Reduced activity in middle-aged thick-billed murres: evidence for age related trends in fine-scale foraging behaviour

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Several biological functions, such as reproductive success, peak during middle age in long-lived vertebrates. One possible mechanism for that peak is improved foraging performance during middle age, after a period of youthful inexperience and before senescence. Age may be particularly important in relating foraging behaviour to fitness for diving animals as altered skeletal muscle contraction efficiency or cardiovascular function could play a strong role at the scale of a single dive. Miniaturized accelerometers provide the opportunity to measure fine-scale foraging behaviour at the scale of a single wing beat. To examine the relationship between age and foraging behaviour in a diving seabird, whose reproductive success peaks during middle age, we equipped 115 thick-billed murres, Uria lomvia, with accelerometers and depth loggers. Murre activity (i.e. dynamic body acceleration) decreased with increasing dive depth during descent but increased with increasing maximum depth achieved. These patterns were inversed during ascent. After accounting for depth and maximum depth, middle-aged birds had low activity levels during the dive, compared with old and young birds, suggesting that old and young birds were less efficient at diving and foraging than middle-aged birds. Young individuals appeared to struggle at depths above 20 m during descent and throughout ascent when compared to middle-aged birds, while old individuals struggled at the end of deep dives during descent and during the initial parts of ascent when compared to the same middle-age class. We conclude that there is a link between foraging behaviour and age, contrary to previous findings. By examining foraging behaviour at a fine-scale, such as a dive, different energy expenditures across age groups were revealed, giving us insight on how seabirds are affected by senescence in the wild.
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Ageing, the process of deterioration of biological functions with chronological age, occurs in virtually all multicellular life forms, from microscopic organisms to large marine mammals (Jones et al., 2014; Péron, Gimenez, Charmantier, Gaillard, & Crochet, 2010). However, ageing is far better understood in short-lived, laboratory organisms, such as round worms (Caenorhabditis elegans) or fruit flies (Drosophila melanogaster), than long-lived, wild animals (Jones et al., 2014; Péron et al., 2010; Ricklefs, 2010; Williams, 1957). Across a wide range of wild vertebrates, reproductive success peaks at middle ages (e.g. Elliott, O'Reilly, et al., 2014; Reid, 1988; Rockwell, Findlay, & Cooke, 1985). Likewise, a common pattern for vertebrates in the natural environment is an increase in foraging performance until middle age, followed by a decline in foraging performance as the organism senesces (Martin, 1995; Péron et al., 2010). In particular, mass gained per time spent foraging is higher in middle-aged seabirds than in young (e.g. Fayet et al., 2015) or old (e.g. Catry, Phillips, Phalan, & Croxall, 2006; Lecomte et al., 2010) individuals. Thus, the peak in reproductive success at middle ages is mirrored with a peak in foraging success.

Lower foraging success in young animals can be attributed to being physically immature or lacking foraging experience (Desrochers, 1992; Martin, 1995; Sullivan, 1988). Likewise, in old

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animals, lower foraging success is thought to be linked to physiological senescence through reduced muscle function affecting athletic ability (Hindle, Horning, Mellish, & Lawler, 2009; Hindle, Lawler, Campbell, & Horning, 2010). However, in some cases, old animals have similar foraging time budgets to middle-aged animals (Elliott, Hare, et al., 2014; Froy et al., 2015; Hindle & Horning, 2010), perhaps, because increased experience among old animals masks any decline in athletic ability (e.g. by better choice of foraging location, time of day, etc.), or, perhaps, because old animals reduce investment in body maintenance, their offspring, or both to maintain a balanced time budget (e.g. seabirds could adjust their underwater behaviour so that overall time budgets are not affected). To examine relative likelihood of these two explanations, it is important to understand how physiological senescence reduces foraging performance in old birds.

Connections between foraging behaviour and age may be particularly apparent in diving animals because changes in foraging efficiency are likely to have measurable and important implications at the scale of a dive (Hindle & Horning, 2010; Le Vaillant et al., 2012; Zimmer, Ropert-Coudert, Kato, Ancel, & Chiaradia, 2011). Oxygen stores, oxygen consumption rate, swimming speed and buoyancy affect the energetic costs of diving (Biuw, McConnell, Bradshaw, Burton, & Fedak, 2003; Elliott, Davoren, & Gaston, 2007; Ropert-Coudert et al., 2004) and vary with the age of an individual (Elliott, Hare, et al., 2014; Kooyman & Ponganis, 1998; Le Vaillant et al., 2012). Optimal inhalation of oxygen is also a key factor in diving that can affect the behaviour of a diving bird (Croll, Gaston, Burger, & Konnoff, 1992; Le Vaillant et al., 2012; Sato et al., 2002) and ultimately dive efficiency. The amount of oxygen inhaled prior to diving is related to the energy expended during a series of dives (Wilson et al., 2003): large inhalations prior to dives are disadvantageous due to increased buoyancy in shallow water, but are also needed to maintain sufficient oxygen stores during dives (Le Vaillant et al., 2012; Wilson, Hustler, Ryan, Burger, & Noldeke, 1992). In general, diving seabirds must work hard as they descend the water column to overcome the effects of buoyancy, but work progressively less as they reach the point of neutral buoyancy. It is at this depth from which they ascend passively during ascent (e.g. Elliott et al., 2007; Lovvorn, Croll, & Liggins, 1999; Lovvorn, Watanuki, Kato, Naito, & Liggins, 2004). With experience comes a greater ability to optimize diving compared to young and middle-age seabirds, as in the case with king penguins, *Aptenodytes patagonicus* (Le Vaillant et al., 2012). There are no studies involving the differences in biomechanical parameters with ageing seabirds, although dive behaviour could change with age at a fine scale within a dive.

Here we used accelerometers to investigate how fine-scale behaviour changes with age in long-lived diving birds, thick-billed murres, *Uria lomvia*. The application of miniaturized accelerometers to behavioural ecology offers the possibility of measuring reduced athleticism due to altered muscle performance independent of other potential causes of senescence, such as reduced brain function leading to impaired ability to find or remember food locations. Indeed, altered muscle performance should manifest itself primarily at very short timescales such as quick bursts of speed generated by intense short-term wing beats (Le Vaillant et al., 2012). Dynamic body acceleration (DBA) is the dynamic component of activity measured by accelerometry that is obtained after removing the component due to gravity associated with body posture (Wilson et al., 2006). DBA is an interesting variable to use in examination of physical ageing processes as DBA correlates strongly with activity, wing beat frequency and amplitude and energy expenditure in captive or free-ranging birds (Elliott, Chivers, et al., 2014; Elliott, Le Vaillant, Kato, Speakman, & Ropert-Coudert, 2013; Green, Halsey, Wilson, & Frappell, 2009;

Halsey, Green, Wilson, & Frappell, 2009; Stothart, Elliott, Wood, Hatch, & Speakman, 2016). Murres must utilize muscles for different wing beat frequencies in air and water, which could increase the wear and tear of muscles and aggravate the ageing process (Elliott, Hare, et al., 2014; Elliott, Ricklefs, et al., 2013;. For instance, physiological systems (oxygen stores and consumption rate) decay with age in murres, yet these processes cancel one another such that dive duration is unchanged (Elliott, Hare, et al., 2014).

Assuming that individuals control inhaled air volume (Sato et al., 2002; Wilson et al., 1992), we predicted that buoyancy, and therefore DBA, would decrease with depth and increase with maximum depth in thick-billed murres. We expected foraging effort to follow a nonlinear relationship similar to that between reproductive behaviour and age (Elliott, O'Reilly, et al., 2014), and we predicted that there would be a nonlinear relationship between DBA and age. We considered two possible hypotheses aside from the null hypothesis that age does not affect dive activity: (1) the 'activity peak hypothesis', in which middle-aged birds have the ability to expend more energy, enabling more intense foraging periods compared to younger and older birds, predicting that DBA per dive would peak in middle age; (2) the 'inactivity peak hypothesis', in which middle-aged birds would be more efficient divers and expend less energy than other age classes when foraging, predicting that DBA per dive would be lower in middle age compared to other age classes. We also examined how body angle during diving varied across ages, as this is an important characteristic of a dive and could help decipher any results from DBA.

