



Swansea University
Prifysgol Abertawe



Cronfa - Swansea University Open Access Repository

This is an author produced version of a paper published in:
Proceedings of the Royal Society B: Biological Sciences

Cronfa URL for this paper:

<http://cronfa.swan.ac.uk/Record/cronfa36822>

Paper:

Wilson, R., Gómez-Laich, A., Sala, J., Dell'Omo, G., Holton, M. & Quintana, F. (2017). Long necks enhance and constrain foraging capacity in aquatic vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, 284 (1867), 20172072

<http://dx.doi.org/10.1098/rspb.2017.2072>

This item is brought to you by Swansea University. Any person downloading material is agreeing to abide by the terms of the repository licence. Copies of full text items may be used or reproduced in any format or medium, without prior permission for personal research or study, educational or non-commercial purposes only. The copyright for any work remains with the original author unless otherwise specified. The full-text must not be sold in any format or medium without the formal permission of the copyright holder.

Permission for multiple reproductions should be obtained from the original author.

Authors are personally responsible for adhering to copyright and publisher restrictions when uploading content to the repository.

<http://www.swansea.ac.uk/library/researchsupport/ris-support/>

**Long necks enhance and constrain foraging capacity in
aquatic vertebrates**

Journal:	<i>Proceedings B</i>
Manuscript ID	Draft
Article Type:	Research
Date Submitted by the Author:	n/a
Complete List of Authors:	Wilson, Rory; Swansea University, Department of Biosciences, College of Science Gómez-Laich, Agustina; Consejo Nacional de Investigaciones Cientificas y Tecnicas, Instituto de Biología de Organismos Marinos (IBIOMAR) Sala, Juan; Consejo Nacional de Investigaciones Cientificas y Tecnicas, Instituto de Biología de Organismos Marinos (IBIOMAR) Dell'Omo, Giacomo; Technosmart, Holton, Mark; Swansea University, College of Engineering Quintana, Flavio; Consejo Nacional de Investigaciones Cientificas y Tecnicas, Instituto de Biología de Organismos Marinos (IBIOMAR)
Subject:	Behaviour < BIOLOGY, Ecology < BIOLOGY, Evolution < BIOLOGY
Keywords:	diving birds, neck length, accelerometry, energy expenditure
Proceedings B category:	Behaviour

SCHOLARONE™
Manuscripts

1 Long necks enhance and constrain foraging capacity in aquatic vertebrates

2

3

4

5 Rory P. Wilson^{a,*}, Agustina Gómez-Laich^b, Juan-Emilio Sala^b, Giacomo Dell’Omo^c,
6 Mark D. Holton^a and Flavio Quintana^b

7

8

9

10 ^aDepartment of Biosciences, College of Science, Swansea University, Swansea SA2
11 8PP, UK

12 ^bInstituto de Biología de Organismos Marinos (IBIOMAR), CONICET. Boulevard
13 Brown 2915, U9120ACD, Puerto Madryn, Chubut, Argentina

14 ^c*Ornis Italica*, Rome 00199, Italy

15

16

17 *Correspondence r.p.wilson@swansea.ac.uk

18

19

20 Abstract

21

22

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.

40

41

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 ($43^{\circ}04'S$, $64^{\circ}29'W$), and 8 Magellanic penguins brooding chicks at San Lorenzo,
94 Argentina ($42^{\circ}04'S$, $63^{\circ}49'W$) (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

201

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;

$$262$$

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

$$264$$

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;

$$277$$

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

$$279$$

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

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

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

341 Funding

342

343 This study was funded by the Consejo Nacional de Investigaciones Científicas y
344 Técnicas de la República Argentina (CONICET), the Agencia Nacional de Promoción
345 Científica y Tecnológica (grant number: PICT-2013-1229) (to FQ, AGL and JES) and
346 the Santander Bank (to RPW). The visualisations in this work were possible due to a
347 generous donation made by the Royal Society/Wolfson Laboratory fund.

