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Long necks enhance and constrain foraging capacity in aquatic vertebrates

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Highly specialized diving birds display substantial dichotomy in neck length with, for example, cormorants and anhingas having extreme necks, while penguins and auks have minimized necks. We attached acceleration loggers to Imperial cormorants *Phalacrocorax atriceps* and Magellanic penguins *Spheniscus magellanicus*, both foraging in waters over the Patagonian Shelf, to examine the difference in movement between their respective heads and bodies in an attempt to explain this dichotomy. The penguins had head and body attitudes and movements that broadly concurred throughout all phases of their dives. By contrast, although the cormorants followed this pattern during the descent and ascent phases of dives, during the bottom (foraging) phase of the dive, the head angle differed widely from that of the body and its dynamism (measured using vectorial dynamic acceleration) was over four times greater. A simple model indicated that having the head on an extended neck would allow these cormorants to half the energy expenditure that they would expend if their body moved in the way their heads did. This apparently energy-saving solution is likely to lead to greater heat loss though and would seem tenable in slow-swimming species because the loss of streamlining that it engenders would make it detrimental for fast-swimming taxa such as penguins.

1. Introduction

Most animal forms consist of a single, simple central body mass, from which extensions, primarily limbs and heads, project [1]. Among vertebrates, the evolution of limbs has facilitated travel [2,3] with, terrestrially at least, longer limbs appearing to confer greater speed [4]. The evolution of a head that operates independently of the body, modulated by the neck, allows animals with long limbs, such as ungulates, to feed on the ground by lowering the head, rather than the whole body, to that level [5]. The specific advantage of this is that the lesser mass of the head being moved up and down requires less energy for its changes in potential energy than would be necessary for the whole body. But there are also animals with long necks that operate in the water, where upthrust negates gravity-based potential energy changes anyway. Some birds, such as cormorants (Phalacrocoracidae) and anhingas (Anhingidae), adhere to this body plan, in contrast with other fish-eating taxa, like penguins (Spheniscidae) and auks (Alcidae), that do not [6].

This divergence of strategies between cormorants and penguins is perplexing because both families are homeothermic and forage in cold water. Given that water has a much higher heat conductivity than air [7] and that long necks will increase the surface area to volume ratio [8], cormorants should lose more energy as heat as a consequence. Clearly, they must offset this detriment with some advantage such as their ability to 'grab prey underwater' [5,6]. In fact, in

a comprehensive review of the evolution of long necks, Wilkinson & Ruxton [5] suggest that short-necked piscivores, such as penguins and auks, operate in 'clear, surface oceanic waters' where 'predators and prey can see each other from a long distance away' while long-necked species, such as cormorants, forage in 'murkier waters … where the predator will only see the prey at very close range'. They conclude that poor visibility 'selects for a long neck, because it is easier to accelerate a small head than the whole body at such close-range'.

We examined this explanation by attaching accelerometers simultaneously to the heads and bodies of Magellanic penguins *Spheniscus magellanicus* and Imperial cormorants *Phalacrocorax atriceps*, both of which forage in the waters of the Patagonian Shelf. Our intent was to quantify differences in the head-based acceleration between the two species to examine the movement-based causes and consequences of the disparity in morphology while acknowledging that other factors will also play a role.

2. Material and methods

Imperial cormorants and Magellanic penguins in Argentinian Patagonia both breed at the same time (October–February) [9,10] and forage during daylight [11,12] at similar depths [12,13]. Both show predominantly U-shaped dive profiles [13,14] and allocate more time to all dive phases (descent, bottom phase and ascent) when diving to greater depths [12,14,15]. For a typical dive to 30 m, the Magellanic penguin consecrates 30, 38 and 29 s to the descent, bottom and ascent phases, respectively [14], while the equivalent figures for the Imperial cormorant are 22, 61 and 21 s, respectively [15]. Although both species execute benthic and pelagic dives, Imperial cormorants forage predominantly benthically [16], which may expose them to more turbid water conditions (cf. [5]), while Magellanic penguins do so pelagically [12]. Both species normally swallow multiple prey items underwater within each dive [17,18].