METHODS

Ethical Note

All works adhere to the ASAB/ABS Guidelines for the use of animals in research. Methods were approved by the University of Manitoba in accordance with the guidelines of the Canadian Council on Animal Care (Protocol number F11-020; Elliott, Hare, et al., 2014), and permits for the handling of wild birds were acquired from the Canadian Wildlife service (2009-10: NUN-SCI-08-55, NUN-SCI-09-01; 2011: NUN-SCI-11-07) and the Government of Nunavut (2009-044, 2009-046, 2010-032, 2011-048). Birds were fitted with an accelerometer-depth logger (M190-D2GT, Little Leonardo, Tokyo, Japan) on the posterior end of their back, and released for 24–48 h (depth sampled at 1 Hz, acceleration along two axes (surging and heaving) at 16 Hz in 2009, 32 Hz in 2010–2011). Devices were 18 g, or $1.8 \pm 0.1\%$ of the bird's body weight, which was below the recommended limit of 3% for flying birds (Phillips, Xavier, & Croxall, 2003), yet likely still had a small impact on dive depth, duration and drag and offspring provisioning rates (Elliott et al., 2007; Paredes, Jones, & Boness, 2005; Vandenabeele et al., 2015). Larger back-mounted devices reduce dive depth and duration (Elliott et al., 2007) and offspring provisioning rates (Elliott, Woo, et al., 2008). During this study, no chick-rearing individuals were observed losing a chick after accelerometer deployment; however, two of the 24 individuals sampled during incubation lost their egg, which is not an unusual rate of failure at this study site.

Study Organism

The murre was chosen as a suitable model organism for studying the effect of senescence on the foraging behaviour of long-lived diving birds because of the high energy costs that accompany flying and diving throughout their long life span (Elliott, Ricklefs,

et al., 2013), with the possibility that improvement early in life and deterioration late in life might be associated with changes in energy expenditure. Through the sampling of many hundreds of thousands of banded murres, the oldest recorded murre was 32 years old (Elliott, Hare, et al., 2014). Furthermore, reproductive success increases with age over the first 10 years of life, and then reaches a plateau, before declining later in life (mid-20s; Elliott, O'Reilly, et al., 2014). Thus, the age range used in this study (4–28 years of age) was representative of the age range present in wild murres and known to be associated with variation in reproductive success. The colony at which murres were sampled has been followed extensively since 1981.

Data Collection and Analysis

We used a noose pole to capture chick-rearing ($N = 112$ sample periods from 95 individuals) and incubating ($N = 24$ sample periods from 24 individuals) murres breeding on Coats Island, NU, Canada (62°34′60″N, 82°45′W; Gaston, Gilchrist, & Hipfner, 2005), during July and August from 2009 until 2011. We deployed in groups of five to eight individuals, and we categorized each deployment as a 'deployment period'. Many of the sampled birds were banded at their nest sites the year they hatched. Individuals that were not banded as a chick, had 5 years added to the number of years since they were first banded to give an estimated age, as very few birds are captured before the age of 5 (Table 1; Elliott, Hare, et al., 2014; de Forest & Gaston, 1996).

The accelerometers recorded accelerometry data in bits, which were later converted to acceleration (g) by subtracting the zero offset and dividing the bit value by 500. To provide balanced sample sizes across environmental conditions, and according to breeding categories, we deployed two to three accelerometers on young birds (<10 years old), two to three accelerometers on middle-aged birds (10–20 years old) and two to three accelerometers on old birds (>20 years old) during each deployment session (every 2–3 days), although in two cases, the accelerometer data became corrupt and no data was obtained (Table 1). Six sampled birds were excluded as they were banded as adults outside of the sampling plot and thus were of an unknown age. All raw data files are archived with Elliott, Hare, et al. (2014).

Data collected from sampled murres were analysed in IGOR Pro (v.6.35A5, WaveMetrics, Portland, OR, U.S.A.). To calculate partial dynamic body acceleration, PDBA, we used the box smooth function of IGOR Pro, with time intervals of 1 s, to generate the static component ($\overline{A}$). The term 'partial' in PDBA refers to the absence of data from a third axis in our accelerometers, in contrast with the original Overall Dynamic Body Acceleration defined by Wilson et al. (2006). PDBA is then given by the formula:

$$\text{PDBA} = \left| A_x - \overline{A_x} \right| + \left| A_y - \overline{A_y} \right|$$

where A is acceleration in either the x (dorso–ventral) or y (head–tail) axis. PDBA was averaged at 1 Hz intervals. Dives were then analysed using a Microsoft Excel (for Mac, v.14.1.0, Microsoft Corporation) macro that would recognize a dive (defined as >3 m in depth, to ensure dives were for foraging purposes; Croll et al., 1992). Dives were split into three phases: descent and ascent phases, separated by a bottom phase defined as occurring below 80% of the maximum depth for each dive. For each dive, we recorded maximum depth achieved, current depth for each second sampled, and the PDBA for each second sampled during the dive.

Given the complex nonlinear relationships between PDBA, depth and maximum depth, we binned the data in each dive phase into maximum dive depth and current depth bins of 10 m intervals from 0 m to 90 + m. Each bin was given a letter code that defined the current depth–maximum depth combination for that bin in our statistical analyses (e.g.: 'A' was assigned to a current depth of 0–10 m for dives with a maximum depth of 0–10 m; 'B' was assigned to a current depth of 0–10 m for dives with a maximum depth of 10–20 m, etc.). Thus, every second sampled was associated with a bin letter. For the descending and ascending dive phases, PDBA per second of diving was averaged for each bin. These PDBA averages within each bin were plotted against depth (m) and maximum depth (m) to create the graphs in Fig. 1 and were not used in the statistical analysis. Deployment period (a letter accounting for the time of deployment, with each group of five to eight accelerometers receiving a different letter) accounted for the year and reproductive stage of sampled individuals. Intrinsic differences, such as age of chick or reproductive status (egg versus chick), and extrinsic differences, such as wind speed, food availability or year, was accounted for within the deployment period term as all individuals within a given deployment were of the same status and, if they had a chick, with a chick of approximately the same age. Because each second sampled was associated with an individual, it was also associated with a deployment period as well.

Similarly to PDBA, logger angles were calculated from the static component of acceleration using the following equation:

$$\text{Logger angle} = \arctan\left(\overline{A_y} \big/ \overline{A_x} \right)$$

Assuming the bird's body angle was ~0° when it rested at the surface of the water, logger angles were converted to body angles using the following equation:

$$\theta = \text{logger angle} - \alpha$$

where θ is body angle in relation to the horizon, logger angle is the angle recorded during sampling, and α is the angle at which the logger was attached to the bird's back, or attachment angle (Sato, Mitani, Cameron, Siniff, & Naito, 2003; Watanuki, Niizuma, Gabrielsen, Sato, & Naito, 2003; Watanuki & Sato, 2008). Attachment angles were determined by selecting the most consistent logger angle when the bird was resting on the water's surface. Each second of sampling for body angles was associated with the corresponding deployment period and current depth–maximum depth bin combination, as described above for PDBA.