348

349 Acknowledgments

350

351 We are grateful to the Conservation Agency from the Chubut Province, Argentina for
352 the permits to work in the protected area, and the Instituto de Biología de Organismos
353 Marinos (IBIOMAR-CONICET) for institutional and logistical support.

354

355 References

356

357

- 358 1. Minelli A. 2003 The development of animal form: ontogeny, morphology, and
359 evolution (Cambridge University Press).
- 360 2. Pontzer H. 2007 Effective limb length and the scaling of locomotor cost in
361 terrestrial animals. *J Exp Biol* 210 (10), 1752-1761.
- 362 3. Biewener AA. 2003 Animal locomotion (Oxford University Press).
- 363 4. Christiansen P. 2002 Locomotion in terrestrial mammals: the influence of body
364 mass, limb length and bone proportions on speed. *Zool J Linn Soc-Lond* 136(4),
365 685-714.
- 366 5. Wilkinson DM, Ruxton GD. 2012 Understanding selection for long necks in
367 different taxa. *Biol Rev* 87(3), 616-630.
- 368 6. Nelson J, Pelicans C, Relatives T. 2005 The Pelecaniformes. (New York:
369 Oxford University Press).
- 370 7. Kooyman G, Gentry R, Bergman W, Hammel H. 1976 Heat loss in penguins
371 during immersion and compression. *Comp Biochem Phys A* 54(1), 75-80.
- 372 8. Sander PM, Clauss M. 2008 Sauropod gigantism. *Science* 322(5899), 200-201.
- 373 9. Frere E, Quintana F, Gandini P. 2005 Cormoranes de la costa patagónica: Estado
374 poblacional, ecología y conservación. *El Hornero* 20(1), 35-52.
- 375 10. Schiavini A, Yorio P, Gandini P, Raya Rey A, Boersma PD. 2005 Los pingüinos
376 de las costas argentinas: Estado poblacional y conservación. *El Hornero* 20(1):
377 5-23.
- 378 11. Harris S, Raya Rey A, Phillips RA, Quintana F. 2013 Sexual segregation in
379 timing of foraging by imperial shags (*Phalacrocorax atriceps*): is it always ladies
380 first? *Mar Biol* 160, 1249-1258.
- 381 12. Wilson RP, *et al.* 2005 How do Magellanic penguins cope with variability in
382 their access to prey. *Ecol Monogr* 75(3), 379-401.
- 383 13. Quintana F, Wilson RP, Dell'Arciprete P, Shepard E, Gómez Laich A. 2011
384 Women from Venus, men from Mars: Inter- sex foraging differences in the