During the early chick-rearing period between November 2014 and December 2015, 10 Imperial cormorant (five each year) brooding chicks at Punta Leon, Argentina (43°04′ S, 64°29′ W), and eight Magellanic penguin brooding chicks at San Lorenzo, Argentina (42°04′ S, 63°49′ W) (six in 2015 and two in 2016), were fitted with tri-axial, orthogonal accelerometers set to record at 25 Hz. Each animal had a unit attached to the dorsal surface of its head and to the centre of the back using tape as described in Wilson *et al.* [19]. Head tags (Technosmart, Rome, Italy) weighed 3 g (dimensions $4 \times 10 \times 40$ mm) while the back-mounted tags (Technosmart) weighed 6 g (dimensions $11 \times 12 \times 30$ mm). In addition to acceleration, the back-mounted tags recorded depth at 1 Hz. After tag attachment, birds were replaced on their nests and left to go to sea for a single foraging trip after which the tags were retrieved. This work was granted approval by the Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina and the Organismo Provincial de Turismo.

Data were then examined to identify periods of diving and between 17 and 28 dives were selected from each penguin's data, while between 10 and 13 dives were selected from each cormorant (cormorants conduct fewer dives per foraging trip than penguins). All selected dives terminated between 40 and 60 m and corresponded to the first part of the foraging trip of each animal. Each dive was then divided into the descent, bottom and ascent phases (see [20] for definition) (electronic supplementary material) and the corresponding acceleration data separated. These data were used to calculate the 'static' acceleration, by using a running mean of 2 s through each acceleration axis, as recommended by Shepard *et al.* [21] from which (both head and body) posture can be derived [22], and the dynamic

acceleration, by subtracting the static acceleration from the raw acceleration for each axis [21]. This assumes that the smoothing algorithm effectively isolates the gravity-dependent acceleration [22]. The vectorial sum of the dynamic body acceleration (VeDBA), a powerful proxy for energy expenditure [23], was calculated for both head- and body-mounted accelerometers. This is effectively equivalent to another commonly used metric used as a proxy for energy expenditure, the overall dynamic body acceleration (ODBA), where the dynamic acceleration components are simply added [24].

Raw acceleration data from the selected dives of both species were then treated following Wilson *et al.* [25], to be normalized and thereby sit on the surface of a sphere. These data were then incorporated within spherical plots showing body and head attitude with respect to gravity on the surface of a sphere [25]. Here, points on the north pole of the sphere indicate horizontal orientation of the tag (and therefore either the body or the head), while points leading to the equator on one side show increasing head pitched-down, with points leading to the equator on the other side show increasing head pitched-up. The location of points on this spherical plot thus indicates bird body- or bird head posture. However, large numbers of points at one location obscure each other, a problem that can be dealt by dividing the surface of the sphere into facets and summing the total number of points within each facet [25]. These values can then be displayed as spherical histograms, with single bars emanating from each facet, to visualize the time allocation adopted to head or body attitude. Such plots, however, do not show the VeDBA allocation to body or head orientation. To do this, all the data within each facet were separated into bins according to their VeDBA values and displayed in frequency distributions, represented by discs placed over spines emanating from the centre of the sphere facets. Here, disc diameter represented the frequency count and disc width represented the width of the frequency bins. Lower values of VeDBA were located closer to the sphere surface (for details, see [25]). This allows allocation of movement-based power to be visualized as a function of head or body attitude.

As part of this study, the length of the outstretched neck of 10 Imperial cormorants was also measured. Specifically, the neck was extended for the measurements in an attempt to simulate the position used by birds foraging underwater. Neck diameter was also taken by using a measuring tape placed round the neck at its mid-point.