Table 1
Number of sampled individuals of each age class (young≤10 years old; middle-aged = 11–19 years old; old≥20 years old) banded as chicks or adults for each sampled year and reproductive stage

Age class	Incubation		Chick rearing					
	Banded as chick	Banded as adult	Banded as chick			Banded as adult		
	2009	2009	2009	2010	2011	2009	2010	2011
Young	9[a]	0	15	8	0	2	4	6
Middle-aged	7[a]	0	15	18	5	1	7	3
Old	4	4	11	8	3	4	1	1

[a] Indicates samples where data from one individual was not available because the data became corrupt.
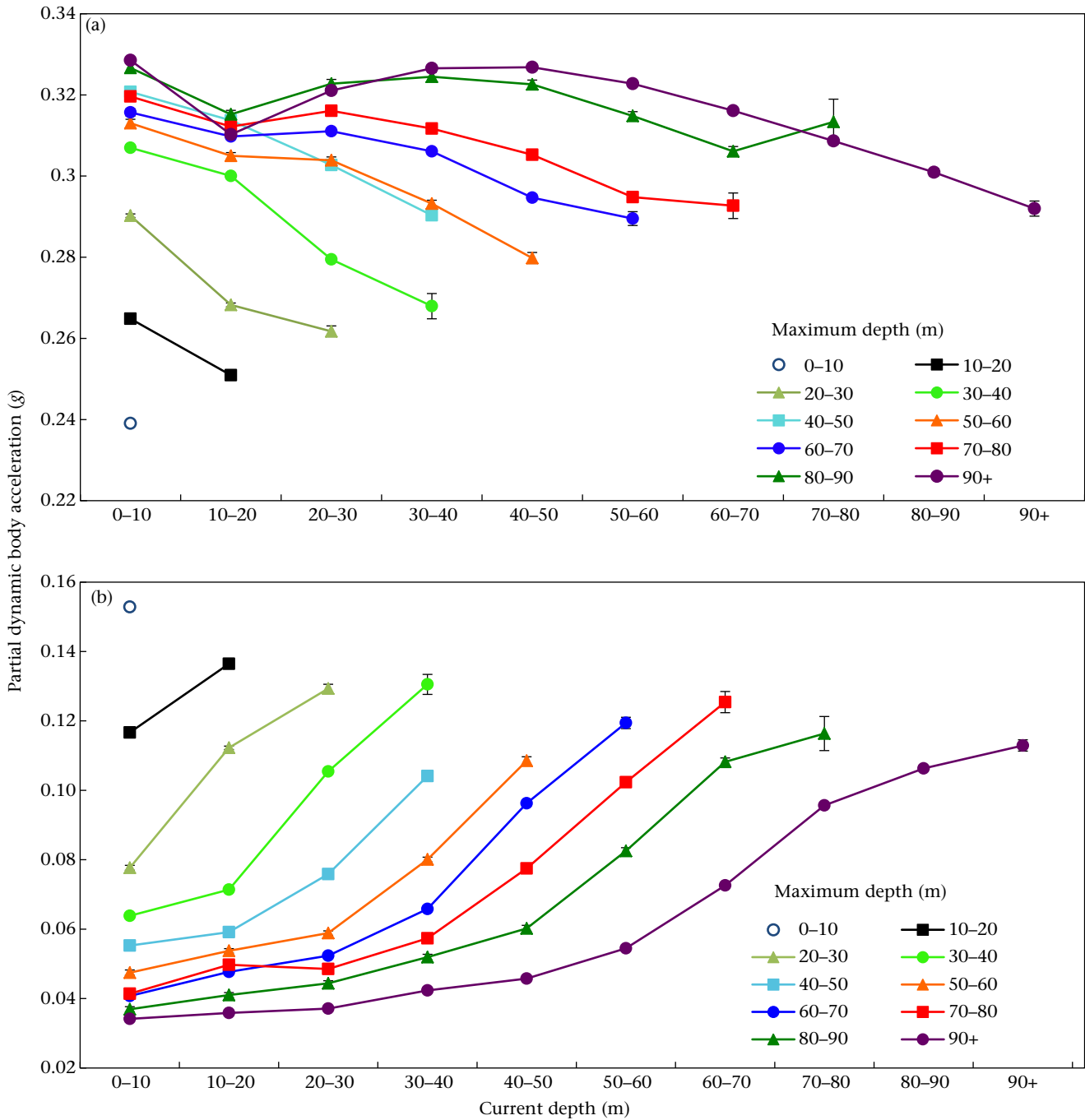
Figure 1. Relation between mean partial dynamic body acceleration (*g*), current depth (m) and maximum depth (m) during the (a) descending phase and (b) ascending phase of a dive for chick-rearing thick-billed murres. Symbols represent average dynamic body acceleration (with respective standard error bars) for sampled individuals within each 10 m bin of maximum depth achieved. Descent and ascent phase depths were defined as 80% of the maximum depth achieved.

Statistical Analysis

All statistical tests were run in the R statistical environment (R Core Team, 2014). A linear mixed effects model ('lme4' package; Bates, Maecheler, Bolker, & Walker, 2014) was created with PDBA as an output, comparing mass, age and age^2 (as covariates) between the murres in each bin group (the given combination of maximum depth and current depth), with individual, bin and deployment period as random effects for every second sampled during the descending, bottom and ascending phases. An identical linear mixed effects model was also created with body angle as the output

for the descending and ascending phases of the dives to test for differences between ages. Age^2 was included in both models to account for potential nonlinear relationships between age and PDBA or body angle.

Filled contour plots were created to assess the inter-age difference of activity and body angle between younger (≤15 years old) and older (>15 years old) individuals ('akima' package; Akima & Gebhardt, 2015). These age classes were defined using the age at which PDBA bottomed out in our previous models, showing that before the age of 15, PDBA decreases per year of age, and after 15, PDBA increases per year of age, allowing comparison of PDBA

differences between each side of this 'peak'. We also used these plots to assess activity and body angle differences between young ($\leq$10 years old) and middle-aged (11—19 years old) individuals, and between middle-aged and old ($\geq$20 years old) individuals. A P value of less than 0.05 was considered statistically significant for all analyses. We tested for homogeneity of variance, normality of residuals via Cook's distance prior to using linear mixed effects models.

RESULTS

PDBA decreased with an increase in current depth during the descent phase (Fig. 1a) and decreased over the ascent phase with decreasing current depth (Fig. 1b). For a given depth, PDBA increased with maximum depth during descent and decreased with maximum depth during ascent (Fig. 1). PDBA varied non-linearly with age and mass during all three of the dive phases (Table 2). PDBA decreased with age until the age of 15 during the descent (Fig. 2a) and bottom (Fig. 2b) phases, and until the age of 16 during the ascent phase of the dive (Fig. 2c). When two defined age classes were compared to each other, young individuals ($\leq$15 years old) had a higher PDBA than old individuals (>15 years old) throughout the descent (Fig. 3a). During the ascent, young individuals had higher PDBA than old individuals in between depths of 40 m and 70 m (the depth of neutral buoyancy; Lovvorn et al., 1999; Lovvorn et al., 2004) during dives with a maximum depth over 60 m, and during shallow dives to a maximum depth of 30 m (Fig. 3b). When a middle-aged class (11—19 years old) was introduced and compared to young ($\leq$10 years old) individuals, young murres had a higher PDBA compared to middle-aged murres during the first 20 m of descent (Fig. 4a) and throughout the ascent of the dive (Fig. 4b). When comparing middle-aged murres and old ($\geq$20 years old) murres, old individuals had a higher PDBA in the later parts (>70 m) of the dive's decent, for dives over 90 m in depth (Fig. 5a). During ascent, old birds generally had a higher PDBA than middle-aged birds during the start of ascent for all dives except those in between 60 m and 80 m in maximum depth (Fig. 5b).

Body angle decreased with age and increased with age[2] and mass (Table 3). When body angle was limited to two age classes, young ($\leq$15 years old) and old (>15 years old), old individuals tended to descend with a steeper body angle during dives over a maximum depth of 60 m, while young individuals descended with a steeper body angle during shallower dives (<50 m in maximum depth) (Fig. 6a). Old individuals ascended with a steeper body angle throughout the ascent phase (Fig. 6b). When age was split into three classes: young ($\leq$10 years old), middle-aged (11—19 years old) and old ($\geq$20 years old), middle-aged individuals generally positioned themselves with steeper body angles during descent and ascent, when compared to the young and old age classes. Specifically, middle-aged individuals performed dives with steeper body angles throughout the whole dive when compared to young individuals (Fig. 7) and throughout the descent phase when compared to old individuals (Fig. 8a). However, old individuals ascended with a steeper body angle during dives over 70 m, and within 20 m of the water's surface, during dives in between 30 m and 50 m in maximum depth (Fig. 8b).

