were 125.1 ± 7.6 and $120 \pm 3.4\text{ mm}$ for the older and younger birds, respectively; means \pm s.d.), the only factor that can possibly be ascribed as different is the drag coefficient (C_d , Eqn 2). In fact, we can incorporate values

for a greater air volume for older birds and a higher drag coefficient in younger birds to create a scenario that would account for the depth-dependent patterns in performance-related effort that we observed in diving king penguins (Fig. 3). Importantly, although variations in e.g. air volume and drag coefficients change the details of the patterns obtained, it is only a combination of these two parameters that can actually produce a pattern that is consistent with our observations.

Inhaled air volume

It has already been shown that some penguin species inhale variable volumes of air according to maximum dive depth (Sato et al., 2002; Wilson and Zimmer, 2004), thus minimizing upthrust, and therefore energy expenditure (Wilson et al., 1992), at foraging depths (Wilson and Zimmer, 2004). This necessitates that birds anticipate the foraging depths and react accordingly (by inhaling correctly) and either, or both, of these processes may be learnt. If so, we would expect enhanced abilities in modulating inhaled air volumes in older birds although the time scale over which this might operate is unclear. There is certainly evidence that younger penguins benefit in general from the experience of older birds during foraging in groups (Ryan et al., 1987) and that there are clear leaders within synchronously diving penguins (Tremblay and Cherel, 1999). We note that, as in most species of penguin, king penguins are highly social, both at sea and on land (Barrat, 1976; Pütz and Cherel, 2005). Presumably, leaders benefit by being able to anticipate the depths to which they are diving and therefore modulate the inhaled air accordingly (see Sato et al., 2002; Wilson and Zimmer, 2004). Conversely, while followers may not be able to inhale air optimally, they can at least benefit from the experience of the leaders with respect to prey location and exploitation (see Ryan et al., 2012). Importantly, king penguins dive to a wide variety of depths, and intersperse shallow surface dives with deeper foraging dives (e.g. Kooyman et al., 1992). During shallow dives it is disadvantageous for birds to inhale greatly, while during deep dives it is disadvantageous to inhale little for reasons documented elsewhere (Wilson et al., 1992). Thus, by being followers rather than leaders, young birds may simply not be inhaling optimally because of an inability to anticipate the depth of the next dive. We note that the difference in the amount of air inhaled by young (0.081 kg^{-1}) and older birds (0.211 kg^{-1}) in our model varies by a factor of 2.6 (Fig. 3). This compares favourably with calculations by Sato and colleagues (Sato et al., 2002) who deduced that the air inhaled by king penguins prior to dives may vary by a factor in excess of 2 in apparent response to dive depth alone. If we assume our values to be realistic (although the figures were adopted primarily for demonstration), young and older birds weighing 12 kg would take down 0.96 and 2.52 l of air in their respiratory system, respectively, which, assuming that oxygen accounts for 21% of the air, equates to 530 and 200 ml oxygen, respectively. Assuming that oxygen can be converted to joules using a factor of $20.1\text{ kJ l}^{-1}\text{ O}_2$ (Schmidt-Nielsen, 1997), these values represent 10.653 and 4.02 kJ , respectively. With swimming metabolic rates of 9.6 W kg^{-1} (Kooyman et al., 1992), which equates to 115.2 W bird^{-1} (if birds weigh 12 kg), this would enable young and older penguins to remain underwater for 35 and 92 s , respectively. These values are 88 and 66% , respectively, less than the mean dive duration of about 270 s recorded in our study. This illustrates at once the apparent reduced contribution of respiratory air to the dive duration and the fundamental importance of non-respiratory oxygen stores against a backdrop of problems in accounting for aerobic dives in king penguins (see Kooyman et al., 1992). To summarize, therefore, we speculate that younger birds

may take down less air than older penguins during deep dives and although this should compromise their diving capabilities the effect on foraging performance may not be as dramatic as it might at first seem.