For each species and for each dive phase, the effect of depth and body part on VeDBA was analysed using linear mixed-effects models (LMM) fitted by maximum likelihood. In these analyses, depth and body part were set as fixed factors (because depth affects buoyancy in diving birds and thereby power to swim, and the dynamism of the body [26]), while bird identity was set as a random factor. Owing to the fact that data were not normally distributed, we applied a log transformation. After transformation, visual inspection of residual plots did not reveal obvious deviations from homoscedasticity or normality. For the descent and ascent phase analyses, only depths between 0 and 30 m were selected so as to preclude depths when the descent angle might be levelling out in preparation for the bottom phase, while bottom phase analyses used dives terminating between the prescribed 40 and 60 m (see above). LMM were performed using the function *lmer* from the package *lme4*. *p*-values were obtained by likelihood tests of the full model with the effect in question against the model without the effect in question. Models with progressively simplified fixed effects were compared using the *anova* function from the package *stats*. Equations showing the relationship between body and head VedBA versus body and head ODBA (because much energy expenditure data in the literature for cormorants are expressed in terms of ODBA) were constructed with the significant parameters obtained from each mixed-effects model. LMM statistical analyses were
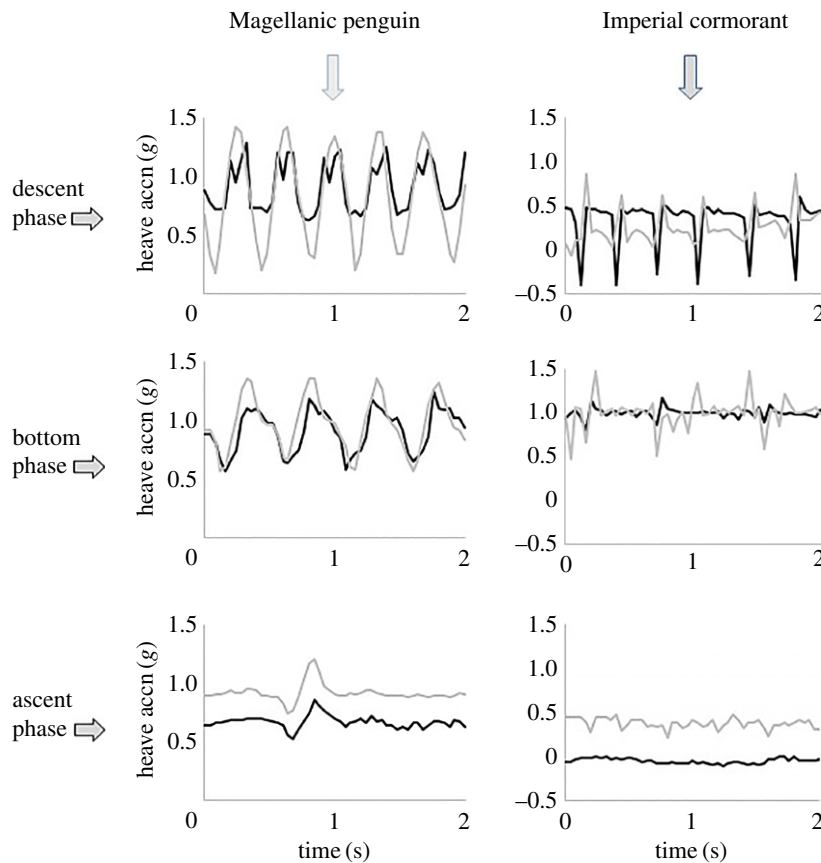
Figure 1. Examples of (heave) acceleration data attained from head-mounted (grey lines) and body-mounted (black lines) accelerometers deployed on penguins and cormorants during the three main dive phases (descent, bottom and ascent). Note that flipper and leg beats are apparent, and coupled, in signals from both body parts for all examples except during the bottom phase for the cormorant. These swimming signals are strongest when the birds have to work more against upthrust (descent > bottom > ascent).

performed using the open source statistical package R v. 3.0.2 [27] with a level of significance of $p < 0.05$.