DISCUSSION

Similar to our initial prediction, we found that PDBA decreased with depth and increased with maximum depth during descent. Likewise, PDBA varied with age during all dive phases. Middle-aged birds expended less energy during dives compared to older and younger birds in support of the 'inactivity peak hypothesis'. The increased activity in the young and old age classes could represent a lack of foraging experience and a decline in physique, respectively. PDBA is considered a proxy for energy expenditure, and thus, PDBA can be reflective of how hard an individual 'worked' during a specific current depth—maximum depth combination. Body angle varied with age, with middle-aged birds diving at a steeper angle than young or old birds, consistent with the 'inactivity peak hypothesis' that middle-aged birds are more efficient divers. PDBA and body angle also varied with mass, but it has been shown that changes in mass are related to age (noticeably in birds under the age of 12) and reproductive stage (a significant decline in body mass occurs from incubation to chick-rearing periods) in thick-billed murres (Croll, Gaston, & Noble, 1991; Gaston & Hipfner, 2006), and because acceleration itself is inversely proportional to body mass by Newton's second law.

Relationship Between Maximum Depth, Current Depth and Dynamic Body Acceleration

During the descent phase of the dive, murres expended more energy near the surface and displayed a secondary peak in PDBA beginning at a depth of 20—30 m (Fig. 1a). This is the depth at which the effects of buoyancy are most prevalent, and the increase in PDBA at this depth indicates that murres were working hard to overcome this effect (Lovvorn et al., 1999, 2004). However, as they continued the dive, they became less buoyant, requiring less energy or work (a lower PDBA) to move deeper (Elliott et al., 2007; Lovvorn et al., 1999, 2004). PDBA during descent also increased with maximum depth, possibly because birds are aware of the maximum depth they are going to achieve prior to diving and adjust the amount of oxygen they inhale (Elliott et al., 2007; Sato et al., 2002; Wilson et al., 2003; Wilson & Zimmer, 2004). Constraints associated with deeper dives could also influence the PDBA of individuals. Deeper dives require more time underwater, and this can cause murres to push the boundaries of their aerobic dive limit (ADL; Croll et al., 1992). As small divers, murres are at a disadvantage during lengthy dives (Croll et al., 1992) and commonly exceed their predicted ADL, despite this activity being physiologically costly (Croll et al., 1992; Elliott, Davoren, & Gaston, 2008). However, the effect of exceeding ADL has not been studied with respect to age and may influence the PDBA of individuals in different age classes. Similarly to the descent, murres worked harder during ascent when starting at shallow depths (Fig. 1b). When ascending from deeper depths, individuals worked hard until 50—60 m, at which they are neutrally buoyant and used their natural buoyancy to return to the surface, showing the decrease in PDBA as the bird ascended in Fig. 1b. In parallel to the patterns during descent, birds diving to a deeper maximum depth ascended passively from a deeper depth because they presumably inhaled more air prior to deep dives and

Table 2
Partial dynamic body acceleration as function of age, age[2] and body mass, with deployment period, bin and individual as random effects

Dive phase	Intercept	SE	Age	Age[2]	Mass (g)
Descent	0.94	0.08	$t_{180}=-8.10, P<0.001$	$t_{180}=10.56, P<0.001$	$t_{180}=-10.97, P<0.001$
Bottom	0.88	0.05	$t_{130}=-8.10, P<0.001$	$t_{130}=9.57, P<0.001$	$t_{130}=-18.23, P<0.001$
Ascent	0.18	0.03	$t_{180}=-2.02, P=0.045$	$t_{180}=2.00, P=0.047$	$t_{180}=-4.04, P<0.001$

t values, degrees of freedom and P values are shown for age, age[2] and mass for each dive phase ($N = 136$).
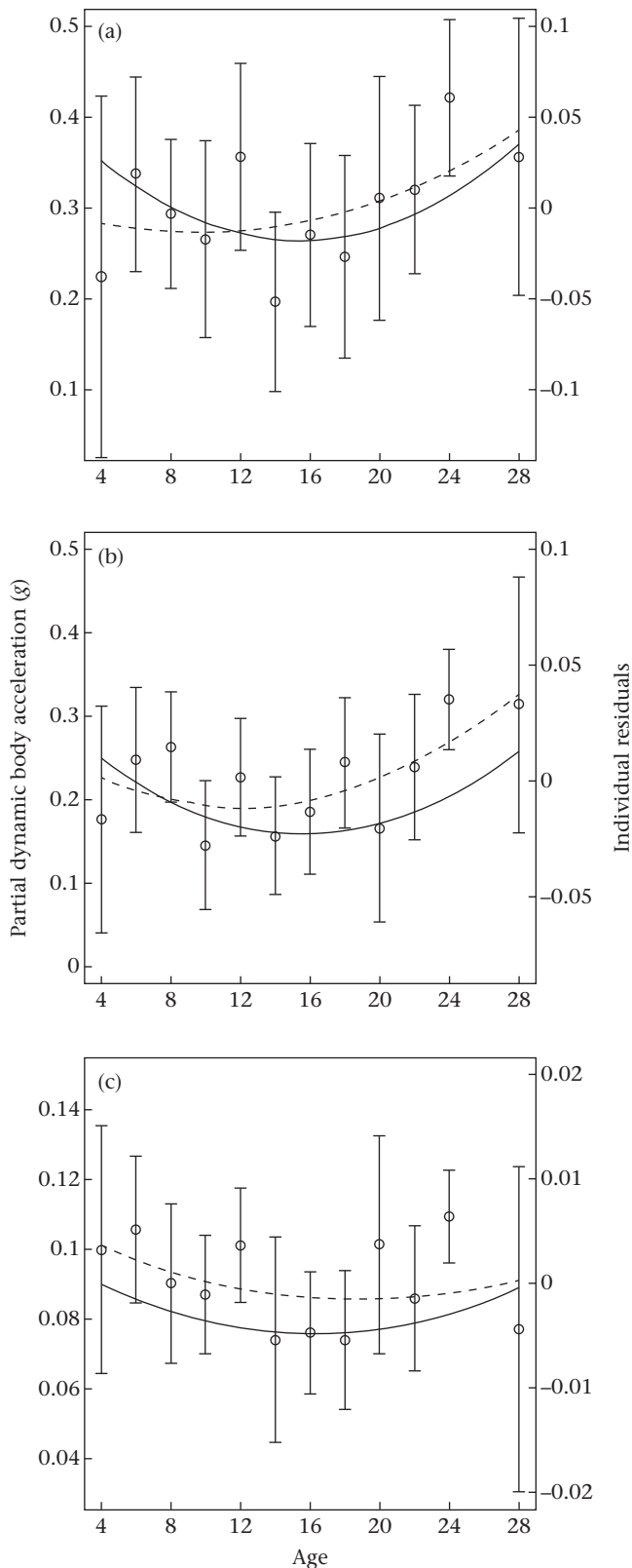
Figure 2. Partial dynamic body acceleration as a function of age during (a) descent ($R^2 = 0.30$), (b) bottom phase ($R^2 = 0.46$) and (c) ascent ($R^2 = 0.14$) for thick-billed murres. Solid lines are derived from the model outputs (model parameters described in Table 2) after accounting for current depth and maximum depth. Individual residuals are binned in 2-year increments (e.g. 4 = averaged over all 4–5-year-olds; 6 = averaged over all 6–7-year-olds, etc.) in order to account for the bias of some ages being represented by a single individual. Dotted lines represent the line of best fit from which the R^2 were acquired.

therefore were more buoyant and required less effort (fewer or weaker wing beats per second) to ascend.

