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Long necks enhance and constrain foraging capacity in aquatic vertebrates

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1   Long necks enhance and constrain foraging capacity in aquatic vertebrates

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19

20　Abstract
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23　　　　Highly specialised diving birds display substantial dichotomy in neck length

24　with, for example, cormorants and anhingas having extreme necks while penguins and

25　auks have minimized necks. We attached acceleration loggers to Imperial Cormorants

26　*Phalacrocorax atriceps* and Magellanic Penguins *Spheniscus magellanicus,* both

27　foraging in waters over the Patagonian shelf, to examine the difference in movement

28　between their respective heads and bodies in an attempt to explain this dichotomy. The

29　penguins had head and body attitudes and movements that broadly concurred

30　throughout all phases of their dives. In contrast, although the cormorants followed this

31　pattern during the descent and ascent phases of dives, during the bottom (foraging)

32　phase of the dive, the head angle differed widely from that of the body and its

33　dynamism (measured using vectorial dynamic acceleration - *VeDBA*) was over 4 times

34　greater. A simple model indicated that having the head on an extended neck would

35　allow these cormorants to half the energy expenditure that they would expend if their

36　body moved in the way their heads did. This apparently energy-saving solution is likely

37　to lead to greater heat loss though and would seem tenable in slow-swimming species

38　since the loss of streamlining that it engenders would make it detrimental for fast-

39　swimming taxa such as penguins.

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42　Keywords: diving birds, neck length, accelerometry, energy expenditure

43

44   Introduction

45

46   Most animal forms consist of a single, simple central body mass, from which

47   extensions, primarily limbs and heads, project [1]. Amongst vertebrates, the evolution

48   of limbs has facilitated travel [2, 3] with, terrestrially at least, longer limbs appearing to

49   confer greater speed [4]. The evolution of a head that operates independently of the

50   body, modulated by the neck, allows animals with long limbs, such as ungulates, to feed

51   on the ground by lowering the head, rather than the whole body, to that level [5]. The

52   specific advantage of this is that the lesser mass of the head being moved up and down

53   requires less energy for its changes in potential energy than would be necessary for the

54   whole body. But there are also animals with long necks that operate in the water, where

55   upthrust negates gravity-based potential energy changes anyway. Some birds, such as

56   cormorants (Phalacrocoracidae) and anhingas (Anhingidae), adhere to this body plan, in

57   contrast to other fish-eating taxa, like penguins (Spheniscidae) and auks (Alcidae), that

58   do not [6].

59   This divergence of strategies between cormorants and penguins is perplexing

60   because both families are homeothermic and forage in cold water. Given that water has

61   a much higher heat conductivity than air [7] and that long necks will increase the

62   surface area to volume ratio [8], cormorants should lose more energy as heat as a

63   consequence. Clearly, they must offset this detriment with some advantage such as their

64   ability to 'grab prey underwater' [5, 6]. In fact, in a comprehensive review of the

65   evolution of long necks, Wilkinson and Ruxton [5] suggest that short-necked piscivores,

66   such as penguins and auks, operate in 'clear, surface oceanic waters' where 'predators

67   and prey can see each other from a long distance away' while long-necked species, such

68   as cormorants, forage in 'murkier waters… where the predator will only see the prey at

69   very close range'. They conclude that poor visibility 'selects for a long neck, because it

70   is easier to accelerate a small head than the whole body at such close-range'.

71   We examined this explanation by attaching accelerometers simultaneously to the

72   heads and bodies of Magellanic penguins *Spheniscus magellanicus* and Imperial

73   cormorants *Phalacrocorax atriceps*, both of which forage in the waters of the

74   Patagonian Shelf. Our intent was to quantify differences in the head-based acceleration

75   between the two species, and to examine the causes and consequences of the disparity in

76   morphology.

77

78   Materials and Methods

79

80   Imperial cormorants and Magellanic penguins in Argentinian Patagonia both breed

81   at the same time (October-February) [9, 10] and forage during daylight [11, 12] at

82   similar depths [12, 13]. Both show predominantly U-shaped dive profiles [13, 14] and

83   consecrate more time to all dive phases (descent, bottom phase and ascent) when diving

84   to greater depths [12, 14, 15]. For a typical dive to 30 m, the Magellanic penguin

85   consecrates 30, 38 and 29 s to the descent, bottom and ascent phases, respectively [14],

86   while the equivalent figures for the Imperial cormorant are 22, 61 and 21 s, respectively

87   [15]. Although both species execute benthic and pelagic dives, Imperial cormorant

88   forage predominantly benthically [16] while Magellanic penguins do so pelagically

89   [12]. Both species normally swallow multiple prey items underwater within each dive

90   [17, 18].