3. Results

During much of the dives, most notably during descent and ascent, both head- and body-mounted accelerometers showed very similar acceleration patterns over time for both species with the wingbeats (penguins) and foot kicks (cormorants) being clearly visible (figure 1). However, during the bottom phases of dives for both species, when most foraging occurs [13,14], body and head acceleration patterns frequently uncoupled in the case of the cormorants (figure 1).

Using VeDBA to quantify the dynamism of both head and body movement showed good concurrence in VeDBA for both body parts according to depth for descent and ascent phases of the dive (figure 2) in both penguins and cormorants (electronic supplementary material), with head dynamism being marginally greater than body dynamism in both species (electronic supplementary material). However, during the bottom (foraging) phase of the dives, patterns in body and head dynamism differed between species. In penguins, the head and body movements were similarly dynamic, but there was a substantial difference between head and body dynamism in the cormorants at this time, with the mean VeDBA head values being over four times higher than the body (electronic supplementary material) (figure 2).

Closer examination of how posture and movement dynamism interacted for head and body in penguins during the

bottom phase of dives showed that penguins moved their body mainly within an approximately 60° arc around the approximately horizontal (figure 3) and this was broadly mirrored by the head, although there was some allocation to time where the head was tilted back (figure 3). Both head and body had similar distributions of dynamism (via VeDBA [23]) to posture (figure 3).

By contrast, cormorants had a slightly downward-tilted body posture, predominantly within an arc of approximately 30° (figure 4), and a head posture that was essentially quadrimodal. Three of these modes had the head level or angled down, while one mode had the head completely inverted (figure 4). The much higher head than body dynamism was primarily manifest in three obvious modes in head pitch corresponding to slightly upward-angled, pointing directly down and over-inverted (figure 4). Neither penguins nor cormorants rolled their heads appreciably at any time during the dives (figures 3 and 4).

4. Discussion

Our results show the concurrence of head and body accelerations in both penguins and cormorants over the descent and ascent phases of the dive cycle (figure 1). This is expected because motion of the body, reacting to the drive forces of the propelling limbs [28], will transfer to extremities [29] with, normally, some attrition in dynamism expected with extremity length when the extremity is passive [30]. We suppose, therefore, that the increase in VeDBA in the head