- 385 Imperial cormorant *Phalacrocorax atriceps* a colonial seabird. *Oikos* 120, 350-
386 358.
- 387 14. Peters G, Wilson RP, Scolaro A, Laurenti S, Upton J, Galleli H. 1995 The diving
388 behaviour of Magellanic Penguins at Punta Norte, Peninsula Valdes, Argentina.
389 *Colon Waterbird* 21, 1-10.
- 390 15. Quintana F, Wilson RP, Yorio P. 2007 Dive depth and plumage air in wettable
391 birds: the extraordinary case of the imperial cormorant. *Mar Ecol Prog Ser* 334,
392 299-310.
- 393 16. Shepard ELC, Wilson RP, Gómez Laich A, Wilson RP. 2010 Buoyed up and
394 slowed down: speed limits for diving birds in shallow water. *Aquat Biol* 8, 259-
395 267.
- 396 17. Gómez-Laich A, Yoda K, Zavalaga C, Quintana F 2015 Selfies of Imperial
397 Cormorants (*Phalacrocorax atriceps*): What Is Happening Underwater? *PLoS*
398 *One* 10(9), e0136980.
- 399 18. Takahashi A, Dunn MJ, Trathan PN, Croxall JP, Wilson RP, Sato K, Naito Y.
400 2007 Krill-feeding behaviour in a chinstrap penguin *Pygoscelis antarctica*
401 compared to fish-eating in Magellanic penguins *Spheniscus magellanicus*: A
402 pilot study. *Marine Ornithology* 32, 47-54.
- 403 19. Wilson RP, Pütz K, Peters G, Culik B, Scolaro JA, Charrassin JB. 1997 Long-
404 term attachment of transmitting and recording devices to penguins and other
405 seabirds. *Wildlife Soc B* 25(1), 101-106.
- 406 20. Halsey L, Bost C-A, Handrich Y. 2007 A thorough and quantified method for
407 classifying seabird diving behaviour. *Polar Biol* 30(8), 991-1004.
- 408 21. Shepard EL, Wilson RP, Halsey LG, Quintana F, Gomez Laich A, Gleiss AC,
409 Liebsch N, Myers AE, Norman B. 2008 Derivation of body motion via
410 appropriate smoothing of acceleration data. *Aquatic Biol* 4, 235-241.
- 411 22. Shepard EL, *et al.* 2008. Identification of animal movement patterns using tri-
412 axial accelerometry. *Endanger Species Res* 10, 47-60.
- 413 23. Qasem L, Cardew A, Wilson A, Griffiths I, Halsey LG, Shepard ELC, Gleiss
414 AC, Wilson RP. 2012 Tri-axial dynamic acceleration as a proxy for animal
415 energy expenditure; should we be summing values or calculating the vector?
416 *PLoS One* 7(2), e31187.

- 417 24. Halsey LG, Shepard ELC, Quintana F, Gomez Laich A, Green JA, Wilson RP.
418 2009 The relationship between oxygen consumption and body acceleration in a
419 range of species. *Comp Biochem Phys S A* 152(2), 197-202.
- 420 25. Wilson RP, *et al.* 2016 A spherical-plot solution to linking acceleration metrics
421 with animal performance, state, behaviour and lifestyle. *Mov ecol* 4(1), 22.
- 422 26. Lovvorn JR, Jones DR. 1991 Body mass, volume, and buoyancy of some aquatic
423 birds, and their relation to locomotor strategies. *Can J Zool* 69, 2888-2892.
- 424 27. Team RC. 2014 R: A language and environment for statistical computing. R
425 Foundation for Statistical Computing, Vienna, Austria. 2013
- 426 28. Gleiss AC, Wilson RP, Shepard EL. 2011 Making overall dynamic body
427 acceleration work: on the theory of acceleration as a proxy for energy
428 expenditure. *Methods Ecol Evol* 2(1), 23-33.
- 429 29. Menz HB, Lord SR, Fitzpatrick RC. 2003 Acceleration patterns of the head and
430 pelvis when walking on level and irregular surfaces. *Gait Posture* 18, 35-46.
- 431 30. Kavanagh JJ, Menz HB. 2008 Accelerometry: A technique for quantifying
432 movement patterns during walking. *Gait Posture* 28, 1-15.
- 433 31. Davies MO, Green PR. 1988 Head bobbing during walking, running and flying:
434 Relative motion perception in the pigeon. *J Exp Biol* 138, 71-91.
- 435 32. Necker R. 2007 Head bobbing of walking birds. *J Comp Physiol A* 193, 1177-
436 1183.
- 437 33. Martin GR. 1999 Eye structure and foraging in King Penguins *Aptenodytes*
438 *patagonicus*. *Ibis* 141(3), 444-450.
- 439 34. White CR, Day N, Butler PJ, Martin GR. 2007 Vision and foraging in
440 cormorants: more like herons than hawks? *PLoS One* 2(7), e639.
- 441 35. Kato A, Ropert-Coudert Y, Gremillet D, Cannell B. 2006 Locomotion and
442 foraging strategy in foot-propelled and wing-propelled shallow-diving seabirds.
443 *Mar Ecol Prog Ser* 308, 293-301.
- 444 36. Lovvorn JR, Liggins GA. 2002 Interactions of body shape, body size and stroke-
445 acceleration patterns in costs of underwater swimming by birds. *Funct Ecol* 16,
446 106-112.
- 447 37. Fish FE, Nicastrò AJ. 2003 Aquatic turning performance by the whirligig beetle:
448 Constraints on maneuverability by a rigid biological system. *J Exp Biol* 206,
449 1649-1656.