91   During the early chick-rearing period between November 2014 and December

92   2015, 10 Imperial cormorants (5 each year) brooding chicks at Punta Leon, Argentina

93   (43°04'S, 64°29'W), and 8 Magellanic penguins brooding chicks at San Lorenzo,

94   Argentina (42°04´S, 63°49´W) (6 in 2015 and 2 in 2016), were fitted with tri-axial,

95   orthogonal accelerometers set to record at 25 Hz. Each animal had a unit attached to the

96   dorsal surface of its head and to the centre of the back using tape as described in Wilson

97   et al. [19]. Head tags (Technosmart, Rome, Italy) weighed 3 g (dimensions; 4 X 10 X

98   40 mm) while the back-mounted tags (Technosmart , Rome, Italy) weighed 6 g

99   (dimensions; 11 X 12 X 30 mm). In addition to acceleration, the back-mounted tags

100   recorded depth at 1 Hz. After tag attachment, birds were replaced on their nests and left

101   to go to sea for a single foraging trip after which the tags were retrieved. This work was

102   granted approval by the Consejo Nacional de Investigaciones Científicas y Técnicas de

103   la República Argentina and the Organismo Provincial de Turismo.

104   Data were then examined to identify periods of diving and between 17 and 28

105   dives were selected from each penguin's data while between 10 and 13 dives were

106   selected from each cormorant (cormorants conduct fewer dives per foraging trip than

107   penguins). All selected dives terminated between 40 and 60 m and corresponded to the

108   first part of the foraging trip of each animal. Each dive was then divided into the

109   descent, bottom and ascent phases [see 20 for definition] (supplementary information)

110   and the corresponding acceleration data separated. These data were used to calculate the

111   'static' acceleration, by using a running mean of 2 s through each acceleration axis, as

112   recommended by Shepard et al. [21] from which (both head and body) posture can be

113   derived [22], and the dynamic acceleration, by subtracting the static acceleration from

114   the raw acceleration for each axis [21]. This assumes that the smoothing algorithm

115   effectively isolates the gravity-dependent acceleration [22]. The vectorial sum of the

116   dynamic body acceleration (*VeDBA*), a powerful proxy for energy expenditure [23], was

117   calculated for both head- and body-mounted accelerometers. This is effectively

118   equivalent to another commonly used metric used as a proxy for energy expenditure, the

119   Overall Dynamic Body Acceleration (*ODBA*), where the dynamic acceleration

120   components are simply added [24].

121   Raw acceleration data from the selected dives of both species were then treated

122   following Wilson et al. [25], to be normalised and thereby sit on the surface of a sphere.

123   These data were then incorporated within spherical plots which show body and head

124   attitude with respect to gravity on the surface of a sphere [25]. Here, points on the North

125   pole of the sphere indicate horizontal orientation of the tag (and therefore either the

126   body or the head), while points leading to the equator on one side show increasing head

127   pitched-down, with points leading to the equator on the other side show increasing head

128   pitched-up. The location of points on this spherical plot thus indicates bird body- or bird

129   head posture. However, large number of points at one location obscure each other, a

130   problem that can be dealt by dividing the surface of the sphere into facets and summing

131   the total number of points within each facet [25]. These values can then be displayed as

132   spherical histograms, with single bars emanating from each facet, to visualize the time

133   allocation adopted to head or body attitude. Such plots, however, do not show the

134   *VeDBA* allocation to body or head orientation. To do this, all the data within each facet

135   were separated into bins according to their *VeDBA* values and displayed in frequency

136   distributions, represented by discs placed over spines emanating from the centre of the

137   sphere facets. Here, disc diameter represented the frequency count and disc width

138   represented the width of the frequency bins. Lower values of *VeDBA* were located

139   closer to the sphere surface (for details see [25]). This allows allocation of movement-

140   based power to be visualized as a function of head or body attitude.

141   As part of this study, the length of the outstretched neck of 10 Imperial

142   cormorants was also measured. Specifically, the neck was extended for the

143   measurements in an attempt to simulate the position used by birds foraging underwater.

144   Neck diameter was also taken by using a measuring tape placed round the neck at its

145   mid-point.