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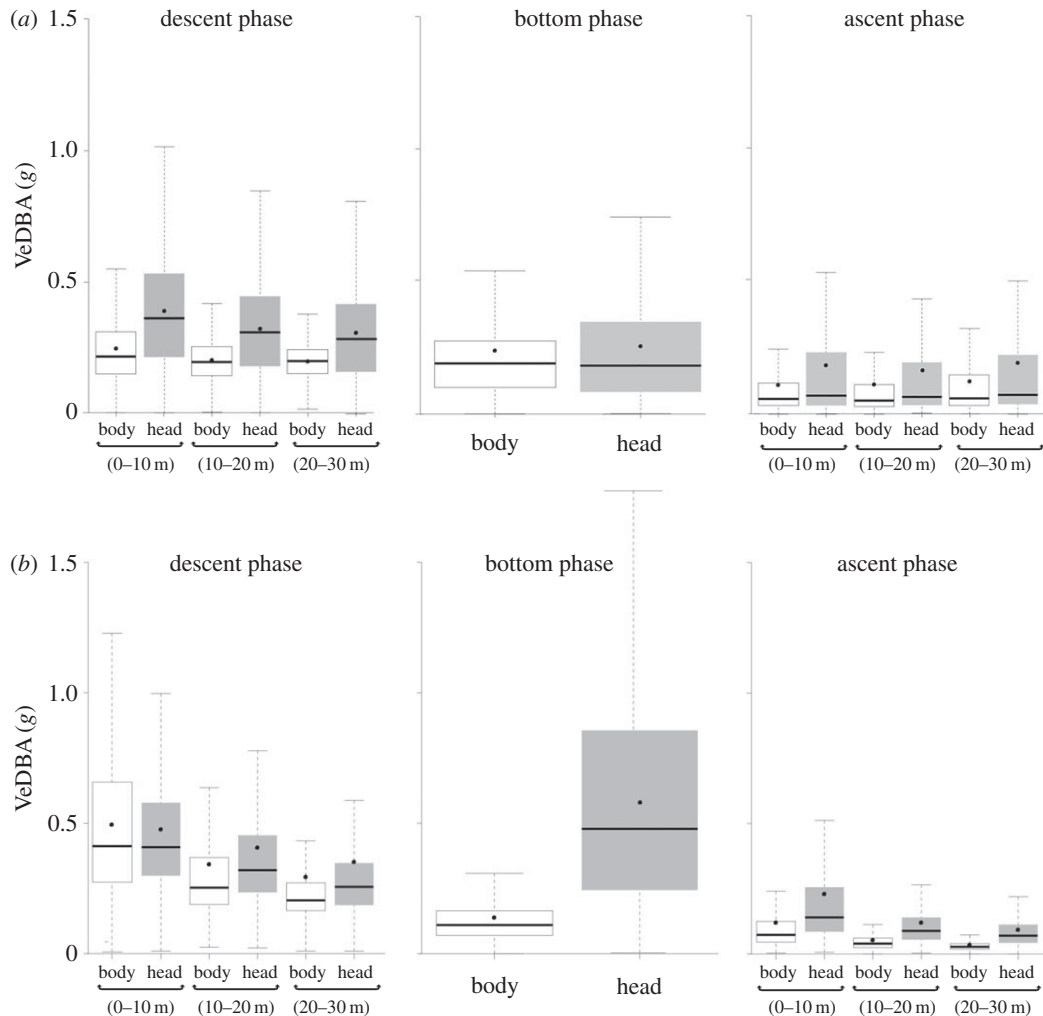
Figure 2. Box–whisker plots of the head (grey) and body (black) dynamism (VeDBA) for penguins (*a*) and cormorants (*b*) according to dive phase and depth (the bottom phases of dives from both species were selected to be approximately similar depths (40–60 m)). Note the substantial difference in head dynamism between the cormorants and the penguins during the primary hunting phases of dives during the bottom phase. The box shows the 25th–75th percentiles, while crosses show the 1st and 99th percentiles.

movements compared with those of the body, in both species, is related to some degree of 'head bobbing', a common phenomenon in birds, normally studied for walking and flying rather than swimming [31,32]. The concurrence between body and head movement is markedly different though, during the bottom, foraging phase. Here, Imperial cormorants had heads that not only adopted a greater range of attitudes with respect to those of the body and did so markedly more than Magellanic penguins, but they also exhibited much more dynamic movements, as exemplified by the VeDBA data. Even though both penguins and cormorants are probably purely visual predators [33,34], the long necks of cormorants would seem advantageous in effectively providing great head manoeuvrability as well as allowing birds to move their heads rapidly to scan around and under rocks and capture prey that is visually detected at a short range [34]. Such behaviour has been observed directly using body-mounted cameras [17].

Given that head manoeuvrability is likely to be a major asset conferred by a long neck, it is appropriate to consider whether the different propulsion mechanisms used by the two species considered might confer differential body man-oeuvrability. If so, this might affect the value of the neck for motility. Kato *et al.* [35] report that foot-propelled cormor-ants have lower stroke rates than wing-propelled penguins,

which would tie in with the perceived higher energy costs of foot-propelled birds for underwater swimming at a given speed and them therefore tending to swim slower [36]. Thus, because turn radius decreases marginally with decreas-ing swim speed [37], cormorants may be expected to be slightly more manoeuvrable than penguins. Against that, no advantage is expected from either party resulting from the body length versus turn rate relationship [38] because both species are similar lengths, and both species have inflex-ible trunks, so no differential advantage is expected in that regard either [39]. Overall, given that both cormorants and penguins are considered to be highly manoeuvrable [40,41], we conclude that no substantive differences are expected between them.