Support for the 'Inactivity Peak Hypothesis'

In support of the 'inactivity peak hypothesis', PDBA was lower in middle-aged birds compared to old and young individuals for the three dive phases (Table 2, Fig. 2). The increased PDBA in old and young murres compared to middle-aged individuals could be explained by an increase in wing beat frequency or wing beat amplitude. Old individuals may need to exert more energy by beating their wings more frequently in order to achieve deep foraging depths to compensate for a declining physique. Similarly, young individuals may lack experience and overexert the number of wing beats required in order to descend the water column, or improperly angle their body during the dive. For example, in this study, young birds had shallower body angles throughout dives, compared to middle-aged and old birds (Figs. 6, 7). This corresponds with results from Watanuki et al. (2006), who found that frequency of wing strokes increased for common murres, *Uria aalge*, that dived with a shallower body angle, especially during shallow dives. During deep dives, murres generally display steep body angles, diving at almost vertical angles (Watanuki & Sato, 2008; Watanuki et al., 2006). In support of that idea, dive angle was steeper in middle-aged birds than in young or old birds (Table 3, Figs. 7, 8). Apparently, young or old birds were unable to maintain accurate buoyancy; thus, they were unable to go as directly as possible from the surface to the bottom and back (steep body angle). Suboptimal buoyancy, either due to variation in air trapped in the plumage or the lungs and airsac, could be the product of either poor feather structure (or inadequate preen oil) or an inability to accurately predict the correct amount of air to inhale. Therefore, improper positioning during diving, caused by suboptimal buoyancy, could increase drag and wing beat frequency, and in turn, increase energy expenditure.

The increased activity (PDBA) during deep dives in old birds may reflect physiological senescence in athletic capacity (Heinze & Schrempf, 2012; Hindle et al., 2009). Note, however, that increased PDBA does not necessarily infer foraging success. For instance, a recent algorithm that calculated foraging attempts in murres also incorporated rapid variation in pitch angle (Chimienti et al., 2016). Elliott, Hare, et al. (2014) found that blood oxygen stores (haematocrit) and resting metabolic rate declined with age in thick-billed murres. The reduction in resting metabolic rate (Elliott, Hare, et al., 2014), likely reflecting basal processes during the dive, may offset increased activity (our study), explaining why dive duration did not change with age.

In support of a connection between reduced athletic ability during diving and age, the differences in PDBA between old and young birds was most pronounced when murres were required to beat their wings strongly. For instance, during ascent the difference was most pronounced around the depth of neutral buoyancy (~70 m) and during shallow dives (<30 m; Fig. 3b). Below the depth of neutral buoyancy, murres must expend energy to ascend, whereas above that depth murres can ascend passively with little effort. During ascent, young individuals appeared to struggle at the depth of neutral buoyancy compared to middle-aged individuals (Fig. 4b). However, middle-aged individuals also appeared to struggle at these depths when compared to old individuals (Fig. 5b). This pattern of old murres performing better at the depth of neutral buoyancy suggests that experience may play a role in efficiently swimming at this transition depth. This point is strengthened by the fact that old individuals also ascended with steeper body angles at these depths (Figs. 6b, 8b), allowing for less drag during the ascent (Watanuki et al., 2006). For young
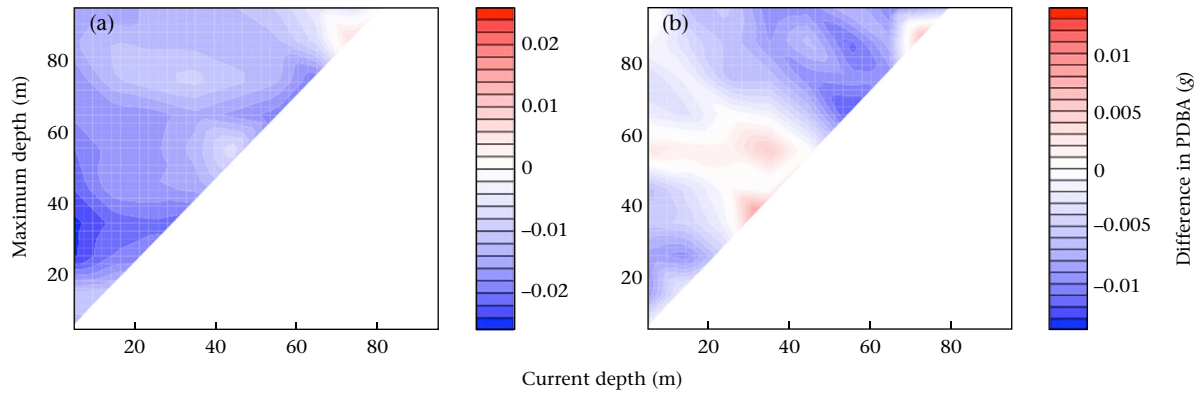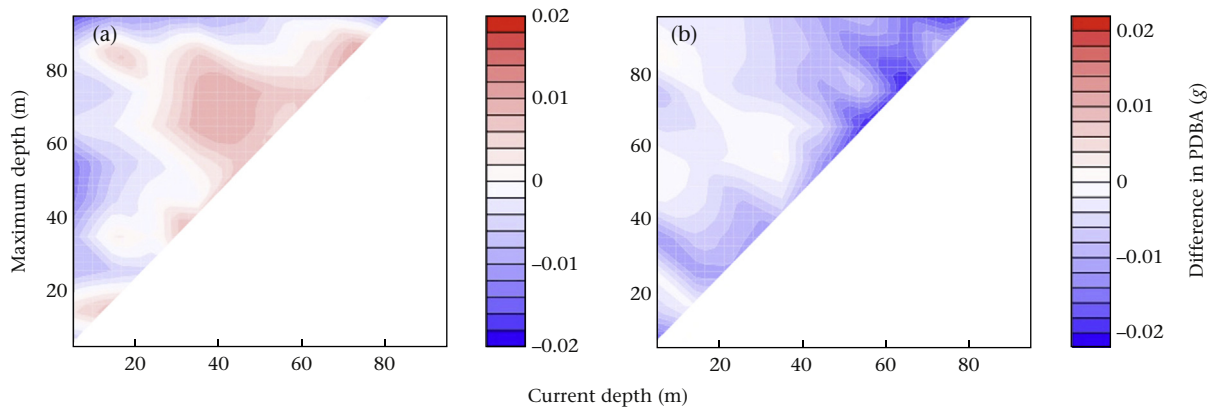
Figure 3. Mean difference in partial dynamic body acceleration (PDBA, *g*) between old (>15 years old) and young (≤15 years old) murres depending on the maximum depth (m) and the current depth (m) during (a) the descent phase and (b) the ascent phase of the dive. Negative values (blue) indicate that younger individuals had a larger PDBA, and positive values (red) indicate that older individuals had a larger PDBA. Darker colours represent a larger difference in PDBA values between age classes. Lighter colours represent a smaller difference in PDBA where values were similar for both age classes. A white colouring represents little to no difference in PDBA between age classes.
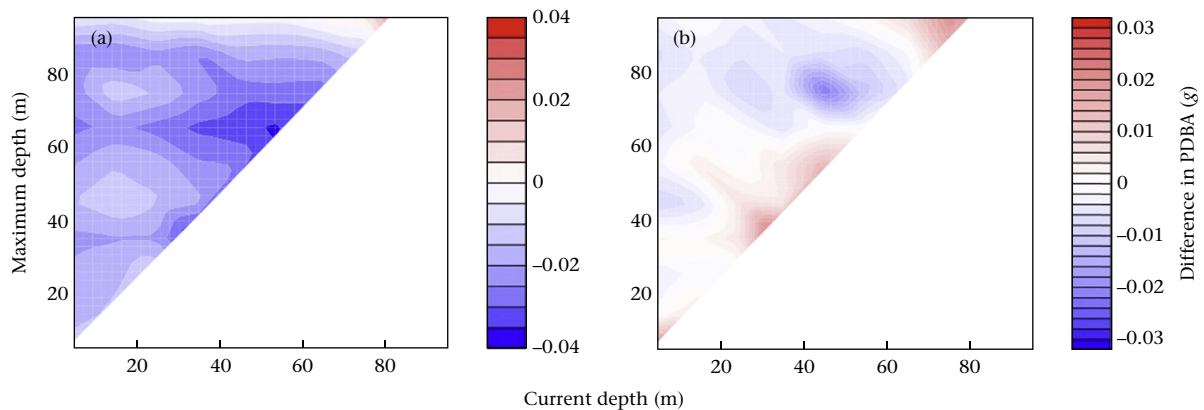

Figure 4. Mean differences in partial dynamic body acceleration (PDBA, *g*) between middle-aged (11–19 years old) and young (≤10 years old) murres depending on the maximum depth (m) and the current depth (m) during (a) the descent phase and (b) the ascent phase of the dive. Negative values (blue) indicate that young individuals had a larger PDBA, and positive values (red) indicate that middle-aged individuals had a larger PDBA. Darker colours represent a larger difference in PDBA values between age classes. Lighter colours represent a smaller difference in PDBA where values were similar for both age classes. A white colouring represents little to no difference in PDBA between age classes.