146   For each species and for each dive phase, the effect of depth and body part on

147   *VeDBA* was analysed using Linear Mixed Effect Models (LMM) fitted by maximum

148   likelihood (ML). In these analyses, depth and body part were set as fixed factors

149   (because depth affects buoyancy in diving birds and thereby power to swim, and the

150   dynamism of the body [26]) while bird identity was set as a random factor. Due to the

151   fact that data was not normally distributed, we applied a log transformation. After

152   transformation, visual inspection of residual plots did not reveal obvious deviations

153   from homoscedasticity or normality. For the descent and ascent phase analyses, only

154   depths between 0 and 30 m were selected so as to preclude depths when the descent

155   angle might be levelling out in preparation for the bottom phase, while bottom phase

156   analyses used dives terminating between the prescribed 40 and 60 m (see above). LMM

157   were performed using the function *lmer* from the package *lme4*. P-values were obtained

158   by likelihood tests of the full model with the effect in question against the model

159   without the effect in question. Models with progressively simplified fixed effects were

160   compared using the *anova* function from the package *stats*. Equations showing the

161   relationship between body and head *VedBA* vs body and head *ODBA* (because much

162   energy expenditure data in the literature for cormorants is expressed in terms of *ODBA*)

163   were constructed with the significant parameters obtained from each mixed effect

164   model. LMM statistical analyses were performed using the open source statistical

165   package R version 3.0.2 [27] with a level of significance of *p<0.05*.

166

167   Results

168

169   During much of the dives, most notably during descent and ascent, both head-

170   and body-mounted accelerometers showed very similar acceleration patterns over time

171   for both species with the wingbeats (penguins) and foot kicks (cormorants) being

172   clearly visible (Fig. 1). However, during the bottom phases of dives for both species,

173   when most foraging occurs [13, 14], body and head acceleration patterns frequently

174   uncoupled in the case of the cormorants (Fig. 1).

175   Using vectorial dynamic body acceleration (*VeDBA*) to quantify the dynamism

176   of both head and body movement showed good concurrence in *VeDBA* for both body

177   parts according to depth for descent and ascent phases of the dive (Fig. 2) in both

178   penguins and cormorants (supplementary information), with head dynamism being

179   marginally greater than body dynamism in both species (supplementary information).

180   However, during the bottom (foraging) phase of the dives, patterns in body and head

181   dynamism differed between species. In penguins, the head and body movements were

182   similarly dynamic but there was a substantial difference between head and body

183   dynamism in the cormorants at this time, with mean *VeDBA* head values being >4 times

184   higher than the body (supplementary information) (Fig. 2).

185   Closer examination of how posture and movement dynamism interacted for head

186   and body in penguins during the bottom phase of dives showed that penguins moved

187   their body mainly within a *ca.* 60□ arc around the approximately horizontal (Fig. 3) and

188   this was broadly mirrored by the head, although there was some allocation to time

189   where the head was tilted back (Fig. 3). Both head and body had similar distributions of

190   dynamism (via *VeDBA* [24]) to posture (Fig. 3).

191   By contrast, cormorants had a slightly downward-tilted body posture,

192   predominantly within an arc of *ca.* 30□ (Fig. 4) and a head posture that was essentially

193   quadri-modal. Three of these modes had the head level or angled down, while one mode

194   had the head completely inverted (Fig. 4). The much higher head- than body dynamism

195   was primarily manifest in three obvious modes in head pitch corresponding to; slightly

196   upward-angled, pointing directly down and over-inverted (Fig. 4). Neither penguin nor

197   cormorant rolled their heads appreciably at any time during the dives (Figs 3 & 4).

198

199

200   Discussion

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202

203   Our results show the concurrence of head and body accelerations in both

204   penguins and cormorants over the descent and ascent phases of the dive cycle (Fig.1).

205   This is expected because motion of the body, reacting to the drive forces of the

206   propelling limbs [28], will transfer to extremities [29] with, normally, some attrition in

207   dynamism expected with extremity length when the extremity is passive [30]. We

208   suppose therefore, that the increase in *VeDBA* in the head movements compared to those

209   of the body, in both species, is related to some degree of 'head bobbing', a common

210   phenomenon in birds, normally studied for walking and flying rather than swimming

211   [31, 32]. The concurrence between body and head movement is markedly different

212   though, during the bottom, foraging phase. Here, Imperial cormorants had heads that

213   not only adopted a greater range of attitudes with respect to those of the body and did so

214   markedly more than Magellanic penguins, but they also exhibited much more dynamic

215   movements, as exemplified by the *VeDBA* data. Even though both penguins and

216   cormorants are probably purely visual predators [33, 34], the long necks of cormorants

217   would seem advantageous in effectively providing great head manoeuvrability as well

218   as allowing birds to move their heads rapidly to scan around and under rocks and

219   capture prey that is visually detected at a short range [34]. Such behaviour has been

220   observed directly using body-mounted cameras [17].