We propose, instead, that cormorants may save energy for their manoeuvres by having a long neck because the amount of force used to make any movement is a function of both acceleration and mass. Specifically, the lower mass of the head than the body means that the rapid movements of the head used to scan the environment and capture prey [17] require lesser absolute force than that if the whole body were accelerated. We can allude to the differences that this might make in terms of energetics by considering a simplistic model based on the relationship between force, mass and acceleration and the use of dynamic body acceleration
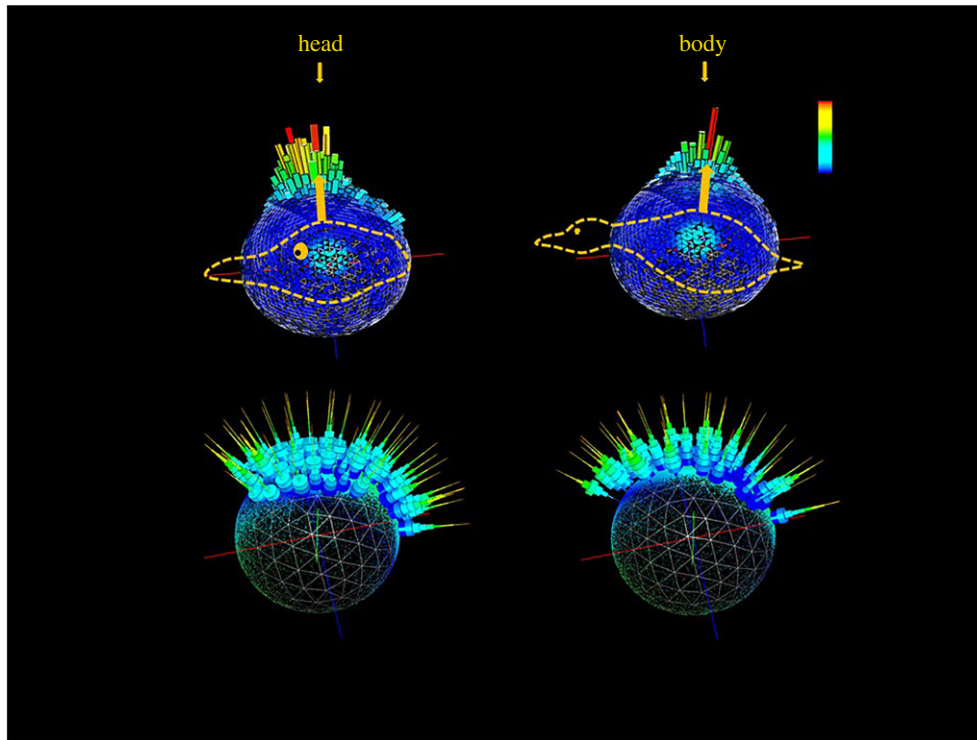
Figure 3. Spherical plots showing the time allocation of head (top, left-hand sphere) and body to attitude (top, right-hand sphere) of Magellanic penguins foraging during the bottom phase of their dives. The length of each histogram represents time. The line drawings are to help interpretation, with the arrows displaying the head and body positions during time modes (indicated by the red columns). The two lower spheres show the distribution of VeDBA frequencies (representing dynamism—discs farthest from the sphere surface indicate highest dynamism) to attitude with each facet normalized to give 100% (maximum values are 1 g for both spheres, and facets containing less than 5% of the data are not shown).