- 450 38. Howard HC. 1974 Optimal strategies for predator avoidance: the relative
451 importance of speed and manoeuvrability. *J Theor Biol* 47, 333-350.
- 452 39. Parson JM, Fish FE, Nicastro AJ. 2011 Turning performance of batoids:
453 limitations of a rigid body. *J Exp Mar Biol Ecol* 402, 12-18.
- 454 40. Ribak G, Weihs D, Arad Z. 2008 Consequences of buoyancy to the maneuvering
455 capabilities of a foot-propelled aquatic predator, the great cormorant
456 (*Phalacrocorax carbo*). *J Exp Biol* 211, 3009-3019.
- 457 41. Hui CA. 1985 Maneuverability of the Humbolt penguin (*Spheniscus humboldti*)
458 during swimming. *Can J Zool* 63, 2165-2167.
- 459 42. Green J, Halsey LG, Wilson R, Frappell P. 2009 Estimating energy expenditure
460 of animals using the accelerometry technique: activity, inactivity and
461 comparison with the heart-rate technique. *J Exp Biol* 212(4), 471-482.
- 462 43. Laich AG, Wilson RP, Gleiss AC, Shepard EL, Quintana F. 2011 Use of overall
463 dynamic body acceleration for estimating energy expenditure in cormorants:
464 does locomotion in different media affect relationships? *J Exp Mar Biol Ecol*
465 399(2), 151-155.
- 466 44. Bannasch R. 1995 Hydrodynamics of penguins—an experimental approach. *The*
467 *penguins*, 141-176.
- 468 45. Ribak G, Weihs D, Arad Z. 2005 Submerged swimming of the great cormorant
469 *Phalacrocorax carbo sinensis* is a variant of the burst-and-glide gait. *J Exp Biol*
470 208(20), 3835-3849.
- 471 46. Lovvorn J, Liggins GA, Borstad MH, Calisal SM, Mikkelsen J. 2001
472 Hydrodynamic drag of diving birds: effects of body size, body shape and
473 feathers at steady speeds. *J Exp Biol* 204(9), 1547-1557.
- 474 47. Wilson RP, Ropert-Coudert Y, Kato A. 2002 Rush and grab strategies in
475 foraging marine endotherms: the case for haste in penguins. *Anim Behav* 63(1),
476 85-95.
- 477 48. Ropert-Coudert Y, Grémillet D, Kato A. 2006 Swim speeds of free-ranging
478 great cormorants. *Mar Biol* 149(3), 415-422.
- 479 49. Wilson RP, Wilson M-PT. 1988 Foraging behaviour in four sympatric
480 cormorants. *J Anim Ecol*, 943-955.
- 481 50. Grémillet D, Tuschy I, Kierspel M. 1998 Body temperature and insulation in
482 diving great cormorants and European shags. *Funct Ecol* 12(3), 386-394.

- 483 51 Mitchell G, van Sitter S, Roberts D, Mitchell D. 2017 Body surface area and
484 thermoregulation in giraffes. *J Arid Environ* 145, 35-42.
- 485 52. Walsberg GE, King JR. 1978 The relationship of the external surface area of
486 birds to skin surface area and body mass. *J Expl Biol* 76(1), 185-189.
- 487 53. Svalgelj WS, Quintana F. 2007 Sexual size dimorphism and sex determination by
488 morphometric measurements in breeding imperial shags (*Phalacrocorax*
489 *atriceps*). *Waterbirds* 30(1), 97-102.
- 490 54. Wilson R, Sala J, Gómez-Laich A, Ciancio J, Quintana F. 2015 Pushed to the
491 limit: food abundance determines tag-induced harm in penguins. *Anim Welfare*
492 24(1), 37-44.
- 493 55. Taylor MP, Wedel, MJ. 2013 Why sauropods had long necks; and why giraffes
494 have short necks. *PeerJ* 1, e36
495
496