Figure 5. Mean differences in partial dynamic body acceleration (PDBA, *g*) between old (≥20 years old) and middle-aged (11–19 years old) murres depending on the maximum depth (m) and the current depth (m) during (a) the descent phase and (b) the ascent phase of the dive. Negative values (blue) indicate that middle-aged individuals had a larger PDBA, and positive values (red) indicate that old individuals had a larger PDBA. Darker colours represent a larger difference in PDBA values between age classes. Lighter colours represent a smaller difference in PDBA where values were similar for both age classes. A white colouring represents little to no difference in PDBA between age classes.

individuals the difference was most pronounced above 20 m in depth during descent (Figs. 3a, 4a), suggesting that young birds faced difficulties at those depths, potentially due to their shallower body angle (Fig. 7a). Old individuals tended to expend more energy

during the final part of the descent during deep dives (>70 m), suggesting that these individuals may begin to chase prey prior to achieving deep foraging depths (Fig. 3a). Similarly, when compared to middle-aged murres during descent, old murres used more

Table 3
Body angle as a function of age, age^2 and body mass, with deployment period, bin and individual as random effects

Dive phase	Intercept	SE	Age	Age^2	Mass (g)
Descent	70.80	21.64	$t_{180}=-22.65, P<0.001$	$t_{180}=26.49, P<0.001$	$t_{180}=2.91, P=0.004$
Ascent	115.25	17.97	$t_{180}=-16.26, P<0.001$	$t_{180}=17.79, P<0.001$	$t_{180}=4.16, P<0.001$

t values, degrees of freedom and P values are shown for age, age^2 and mass for the ascent and descent phase ($N = 136$).
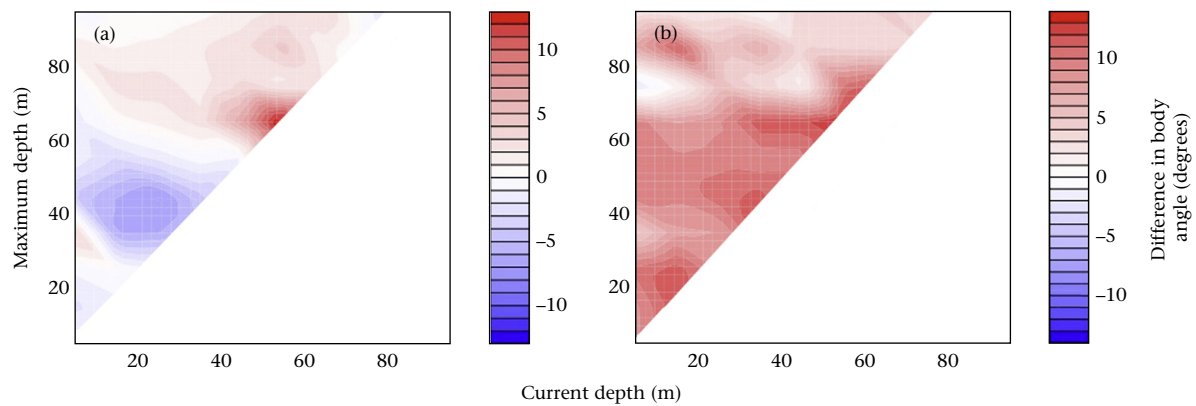
Figure 6. Mean differences in body angle (degrees) between old ($\geq$20 years old) and young ($\leq$15 years old) murres depending on the maximum depth (m) and the current depth (m) during (a) the descent phase and (b) the ascent phase of the dive. Negative values (blue) indicate that young individuals dived with steeper dive angles, and positive values (red) indicate that old individuals dived with steeper dive angles. Darker colours represent a larger difference in body angle between age classes. Lighter colours represent a smaller difference, where body angles were similar for both age classes. A white colouring represents little to no difference in body angle between age classes.
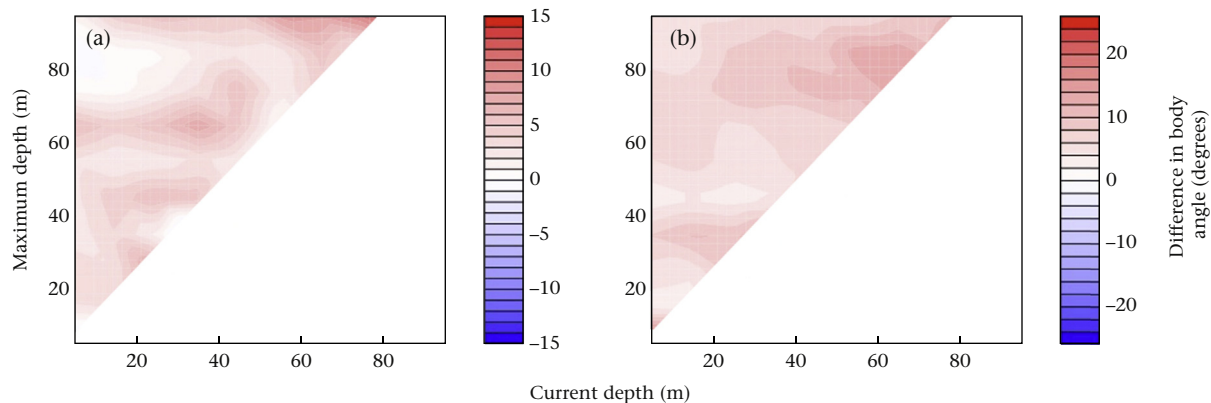

Figure 7. Mean differences in body angle (degrees) between middle-aged (11–19 years old) and young ($\leq$10 years old) murres depending on the maximum depth (m) and the current depth (m) during (a) the descent phase and (b) the ascent phase of the dive. Negative values (blue) indicate that young individuals dived with steeper body angles, and positive values (red) indicate that middle-aged individuals dived with steeper body angles. Darker colours represent a larger difference in body angle between age classes. Lighter colours represent a smaller difference, where body angles were similar for both age classes. A white colouring represents little to no difference in body angle between age classes.

energy at depths over 70 m during deep dives (a maximum depth over 90 m), however middle-aged murres appeared to spend more energy throughout descent (Fig. 5a). This suggests that experience may play a more important role than expected. Similar to our results, young king penguins had higher PDBA during descent than middle-aged birds at deep depths (Le Vaillant et al., 2012). During ascent, young penguins also had higher PDBA than middle-aged penguins, although the study did not include any exceptionally old penguins (Le Vaillant et al., 2012).

One possibility for the high PDBA in young individuals could be attributed to unsuccessful chases. Younger individuals have potentially less developed muscles that are more susceptible to lactate acid build up due to lower lactate dehydrogenase (LDH) activity (Davis & Guderley, 1987; Haggblom, Terwilliger, & Terwilliger, 1988; Hindle et al., 2009). Young birds may also be

less successful at foraging due to improper wing placement and shallower body angles causing an increase in the drag or wing beat frequency as the bird dives (Ainley, 1978; Elliott et al., 2007; Le Vaillant et al., 2012; Martin, 1995; Watanuki et al., 2006). Extra drag would entail greater effort required for reaching foraging depths (Desrochers, 1992; Martin, 1995; Robertson, Cooch, Lank, Rockwell, & Cooke, 1994; Sullivan, 1988). However, this is questionable if murres that are actively breeding already have stable LDH activity (Haggblom et al., 1988) and substantial diving experience (Dunn, 1972; Pärt, 2001).