Variation in drag

We can think of two possible mechanisms to explain why younger birds might have higher drag. First, they may not hold their body, head, flippers and feet in positions that are as optimal as that of the older birds (small differences in shape can produce large differences in drag) (e.g. Lovvorn and Liggins, 2002). Birds less experienced may swim with more body movements because they catch prey with more difficulty. These extra movements, which may increase the drag, could be detected using tri-axial accelerometers, rather than the 2D accelerometers used here. Second, the plumage of these younger birds may be in poorer condition. The compliancy of penguin feathers is likely to play a significant role in reducing drag (e.g. Fish, 2006) so any process that compromises feather condition, such as less attention to preening, may result in the patterns we observed. Changes in drag can fundamentally influence swimming and diving capacities (e.g. Williams and Kooyman, 1985; Lovvorn et al., 2004). For example, Wilson noted how old feathers reduced the maximum speed of African penguins, *Spheniscus demersus*, by almost a third (Wilson, 1985), and drastic alterations in diving behaviour have been noted following an artificial increase in the drag in several other penguin species. For example, handicapped Adélie penguins, *Pygoscelis adeliae*, feed in inshore areas in comparison with non-handicapped ones that can travel further offshore (Beaulieu et al., 2010); little penguins, *Eudyptula minor*, increase the number of dives and the time allocated to prey pursuit with increasing hydrodynamic drag (Ropert-Coudert et al., 2007). Feather age is unlikely to account for drag differences in king penguins as moulting in early breeders is relatively synchronous, i.e. in November (Barrat, 1976), which is nearly 3 months before our study took place. Older breeders in our study did not moult earlier than the young ones (Wilcoxon rank sum test, $W=14$, $P=0.084$), and the time elapsed between moult and the foraging trip studied was not influenced by age class (Wilcoxon rank sum test, $W=29$, $P=0.775$). King penguins devote, on average, 16% of their daily time budget to preening (re-arrangement of feathers) (Viblanco et al., 2011), indicating that plumage integrity is an important component of their activity budget. Preening is often associated with the removal of parasites and foreign items from their plumage (Ainley, 1974). In this context, preening could help re-arrange the feathers and eliminate debris that may otherwise contribute to reduce the drag. Younger king penguins possibly dedicate less time to preening and suffer the consequences by having increased drag.

In addition to the more conventional explanations, Davenport and colleagues suggest that Emperor penguins, *Aptenodytes forsteri*, can reduce drag by losing air from their plumage (Davenport et al., 2011). Although their suggestion only referred to birds just before they leapt out onto the ice, this mechanism may also work during other phases of the dive. This might conveniently explain why older birds dive with more air but the implication would be that penguins could somehow control plumage air volume, which seems unlikely.

Finally, the apparent explanation for differences in drag might be nothing more than younger birds adopting a less direct swim path. Minimal drag will be achieved by birds assuming the ideal shape (see Bannasch, 1995) and also swimming in a direct line. Greater variation from a direct path by younger birds would effectively reduce the efficiency of their locomotion compared with

that of older birds without having to invoke any changes in the drag caused by the plumage.

Thus, considering all factors together, younger breeders had overall higher costs of transport during their dives than older birds even though they ostensibly had the same rate of prey encounter as older birds, as determined by the wiggles in the depth profile (although the use of wiggles to estimate prey capture may be inappropriate as the implication is that the two groups engage in prey capture manoeuvres equally well) (see Simeone and Wilson, 2003). Thus, at best, the overall foraging costs for younger birds seem to be higher, which we would expect to be reflected in body condition or breeding success. Crude body morphometrics indicate no difference in the former. In king penguins, the breeding success is of the order of 40% (Saraux et al., 2011), although as yet there is no information relating to age. Our sample size was too small for us to be able to examine breeding performance. We note, though, that in other penguin species, breeding success increases with age (Nisbet and Dann, 2009) so our findings might point to a potential mechanism for this.

Whatever the diving strategy adopted by older king penguins, it ostensibly contributes to reduce their swimming effort, and should decrease their foraging effort over the whole trip. Age-specific differences in foraging ability are important to explain breeding performance according to age (Lescroël et al., 2010; Daunt et al., 2007). However, our results show that investigations should not just consider the extreme age classes, i.e. juveniles versus mature adults, but should instead include age as a parameter in the examination of foraging capacity (see Zimmer et al., 2011). Future studies should examine change in foraging performance over a broader range of age classes, including much older birds, to investigate the effects of senescence on the physical abilities of birds to dive and hunt prey. Finally, it would also be interesting to explore additional parameters, such as reproductive experience (e.g. Moyes et al., 2009) and hormonal or immunological state (Angelier et al., 2007).

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Table S1

Summaries of best models explaining (a) PDBA, (b) swimming speed, (c) and relationship PDBA/Speed, during the descent phase.