221   Given that head manoeuvrability is likely to be a major asset conferred by a long

222   neck, it is appropriate to consider whether the different propulsion mechanisms used by

223   the two species considered might confer differential body manoeuvrability. If so, this

224   might impact on the value of the neck for motility. Kato et al. [35] report that foot-

225   propelled cormorants have lower stroke rates than wing-propelled penguins, which

226   would tie in with the perceived higher energy costs of foot-propelled birds for

227   underwater swimming at a given speed and them therefore tending to swim slower [36].

228   Thus, since turn radius decreases marginally with decreasing swim speed [37],

229   cormorants may be expected to be slightly more manoeuvrable than penguins. Against

230   that, no advantage is expected from either party resulting from the body length *versus*

231   turn rate relationship [38] because both species are similar lengths, and both species

232   have inflexible trunks so no differential advantage is expected in that regard either [39].

233   Overall, given that both cormorants and penguins are considered to be highly

234   manoeuvrable [40, 41], we conclude that no substantive differences are expected

235   between them.

236   We propose instead, that cormorants may save energy for their manoeuvres by

237   having a long neck because the amount of force used to make any movement is a

238   function of both acceleration and mass. Specifically, the lower mass of the head than the

239   body means that the rapid movements of the head used to scan the environment and

240   capture prey [17] requires lesser absolute force than that if the whole body was

241   accelerated. We can allude to the differences that this might make in terms of energetics

242   by considering a simplistic model based on the relationship between force, mass and

243   acceleration and the use of dynamic body acceleration (*DBA*) as a proxy for energy

244   [28]. This relationship is based on the premise that animals must use energy to apply

245   force (aside from gravitational effects) and incorporates a number of assumptions based

246   on three separate processes; that the ratio of mechanical to metabolic work is constant,

247   that the ratio of external to internal work is done constant, and that the ratio of inertial to

248   *de novo* mechanical work is constant [28].The process also has to recognise that any

249   relationship between movement and dynamic body acceleration will be profoundly

250   affected by the mass of the body being moved and the medium in which movement is

251   conducted (water, air, etc). However, these provisos apart, the dynamism of movement

252   in general terms, derived from body-mounted tags measuring *DBA*, has been found to

253   be a powerful (linear) proxy for energy expenditure for a range of species in disparate

254   taxa [e.g. 24, 42]. Since Force = Mass X Acceleration, where the mass is that of the

255   study animal, the implication is that some element of the energetic costs of moving the

256   head may be accessible by considering the head *DBA* and the mass of the head [cf. 28].

257   Perhaps more realistically though, the costs of moving the body in a similar manner to

258   that of the head can provide a very rough estimate of the costs that cormorants would

259   incur if they had no neck and had to move their body to achieve a similar effect.

260   Gomez-Laich et al. [43] report a relationship between power (*P*, W/kg) and *DBA*, where

261   their dynamic acceleration is measured in terms of *ODBA*, of;

263    $P = 41.31 ODBA_{body} + 12.09$

265   Given the relationship between *VeDBA* and *ODBA* (see results above), this

266   would normally imply mean power costs of about 16 W/kg for birds searching along the

267   bottom from our data using normal body-mounted tags. Using the same approach to

268   convert the head data, however, implies that if the body moved in the same way as the

269   head, it would incur power costs of 29 W/kg, an increase by a factor of almost 2, an

270   indication of the energetic advantages of having a long neck. Such reduced costs have

271   clear value for a diving bird which should benefit from any measures that reduce

272   oxygen consumption and therefore increase dive duration and, potentially, dive depth.

273   The lack of any substantive difference in penguin head and body *VeDBA* means that a

274   comparable scenario for the penguins should make no difference in the energetics.