497 Figure captions

498

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

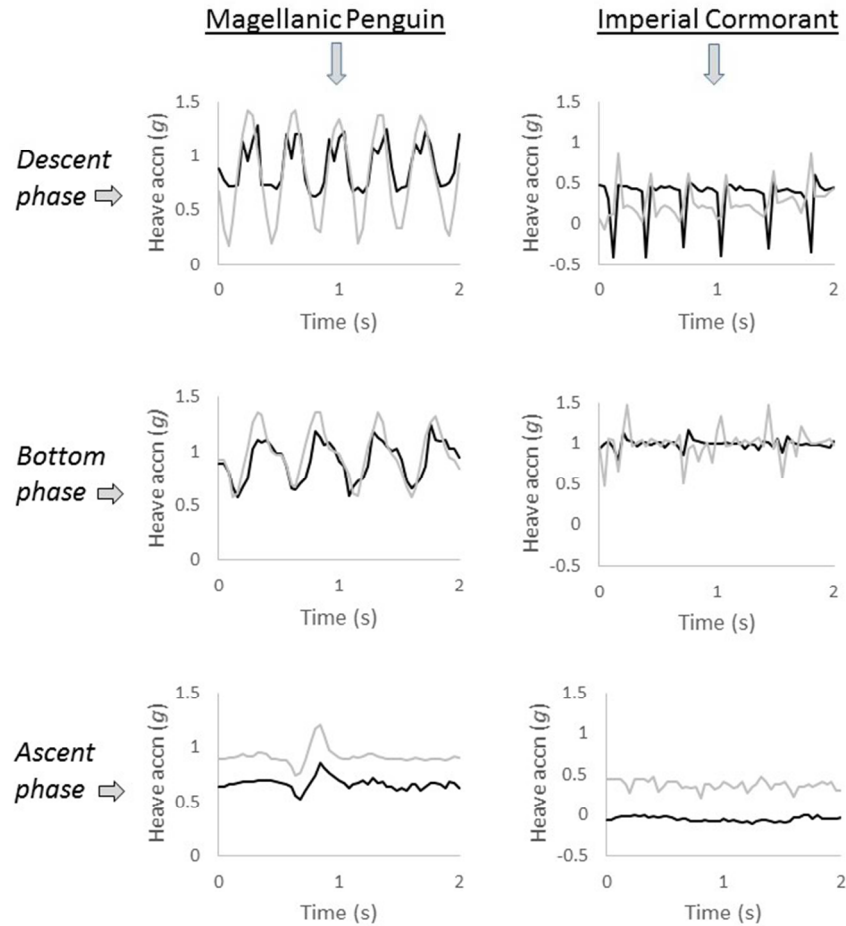
528 normalized to give 100% (max values are 2 g for both spheres and facets containing less
529 than 5% of the data are not shown).

