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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.

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 ± 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,