(A)

	Estimate	Std.Error	t-value	p-value
(Intercept)	1.407	0.022	64.537	<0.001
Maximum Depth	0.001	3×10^{-5}	27.625	<0.001
Current Depth	-0.009	7×10^{-5}	-131.058	<0.001
Age Class (Young-Old)	0.106	0.036	2.908	0.008
Maximum Depth*Current Depth	2×10^{-5}	3×10^{-7}	57.985	<0.001
Maximum Depth*Age Class	-0.001	4×10^{-5}	-13.517	<0.001
Current Depth*Age Class	4×10^{-4}	3×10^{-5}	10.143	<0.001

(B)

	Estimate	Std. Error	t-value	p-value
(Intercept)	2.489	0.107	23.359	<0.001
Maximum Depth	-0.002	7×10^{-5}	-28.949	<0.001
Current Depth	0.009	1×10^{-4}	71.583	<0.001
Sex (Male-Female)	-0.010	0.102	-0.094	0.926
Age Class (Young-Old)	0.140	0.107	1.291	0.212
Year (2010-2009)	-0.416	0.106	-3.920	0.001
Maximum Depth*Sex	-3×10^{-4}	6×10^{-5}	-5.431	<0.001
Current Depth*Sex	0.001	5×10^{-4}	22.467	<0.001
Maximum Depth*Age Class	-5×10^{-4}	7×10^{-5}	-7.941	<0.001
Current Depth*Age Class	0.001	6×10^{-5}	21.284	<0.001
Maximum Depth*Current Depth	-2×10^{-5}	1×10^{-7}	-38.766	<0.001
Maximum Depth*Year	0.002	6×10^{-5}	39.789	<0.001
Current Depth*Year	-0.003	5×10^{-5}	-56.530	<0.001

(C)

	Estimate	Std.Error	t-value	p-value
(Intercept)	-95.227	42.594	-2.236	0.025
Maximum Depth	0.001	2×10^{-5}	32.016	<0.001
Current Depth	-0.004	3×10^{-5}	-118.063	<0.001

Age Class (Young-Old)	0.006	0.020	0.318	0.754
Year (2010-2009)	0.048	0.021	2.250	0.037
Body Condition	-0.027	0.012	-2.363	0.029
Maximum Depth*Current Depth	1×10^{-5}	1×10^{-7}	51.240	<0.001
Maximum Depth *Age Class	-2×10^{-4}	2×10^{-5}	-11.518	<0.001
Current Depth*Age Class	2×10^{-4}	2×10^{-5}	9.530	<0.001

Table S2

Summaries of best models explaining (a) PDBA, (b) swimming speed, (c) and relationship PDBA/Speed, during the ascent phase.

(A)

	Estimate	Std.Error	t-value	p-value
(Intercept)	0.110	0.0290	3.802	<0.001
Maximum Depth	-7×10^{-4}	4×10^{-5}	-18.115	<0.001
Current Depth	0.009	8×10^{-5}	109.983	<0.001
Sex (Male-Female)	-0.006	0.036	-0.178	0.860
Age Class (Young-Old)	0.058	0.038	1.547	0.137
Maximum Depth*Current Depth	-2×10^{-5}	4×10^{-7}	-56.704	<0.001
Maximum Depth*Age Class	-3×10^{-4}	5×10^{-5}	-6.614	<0.001
Current Depth*Age Class	4×10^{-4}	4×10^{-5}	9.741	<0.001
Current Depth*Sex	2×10^{-4}	4×10^{-5}	5.279	<0.001

(B)

	Estimate	Std. Error	t-value	p-value
(Intercept)	2.392	0.087	36.280	<0.001
Maximum Depth	0.002	8×10^{-5}	24.003	<0.001
Current Depth	-0.008	2×10^{-4}	-43.162	<0.001
Sex (Male-Female)	-0.022	0.082	-0.273	0.788
Age Class (Young-Old)	-0.098	0.085	-1.162	0.259
Maximum Depth*Sex	3×10^{-4}	1×10^{-4}	3.477	<0.001
Current Depth*Sex	-2×10^{-4}	1×10^{-4}	-2.681	0.007
Current Depth*Age Class	4×10^{-4}	1×10^{-4}	4.391	<0.001
Maximum Depth*Current Depth	2×10^{-5}	1×10^{-6}	19.996	<0.001

(C)

	Value	Std.Error	t-value	p-value
(Intercept)	0.079	0.014	5.746	<0.001
Maximum Depth	-6×10^{-4}	4×10^{-5}	-16.663	<0.001
Current Depth	0.005	9×10^{-5}	61.860	<0.001
Age Class (Young-Old)	0.034	0.023	1.478	0.154
Maximum Depth*Current Depth	-1×10^{-5}	4×10^{-7}	-31.848	<0.001
Maximum Depth*Age Class	-2×10^{-4}	5×10^{-5}	-4.186	<0.001

Current Depth*Age Class	3×10^{-4}	5×10^{-5}	7.158	<0.001
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