530

531

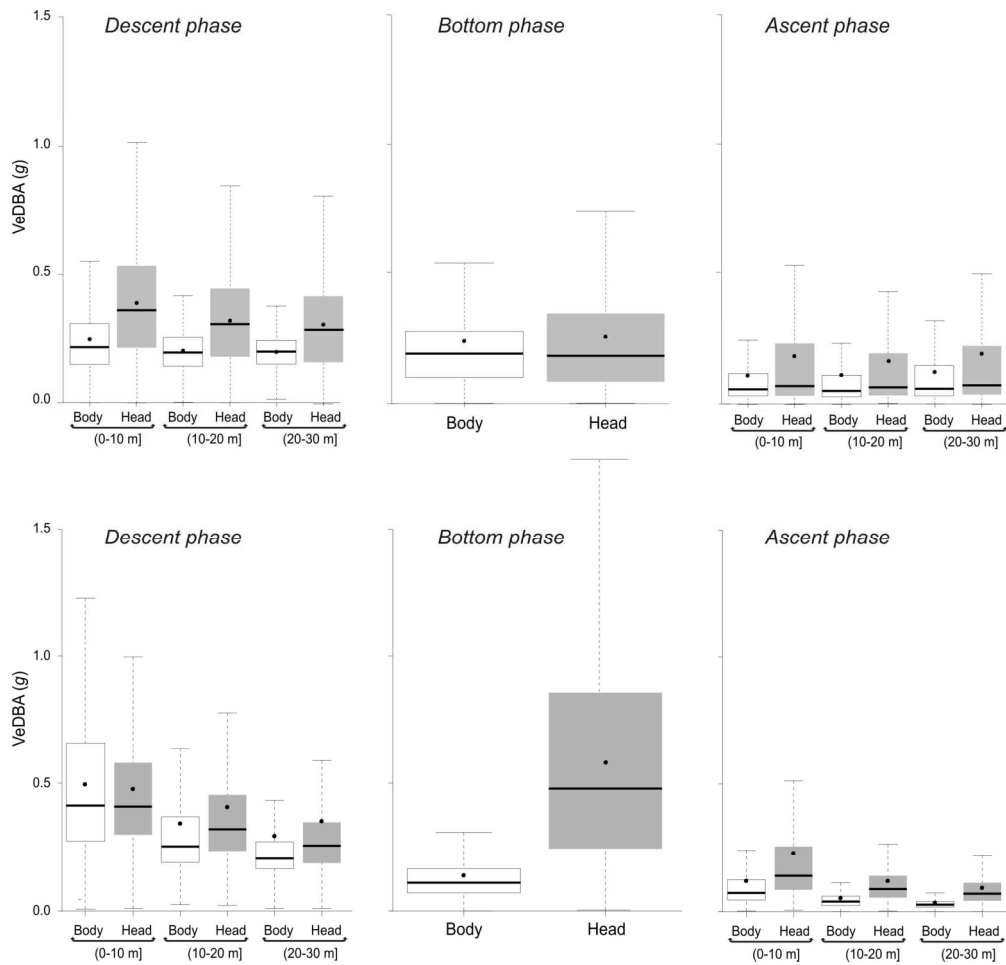
532

533



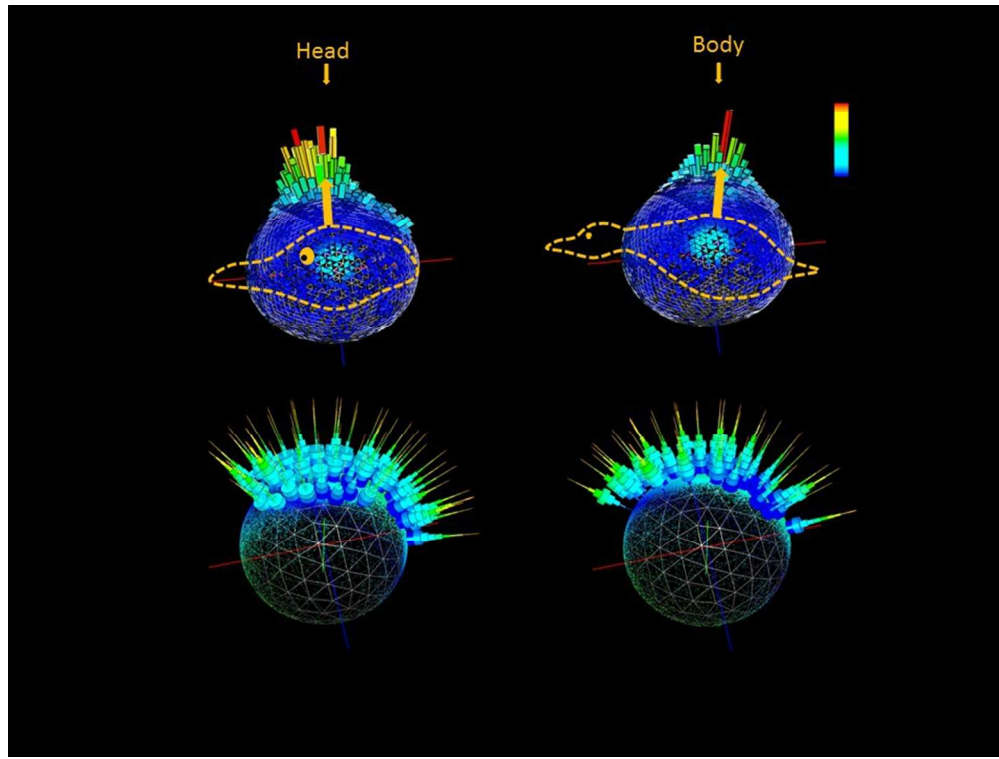
Examples of (heave) acceleration data attained from head mounted (grey lines) and body mounted (black lines) accelerometers deployed on penguins and cormorants during the three main dive phases (descent, bottom and ascent). Note that flipper and leg beats are apparent, and coupled, in signals from both 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)