In summary, we provide evidence for a link between age and fine-scale foraging behaviour. Selective disappearance did not play a strong role in a complementary, longitudinal study of diving (Elliott, Hare, et al., 2014) and, thus, in our cross-sectional study, disappearances of high- or low-activity individuals creating a trend
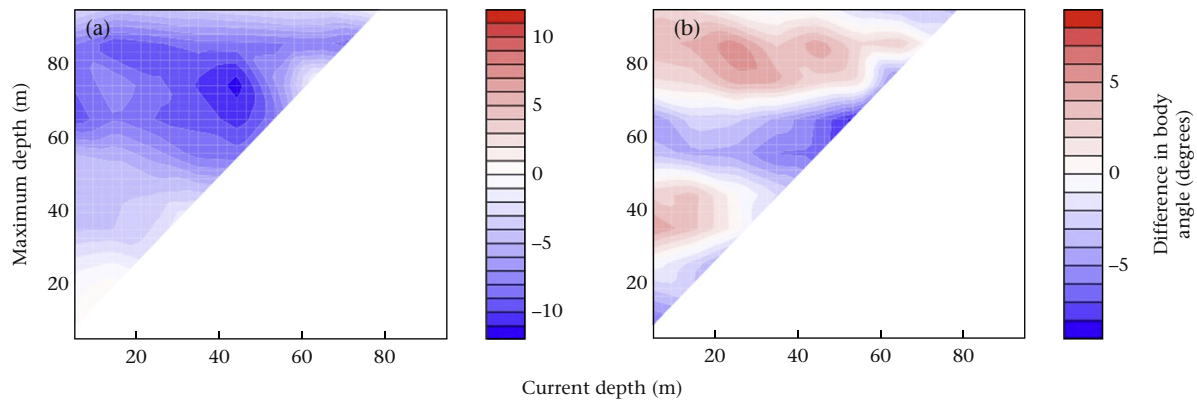
Figure 8. Mean differences in body angle (degrees) between old (≥20 years old) and middle-aged (11–19 years old) murres depending on the maximum depth (m) and the current depth (m) during (a) the descent phase and (b) the ascent phase of the dive. Negative values (blue) indicate that middle-aged individuals dived with steeper body angles, and positive values (red) indicate that old individuals dived with steeper body angles. Darker colours represent a larger difference in body angle between age classes. Lighter colours represent a smaller difference, where body angles were similar for both age classes. A white colouring represents little to no difference in body angle between age classes.

in activity rates with age (e.g. Forslund & Pärt, 1995) is unlikely. Our results are in contrast to a previous study in thick-billed murres, which found diving behaviour to be consistent during senescence and found no significant change in any diving behaviour with age (Elliott, Hare, et al., 2014). By looking at the effects of ageing on diving behaviour at a fine scale, we were able to distinguish differences in diving behaviour for murres of various ages and different reproductive stages. The continued application of accelerometers in behavioural ecology provides the opportunity for measuring fine-scale kinematics in the field and relating fine-scale behaviour to fitness, especially in the context of ageing.

Acknowledgments

References

Ainley, D. G. (1978). Activity patterns and social behavior of non-breeding Adélie penguins. *Condor, 80,* 138–146.

Akima, H., & Gebhardt, A. (2015). *akima: Interpolation of irregularly and regularly spaced data (R package version 0. 5-12).* https://CRAN.R-project.org/package=akima.

Bates, D., Maecheler, M., Bolker, B., & Walker, S. (2014). *lme4: Linear mixed-effects models using Eigen and S4 (R package version 1. 1-7).* Vienna, Austria: R Foundation for Statistical Computing.

Biuw, M., McConnell, B., Bradshaw, C. J. A., Burton, H., & Fedak, M. (2003). Blubber and buoyancy: Monitoring the body condition of free-ranging seals using simple dive characteristics. *Journal of Experimental Biology, 206,* 3405–3423.

Catry, P., Phillips, R. A., Phalan, B., & Croxall, J. P. (2006). Senescence effects in an extremely long-lived bird: The grey-headed albatross *Thalassarche chrysostoma. Proceedings of the Royal Society B: Biological Sciences, 273,* 1625–1630.

Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I. M., Travis, J. M., et al. (2016). The use of an unsupervised learning approach for characterizing latent behaviors in accelerometer data. *Ecology and Evolution, 6*(3), 727–741.

Croll, D. A., Gaston, A. J., Burger, A. E., & Konnoff, D. (1992). Foraging behaviour and physiological adaptation for diving in thick-billed murres. *Ecology, 73,* 344–356.

Croll, D. A., Gaston, A. J., & Noble, D. G. (1991). Adaptive loss of mass in thick-billed murres. *Condor, 93,* 496–502.

Davis, M. B., & Guderley, H. (1987). Energy metabolism in the locomotor muscles of the common murre (*Uria aalge*) and the Atlantic puffin (*Fratercula arctica*). *Auk, 104,* 733–739.

Desrochers, A. (1992). Age and foraging success in European blackbirds: Variation between and within individuals. *Animal Behaviour, 43,* 885–894.

Dunn, E. K. (1972). Effect of age on fishing ability of sandwich terns *Sterna sandvicensis. Ibis, 114,* 360–366.

Elliott, K. H., Chivers, L. S., Bessey, L., Gaston, A. J., Hatch, S. A., Kato, A., et al. (2014). Windscapes shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. *Movement Ecology, 2*(1), 17.

Elliott, K. H., Davoren, G. K., & Gaston, A. J. (2007). The influence of buoyancy and drag on the dive behaviour of an Arctic seabird, the thick-billed murre. *Canadian Journal of Zoology, 85,* 352–361.

Elliott, K. H., Davoren, G. K., & Gaston, A. J. (2008). Time allocation by a deep-diving bird reflects prey type and energy gain. *Animal Behaviour, 75,* 1301–1310.

Elliott, K. H., Hare, J. F., Le Vaillant, M., Gaston, A. J., Ropert-Coudert, Y., & Anderson, W. G. (2014). Ageing gracefully: Physiology but not behaviour declines with age in a diving seabird. *Functional Ecology, 29,* 219–228.

Elliott, K. H., Le Vaillant, M., Kato, A., Speakman, J. R., & Ropert-Coudert, Y. (2013). Accelerometry predicts daily energy expenditure in a bird with high activity levels. *Biology Letters, 9*(1), 20120919.

Elliott, K. H., O'Reilly, K. M., Hatch, S. A., Gaston, A. J., Hare, J. F., & Anderson, W. G. (2014). The prudent parent meets old age: A high stress response in very old seabirds supports the terminal restraint hypothesis. *Hormones and Behaviour, 66,* 828–837.

Elliott, K. H., Ricklefs, R. E., Gaston, A. J., Hatch, S. A., Speakman, J. R., & Davoren, G. K. (2013). High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Proceedings of the National Academy of Sciences of the United States of America, 110,* 9380–9384.

Elliott, K. H., Woo, K., Gaston, A. J., Benvenuti, S., Dall Antonia, L., & Davoren, G. K. (2008). Seabird foraging behaviour indicates prey type. *Marine Ecology Progress Series, 354,* 289–303.

Fayet, A. L., Freeman, R., Shoji, A., Padget, O., Perrins, C. M., & Guilford, T. (2015). Lower foraging efficiency in immatures drives spatial segregation with breeding adults in a long-lived pelagic seabird. *Animal Behaviour, 110,* 79–89. http://dx.doi.org/10.1016/j.anbehav.2015.09.008.

de Forest, L. N., & Gaston, A. J. (1996). The effect of age on timing of breeding and reproductive success in the thick-billed murre. *Ecology, 77,* 1501–1511.

Forslund, P., & Pärt, T. (1995). Age and reproduction in birds: Hypotheses and tests. *Trends in Ecology & Evolution, 10,* 374–378.

Froy, H., Lewis, S., Catry, P., Bishop, C. M., Forster, I. P., Fukuda, A., et al. (2015). Age-related variation in foraging behaviour in the wandering albatross at South Georgia: No evidence for senescence. *PLoS One, 10*(1), e0116415.

Gaston, A. J., Gilchrist, H. G., & Hipfner, J. M. (2005). Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brünnich's guillemot (*Uria lomvia* L.). *Journal of Animal Ecology, 74,* 832–841.