275   Why then, should there be a difference in neck length and strategy between the

276   cormorant and the penguin? Power (*P*) for speed in fluid media is given by;

278    $P = 0.5 \rho v^3 Cd A$

280   where ρ is the density of the medium, *v* is the velocity, *Cd* is the drag coefficient and *A*

281   is the cross-sectional area of the body at its widest point. Penguins have a much lower

282   drag coefficient ($Cd \approx 0.03$ [44]) than cormorants ($Cd \approx 0.14$ [45]), possibly because the

283   long neck of cormorants gives them a non-optimal shape [46]. Consequently, changes in

284   the streamlining due to, for example, a non-aligned head, should tend to result in a

285   proportionately greater variation in Cd in penguins than cormorants, with knock-on

286   consequences for energy expenditure. This would be exacerbated by speed; penguins

287   travel more than twice as fast as cormorants (with foraging speeds of *ca.* 2 m/s [47]

288   compared to *ca*. 0.8 m/s [48, 49]) and, since the power term depends on the cube of the

289   velocity, this provides reason enough for penguins to move their head minimally.

290   The energy savings made by the cormorant by having a long mobile neck are

291   likely to be partly tempered by heat loss though [cf. 8, 50, 51]. If we use the work of

292   Walsberg and King [52], in which the surface area of a bird (S, cm^2) is given by;

293

294    $S = 10 \ M^{0.667}$

295

296   and where M is the mass (g), we can approximate the surface area of an Imperial

297   cormorant weighing a mean of 2.25 kg [53] to be 0.17 m^2. Our measurements of the

298   cormorant neck indicate a surface area of 0.017 m^2 (supplementary information) so that

299   the cormorant's extended neck constitutes about 10% of the total body surface area.

300   Accordingly, we would expect heat loss underwater would be roughly that proportion of

301   the whole. There thus appears a clear energetic disadvantage to aquatic homeotherms

302   having long necks. However, the extent of this disadvantage should depend on how long

303   the animal is exposed to the cold water. Here too, there are substantial differences

304   between penguins and cormorants; Magellanic penguin foraging trips last between 29

305   and 64 h during breeding [54] but these birds are entirely aquatic during 4 months of the

306   winter while Imperial cormorants undertake foraging trips consisting of only about 6 h

307   during breeding [13], and do not have a pelagic phase during the non-breeding season

308   [11].

309   There is thus an emerging pattern which explains why slow-moving, temporarily

310   aquatic, homeotherms (such as cormorants) can benefit from an elongated neck while

311   faster, substantially (or completely) aquatic homeotherms, such as penguins and

312   dolphins, may not.

313

314

315   Conclusion

316

317   We therefore conclude that long necks can be highly advantageous to

318 homeotherms foraging in cold water because they increase search capacity while

319 minimizing energy expenditure, ultimately helping minimize time spent in a thermally

320 challenging environment. However, benefits decrease as travel speed increases, which

321 may explain why high speed aquatic homeotherms have short necks and predominantly

322 immobile heads. This speed *versus* head reach and dynamism framework should help

323 understand the morphology of a suite of animals with variable length necks according to

324 the way they forage, a particularly intractable example being plesiosaurs [5, 55].

325

326 Data accessibility

327

328 Data are available from Swansea University's College of Science T-drive on request to

329 the corresponding author.

330

331 Authors´contributions

332

333 The study was conceived by R.P.W, F.Q. and G.D.O. The work was performed by

334 R.P.W, F.Q., A.G-L., J.E.S. and G.D.O. The data were analysed by M.H., R.P.W. and

335 A.G-L. The manuscript was written by all authors.

336

337 Competing interests

338

339 We have no competing interests

340

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497   Figure captions

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499   Figure 1. Examples of (heave) acceleration data attained from head mounted (grey

500   lines) and body mounted (black lines) accelerometers deployed on penguins and

501   cormorants during the three main dive phases (descent, bottom and ascent). Note that

502   flipper and leg beats are apparent, and coupled, in signals from both body parts for all

503   examples except during the bottom phase for the cormorant. These swimming signals

504   are strongest when the birds have to work more against upthrust (descent> bottom>

505   ascent)

506   Figure 2. Box-whisker plots of the head (grey) and body (black) dynamism (*VeDBA*) for

507   penguins (upper graphs) and cormorants (lower graphs) according to dive phase and

508   depth (the bottom phases of dives from both species were selected to be approximately

509   similar depths (40- 60 m)). Note the substantial difference in head dynamism between

510   the cormorants and the penguins during the primary hunting phases of dives during the

511   bottom phase. The box shows the 25-75 percentile while crosses show the 1% and 99%

512   percentiles.