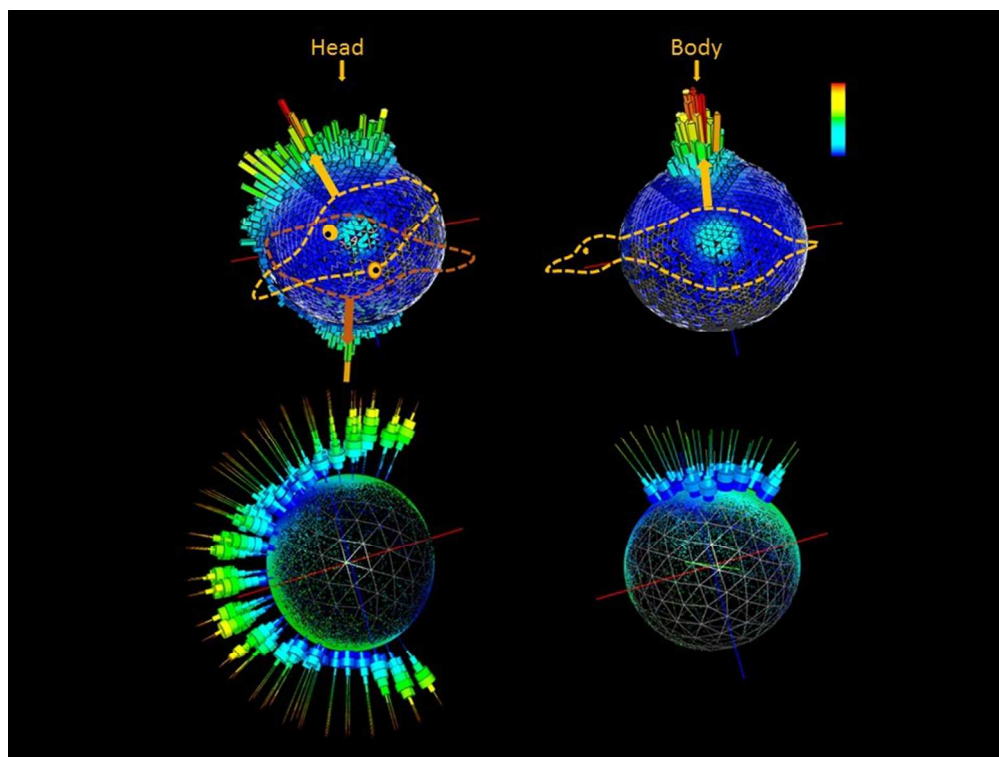
Box-whisker plots of the head (grey) and body (black) dynamism (VeDBA) for penguins (upper graphs) and cormorants (lower graphs) according to dive phase and depth (the bottom phases of dives from both species were selected to be approximately similar depths (40- 60 m)). Note the substantial difference 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).

254x190mm (96 x 96 DPI)