Gaston, A. J., & Hipfner, J. M. (2006). Body mass changes in Brünnich's guillemots *Uria lomvia* with age and breeding stage. *Journal of Avian Biology, 37,* 101–109.

Green, J. A., Halsey, L. G., Wilson, R. P., & Frappell, P. B. (2009). Estimating energy expenditure of animals using the accelerometry technique: Activity, inactivity and comparison with the heart-rate technique. *Journal of Experimental Biology, 212,* 471–482.

Haggblom, L., Terwilliger, R. C., & Terwilliger, N. B. (1988). Changes in myoglobin and lactate dehydrogenase in muscle tissues of a diving bird, the pigeon guillemot, during maturation. *Comparative Biochemistry and Physiology B, 91,* 273–277.

Halsey, L. G., Green, J. A., Wilson, R. P., & Frappell, P. B. (2009). Accelerometry to estimate energy expenditure during activity: Best practice with data loggers. *Physiological and Biochemical Zoology, 82*(4), 396–404.

Heinze, J., & Schrempf, A. (2012). Terminal investment: Individual reproduction of ant queens increases with age. *PLoS One, 7*, e5201.

Hindle, A. G., & Horning, M. (2010). Energetics of breath-hold hunting: Modeling the effects of aging on foraging success in the Weddell seal. *Journal of Theoretical Biology, 264*, 673–682.

Hindle, A. G., Horning, M., Mellish, J.-A. E., & Lawler, J. M. (2009). Diving into old age: Muscular senescence in a large-bodied, long-lived mammal, the Weddell seal (*Leptonychotes weddellii*). *Journal of Experimental Biology, 212*, 790–796.

Hindle, A. G., Lawler, J. M., Campbell, K. L., & Horning, M. (2010). Muscle aging and oxidative stress in wild-caught shrews. *Comparative Biochemistry and Physiology B, 155*, 427–434.

Jones, O. R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C. G., Schaible, R., Casper, B. B., et al. (2014). Diversity of ageing across the tree of life. *Nature, 505*, 169–174.

Kooyman, G. L., & Ponganis, P. J. (1998). The physiological basis of diving to depth: Birds and mammals. *Annual Review of Physiology, 60*, 19–32.

Le Vaillant, M., Wilson, R. P., Kato, A., Saraux, C., Hanuise, N., Prud'Homme, O., et al. (2012). King penguins adjust their diving behaviour with age. *Journal of Experimental Biology, 215*, 3685–3692.

Lecomte, V. J., Sorci, G., Cornet, S., Jaeger, A., Faivre, B., Arnoux, E., et al. (2010). Patterns of aging in the long-lived wandering albatross. *Proceedings of the National Academy of Sciences of the United States of America, 107*, 6370–6375.

Lovvorn, J. R., Croll, D. A., & Liggins, G. A. (1999). Mechanical *versus* physiological determinants of swimming speeds in diving Brünnich's guillemots. *Journal of Experimental Biology, 202*, 1741–1752.

Lovvorn, J. R., Watanuki, Y., Kato, A., Naito, Y., & Liggins, G. A. (2004). Stroke patterns and regulation of swim speed and energy cost in free-ranging Brünnich's guillemots. *Journal of Experimental Biology, 207*, 4679–4695.

Martin, K. (1995). Patterns and mechanisms for age-dependent reproduction and survival in birds. *American Zoologist, 35*, 340–348.

Paredes, R., Jones, I. L., & Boness, D. J. (2005). Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murres equipped with data loggers. *Animal Behaviour, 68*, 197–208.

Pärt, T. (2001). The effects of territory quality on age-dependent reproductive performance in the northern wheatear, *Oenanthe oenanthe*. *Animal Behaviour, 62*, 379–388.

Péron, G., Gimenez, O., Charmantier, A., Gaillard, J. M., & Crochet, P. A. (2010). Age at onset of senescence in birds and mammals is predicted by early-life performance. *Proceedings of the Royal Society B: Biological Sciences, 277*, 2849–2856.

Phillips, R. A., Xavier, J. C., & Croxall, J. P. (2003). Effects of satellite transmitters on albatrosses and petrels. *Auk, 120*(4), 1082–1090.

R Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/.

Reid, W. V. (1988). Age-specific patterns of reproduction in the glaucous-winged gull: Increased effort with age? *Ecology, 69*, 1454–1465.

Ricklefs, R. E. (2010). Insights from comparative analyses of aging in birds and mammals. *Aging Cell, 9*, 273–284.

Robertson, G. J., Cooch, E. G., Lank, D. B., Rockwell, R. F., & Cooke, F. (1994). Female age and egg size in the lesser snow goose. *Journal of Avian Biology, 25*, 149–155.

Rockwell, R. F., Findlay, C. S., & Cooke, F. (1985). Life history studies of the lesser snow goose. V. Temporal effects on age-specific fecundity. *Condor, 87*, 142–143.

Ropert-Coudert, Y., Grémillet, D., Ryan, P., Kato, A., Naito, Y., & Le Maho, Y. (2004). Between air and water: The plunge dive of the Cape gannet *Morus capensis*. *Ibis, 146*, 281–290.

Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B., & Naito, Y. (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *Journal of Experimental Biology, 206*, 1461–1470.

Sato, K., Naito, Y., Kato, A., Niizuma, Y., Watanuki, Y., Charrassin, J. B., et al. (2002). Buoyancy and maximal diving depth in penguins: Do they control inhaling air volume? *Journal of Experimental Biology, 205*, 1189–1197.

Stothart, M. R., Elliott, K. H., Wood, T., Hatch, S. A., & Speakman, J. R. (2016). Counting calories in cormorants: Dynamic body acceleration predicts daily energy expenditure measured in pelagic cormorants. *Journal of Experimental Biology, 219*, 2192–2200.

Sullivan, K. A. (1988). Ontogeny of time budgets in yellow-eyed juncos: Adaptation to ecological constraints. *Ecology, 69*, 118–124.

Vandenabeele, S. P., Shepard, E. L. C., Grémillet, D., Butler, P. J., Martin, G. R., & Wilson, R. P. (2015). Are bio-telemetic devices a drag? Effects of external tags on the diving behaviour of great cormorants. *Marine Ecology Progress Series, 519*, 239–249.

Watanuki, Y., Niizuma, Y., Gabrielsen, G. W., Sato, K., & Naito, Y. (2003). Stroke and glide of wing propelled divers: Deep diving seabirds adjust surge frequency to buoyancy change with depth. *Proceedings of the Royal Society B: Biological Sciences, 270*, 483–488.

Watanuki, Y., & Sato, K. (2008). Dive angle, swim speed and wing stroke during shallow and deep dives in common murres and rhinoceros auklets. *Ornithological Science, 7*(1), 15–28.

Watanuki, Y., Wanless, S., Harris, M., Lovvorn, J. R., Miyazaki, M., Tanaka, H., et al. (2006). Swim speeds and stroke patterns in wing-propelled divers: A comparison among alcids and a penguin. *Journal of Experimental Biology, 209*, 1217–1230.

Williams, G. C. (1957). Pleiotropy, natural selection and the evolution of senescence. *Evolution, 11*, 398–411.

Wilson, R. P., Hustler, K., Ryan, P. G., Burger, A. E., & Noldeke, E. C. (1992). Diving birds in cold water: Do Archimedes and Boyle determine energetic costs? *American Naturalist, 140*, 179–200.

Wilson, R. P., Simeone, A., Luna-Jorquera, G., Steinfurth, A., Jackson, S., & Fahlman, A. (2003). *Journal of Experimental Biology, 206*, 1751–1763.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., et al. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. *Journal of Animal Ecology, 75*(5), 1081–1090.

Wilson, R. P., & Zimmer, I. (2004). Inspiration by Magellanic penguins: Reduced swimming effort when under pressure. *Marine Ecology Progress Series, 278*, 303–307.

Zimmer, I., Ropert-Coudert, Y., Kato, A., Ancel, A., & Chiaradia, A. (2011). Does foraging performance change with age in female little penguins (*Eudyptula minor*)? *PLoS One, 6*, e16098. http://dx.doi.org/10.1371/journal.pone.0016098.