513   Figure 3. Spherical plots showing the time allocation of head (top, left-hand sphere) and

514   body to attitude (top, right-hand sphere) of Magellanic penguins foraging during the

515   bottom phase of their dives. The length of each histogram represents time. The line

516   drawings are to help interpretation, with the arrows displaying the head and body

517   positions during time modes (indicated by the red columns). The two lower spheres

518   show the distribution of *VeDBA* frequencies (representing dynamism - discs farthest

519   from the sphere surface indicate highest dynamism) to attitude with each facet

520   normalized to give 100% (max values are 1 *g* for both spheres and facets containing less

521   than 5% of the data are not shown).

522   Figure 4. Spherical plots showing the time allocation of head (top, left-hand sphere) and

523   body to attitude (top, right-hand sphere) of Imperial cormorants foraging during the

524   bottom phase of their dives. The length of each histogram represents time. The line

525   drawings are to help interpretation, with the arrows displaying the head and body

526   positions during time modes (indicated by the red or orange columns). The two lower

527   spheres show the distribution of *VeDBA* frequencies to attitude with each facet
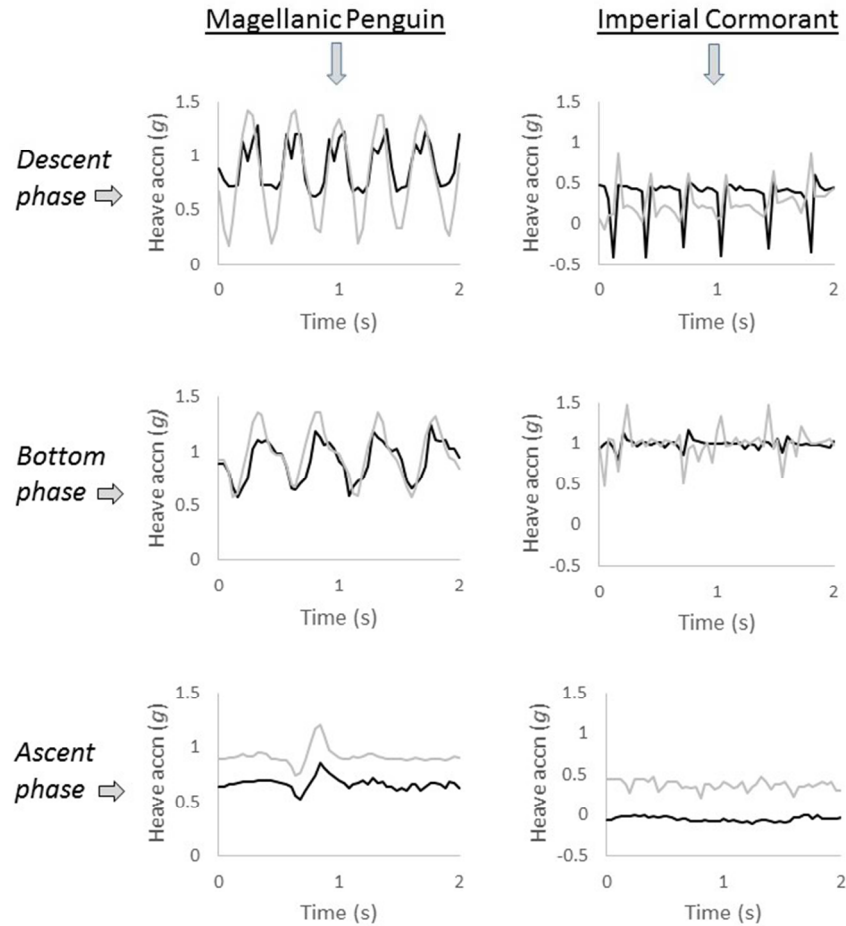
528   normalized to give 100% (max values are 2 g for both spheres and facets containing less

529   than 5% of the data are not shown).