(DBA) as a proxy for energy [28]. This relationship is based on the premise that animals must use energy to apply force (apart from gravitational effects) and incorporates a number of assumptions based on three separate processes: that the ratio of mechanical to metabolic work is constant, that the ratio of external to internal work is done constant and that the ratio of inertial to de novo mechanical work is constant [28]. The process also has to recognize that any relationship between movement and DBA will be profoundly affected by the mass of the body being moved and the medium in which movement is conducted (water, air, etc.). However, these provisos apart, the dynamism of movement in general terms, derived from body-mounted tags measuring DBA, has been found to be a powerful (linear) proxy for energy expenditure for a range of species in disparate taxa (e.g. [24,42]). As force = mass × acceleration, where the mass is that of the study animal, the implication is that some element of the energetic costs of moving the head may be accessible by considering the head DBA and the mass of the head (cf. [28]). Perhaps more realistically though, the costs of moving the body in a similar manner to that of the head can provide a very rough estimate of the costs that cormorants would incur if they had no neck and had to move their body to achieve a similar effect. Laich *et al*. [43] report a relationship between power (P, W kg^{-1}) and DBA, where their dynamic acceleration is measured in terms of ODBA, of

$$P = 41.31\text{ODBA}_{body} + 12.09.$$

Given the relationship between VeDBA and ODBA (see Results), this would normally imply mean power costs of about 16 W kg^{-1} for birds searching along the bottom from our data using normal body-mounted tags. Using the same approach to convert the head data, however, implies that if the body moved in the same way as the head, it would incur power costs of 29 W kg^{-1}, an increase by a factor of almost 2, an indication of the energetic advantages of having a long neck. Such reduced costs have clear value for a diving bird which should benefit from any measures that reduce oxygen consumption and therefore increase dive duration and, potentially, dive depth. The lack of any substantive difference in penguin head and body VeDBA means that a comparable scenario for the penguins should make no difference in the energetics.

Why then, should there be a difference in neck length and strategy between the cormorant and the penguin? Power (P) for speed in fluid media is given by

$$P = 0.5\rho v^3 \text{Cd}A,$$

where ρ is the density of the medium, v the velocity, Cd the drag coefficient and A the cross-sectional area of the body at its widest point. Penguins have a much lower drag coefficient (Cd $\approx$ 0.03 [44]) than cormorants (Cd $\approx$ 0.14 [45]), possibly because the long neck of cormorants gives them a non-optimal shape [46]. Consequently, changes in the streamlining due to, for example, a non-aligned head should tend to result in a proportionately greater variation in Cd in penguins than cormorants, with knock-on consequences for energy expenditure. This would be exacerbated by speed; penguins travel more than twice as fast as cormorants (with foraging speeds of approx. 2 m s^{-1} [47] compared with approx. 0.8 m s^{-1} [48,49]) and, because the power term depends on the cube of the velocity, this provides reason enough for penguins to move their head minimally.
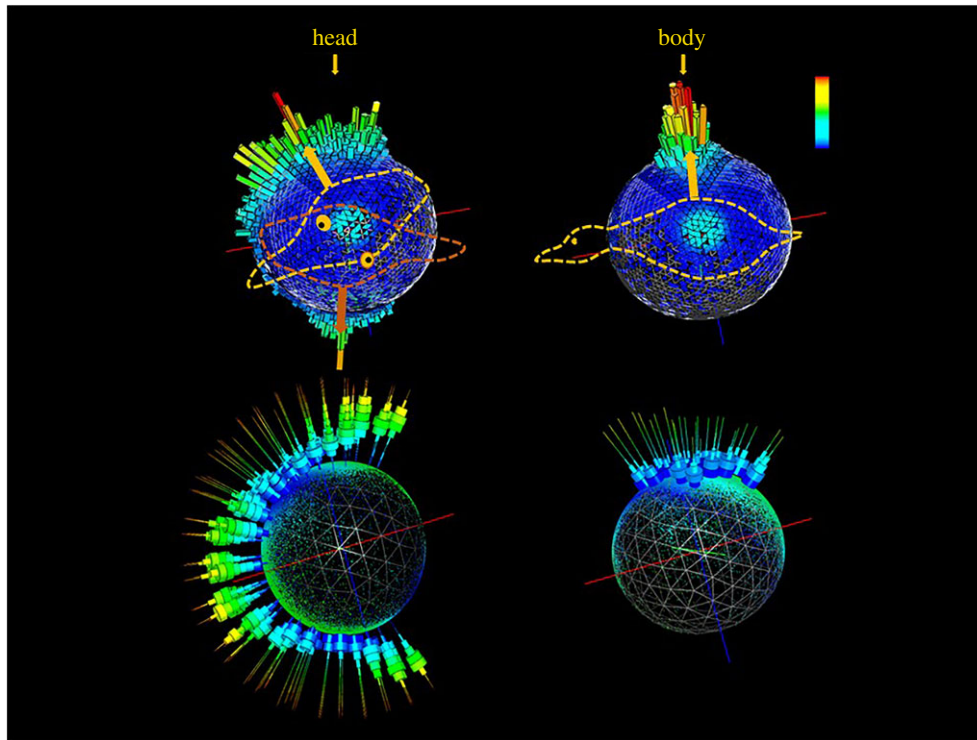
Figure 4. Spherical plots showing the time allocation of head (top, left-hand sphere) and body to attitude (top, right-hand sphere) of Imperial cormorants foraging during the bottom phase of their dives. The length of each histogram represents time. The line drawings are to help interpretation, with the arrows displaying the head and body positions during time modes (indicated by the red or orange columns). The two lower spheres show the distribution of VeDBA frequencies to attitude, with each facet normalized to give 100% (maximum values are 2 g for both spheres, and facets containing less than 5% of the data are not shown).