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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)
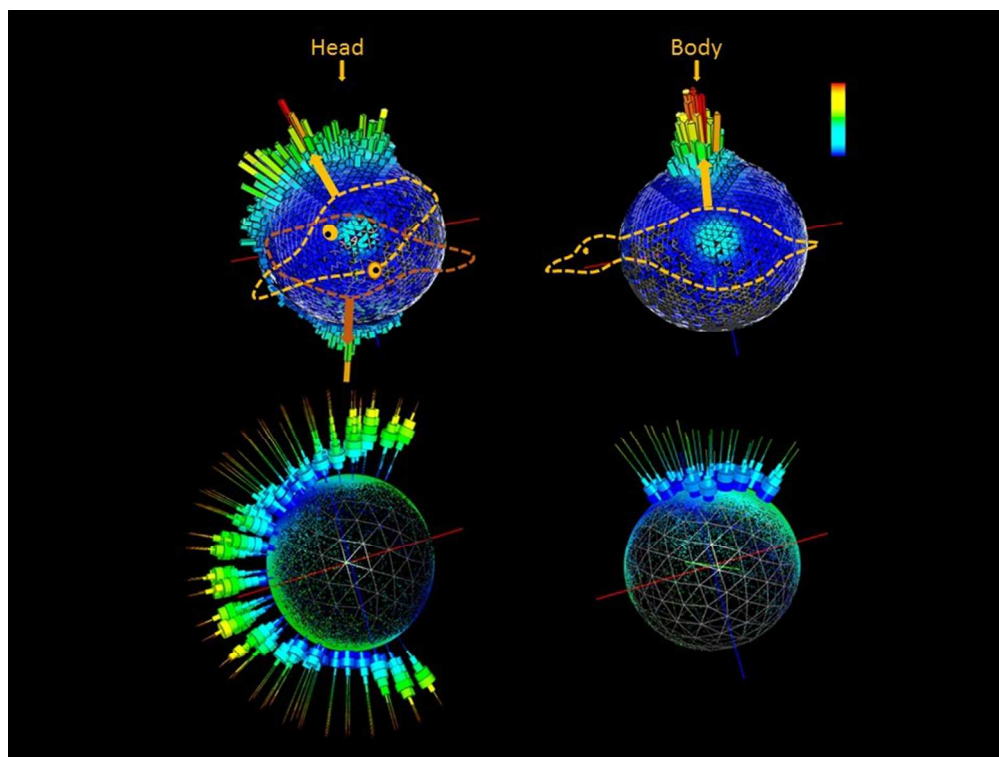
190x254mm (96 x 96 DPI)
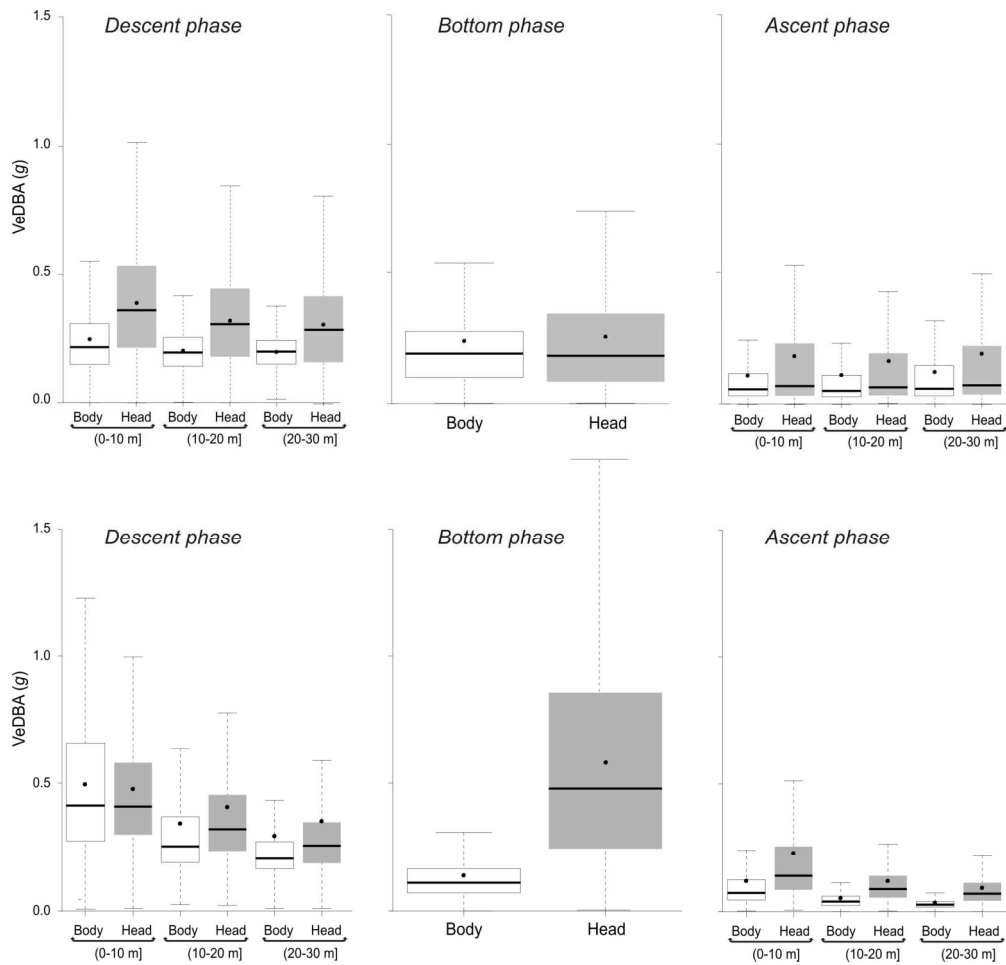
Box-whisker plots of the head (grey) and body (black) dynamism (VeDBA) for penguins (upper graphs) and cormorants (lower graphs) according to dive phase and depth (the bottom phases of dives from both species were selected to be approximately similar depths (40- 60 m)). Note the substantial difference in head dynamism between the cormorants and the penguins during the primary hunting phases of dives during the bottom phase. The box shows the 25-75 percentile while crosses show the 1% and 99% percentiles.

205x195mm (300 x 300 DPI)
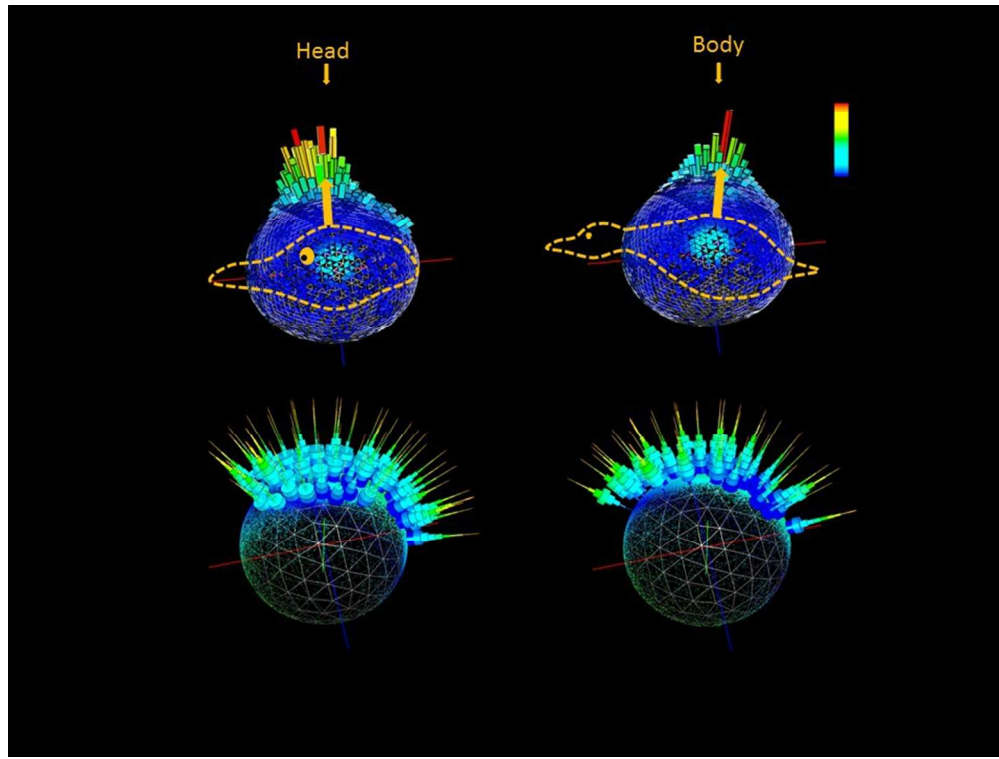
Spherical plots showing the time allocation of head (top, left-hand sphere) and body to attitude (top, right-hand sphere) of Magellanic penguins foraging during the bottom phase of their dives. The length of each histogram represents time. The line drawings are to help interpretation, with the arrows 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% (max values are 1 g for both spheres and facets containing less than 5% of the data are not shown).

254x190mm (96 x 96 DPI)

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% (max values are 2 g for both spheres and facets containing less than 5% of the data are not shown).

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