The energy savings made by the cormorant by having a long mobile neck are likely to be partly tempered by heat loss though (cf. [8,50,51]). If we use the work of Walsberg & King [52], in which the surface area of a bird (S, cm^2) is given by

$$S = 10M^{0.667},$$

and where M is the mass (g), we can approximate the surface area of an Imperial cormorant weighing a mean of 2.25 kg [53] to be 0.17 m^2. Our measurements of the cormorant neck indicate a surface area of 0.017 m^2 (electronic supplementary material), so that the cormorant's extended neck constitutes about 10% of the total body surface area. Accordingly, we would expect heat loss underwater would be roughly that proportion of the whole. There thus appears a clear energetic disadvantage to aquatic homeotherms having long necks. However, the extent of this disadvantage should depend on how long the animal is exposed to the cold water. Here, too, there are substantial differences between penguins and cormorants: Magellanic penguin foraging trips last between 29 and 64 h during breeding [54], but these birds are entirely aquatic during four months of the winter, whereas Imperial cormorants undertake foraging trips consisting of only about 6 h during breeding [13], and do not have a pelagic phase during the non-breeding season [11].

There is thus an emerging pattern that explains why slow-moving, temporarily aquatic homeotherms (such as cormorants) can benefit from an elongated neck while faster, substantially (or completely) aquatic homeotherms, such as penguins and dolphins, may not. Given that there is substantial variation in neck length and flexibility across other aquatic taxa, such as otariids (fur seals and sea lions, which have highly flexible necks) and true seals (with highly diminished necks), further studies using head- and body-mounted technology should help clarify our suggestions. Ultimately, we might even hope that this process will throw light on the differences in ecology between extinct taxa, such as pleisiosaurs and ichthyosaurs, showing similar, or greater, variability.

5. Conclusion

We therefore conclude that long necks can be highly advantageous to homeotherms foraging in cold water because they increase search capacity while minimizing energy expenditure, which should help both increase dive duration and ultimately minimize time spent in a thermally challenging environment. However, benefits decrease as travel speed increases, which may explain why high-speed aquatic homeotherms have short necks and predominantly immobile heads. This speed versus head reach and dynamism framework should help us to understand the morphology of a suite of animals with variable-length necks according to the way they forage, a particularly intractable example being plesiosaurs [5,55].

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