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2 **The diving behaviour of the Manx Shearwater**

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16 Running Head: Shearwater diving

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19 **Summary**

20 The diving capabilities of *Procellariiformes* remain the least understood component of
21 avian diving physiology. Due to their relatively small size shearwaters may have high
22 oxygen consumption rates during diving relative to their available oxygen stores. Dive
23 performance in this group should be strongly limited by the trade-off between oxygen
24 consumption and oxygen stores, and shearwaters could be a good model group for testing
25 predictions of dive theory. Many earlier measurements of shearwater dive behaviour
26 relied on observations from the surface or potentially biased technology, and it is only
27 recently that diving behaviour has been observed using electronic recorders for many of
28 the clades within the family. To rectify this issue, the diving behaviour of Manx
29 Shearwaters (*Puffinus puffinus*) breeding in Wales, United Kingdom, was studied on a
30 large sample of birds using bird-borne time-depth-temperature recorders deployed on
31 chick-rearing shearwaters in July and August over three years (2009-2011). Light
32 availability apparently limited diving as dives only occurred between 4:00 and 19:00 in
33 GMT. All individuals routinely dive deeper than traditional assumptions, to a mean
34 maximum depth of 31m and down to nearly 55m. We compiled all available data for a
35 comparison of the dive depth across shearwater species. There was a positive allometric
36 relationship between maximum dive depth and body mass across *Puffinus* and *Ardenna*
37 shearwater species, as expected, but only if samples of < 2 individuals were excluded.
38 The large intra-specific range in maximum dive depth in our study illustrates that
39 apparent diversity in diving performance across species must be interpreted cautiously.

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43 **Introduction**

44 In breath-holding diving animals, oxygen stores are generally increase with body mass
45 $\propto 1.00$, while metabolic rate increases only with body mass $\propto 0.75$ (Halsey *et al.* 2006).
46 Therefore body mass determines capacity for long and deep dives in breath-hold divers
47 (Kooyman & Kooyman, 1995). Procellariiform seabirds often exceed the dive depth limit
48 expected from allometry, exemplifying adaptation for a pelagic life-style, and widely
49 varied diving performance. Albatrosses, with their long wings, are not morphologically
50 adapted for diving and typically perform shallow (<5m) dives (Prince *et al.* 1994), while
51 diving petrels (*Pelecanoides*), morphologically adapted for underwater pursuit using wing
52 propulsion, can reach maximum diving depths of 10-18 m (Navarro *et al.* 2014,
53 Dunphy *et al.* 2015). The diving behaviour of shearwaters (*Puffinus*, *Ardenna* and
54 *Calonectris*) possess several anatomical adaptations for swimming under water, including
55 a robust sternum and pelvis, laterally compressed “streamlined” tarsi, flattened humeri
56 and relatively short wings compared with many other Procellariiformes (Warham 1977).
57 Some petrel species are known to engage in pursuit plunging and pursuit diving (Warham
58 1990). However, information on dive performance in shearwater species consists of
59 mixed data from maximum depth gauges (Burger & Wilson 1988) and low-sampling rate
60 archival pressure loggers (Rayner *et al.* 2011). The use of high-sampling-rate dive
61 loggers is critical for capturing fine-scale diving behaviour and accurately calculating
62 dive parameters. Lower sampling rates lead to under estimation of the number of dives
63 performed, overestimation of dive duration and potentially underestimation of dive depth
64 (Wilson *et al.* 1995, Elliott *et al.* 2009). To help fill this gap in knowledge we report
65 detailed diving behaviour in a ca. 400 g representative of the group (range: 148-850 g,
66 Table 1), the Manx Shearwater *Puffinus puffinus*, a trans-equatorial migrant
67 predominantly breeding in the UK (Guilford *et al.* 2009). Knowledge of the feeding

68 ecology of marine top predators is essential to understand their potential role in the
69 marine ecosystems, and to conserve and manage those ecosystems (Ashmole, 1971, Hunt
70 and Schneider, 1987), and there is a need for more data for those species that have been
71 seldom studied to date (Phalan et al., 2007). Our goal is two-fold: to describe the diving
72 behaviour of Manx Shearwaters for the first time with a large sample using 1 Hz time-
73 depth recorders (TDR), and to explore whether there is an allometric relationship between
74 body mass and dive depth for shearwater species using currently available published data
75 (including analysis of sample size).

76

77 **Methods**

78 To gain a representative sample of diving behaviour, TDRs were deployed on Manx
79 shearwaters rearing chicks during July and August over three years (2009-2011) at
80 Skomer Island, Wales (51° 44' N, 5° 17' W). Equipped birds were selected from our
81 study plots, all of whom were caring for young during the normal chick-rearing period at
82 this site. With a large number of birds tracked for multiple years and by comparing
83 breeding success with unmonitored plots, our samples are representative of the population
84 as a whole. 2.7g CEFAS G5 TDRs were attached for seven days maximum to four
85 central tail feathers with Tesa marine cloth tape (Wilson & Wilson 1989), configured at 1
86 Hz recording in pressure and temperature, with a resolution of <0.1 m. As part of
87 another study, birds also carried a GPS logger on their back and leg-mounted geolocator-
88 immersion logger: total attachment mass was 17.5-19.0g (4.0-4.8% body mass based on
89 individual body weights; see Dean et al. (2012) for methods, which reported that there
90 was no measurable effects in breeding parameters). Birds were taken from study nests by
91 hand, weighed, devices deployed (or removed), and returned within 15 minutes. Birds

92 were sexed by cloacal inspection (Gray & Hamer 2001) and sex information was
93 recorded as unknown if we missed the laying date. To determine food load from parents
94 to their chicks, we weighed chicks every evening at 8pm before Manx Shearwaters
95 arrived at the colony and checked study burrows every 20 min through the night
96 (typically between 23:00-04:00). To reduce disturbance, we used knock-down sticks at
97 the entrance (Shoji & Gaston, 2010), only checking nests when sticks were displaced.
98 When we found an adult in a study burrow, we blocked the nest and left at least 20 min to
99 allow parents to feed young before weighing both parent and chick. This visual inspection
100 also allowed us to determine trip duration.

101 All analyses were performed in R 3.1.2 (R Development Core Team 2014). We extracted
102 dive depth, dive duration and surface interval duration for each dive, after accounting for
103 device drift, using diveMove (Luque & Fried 2011). Depth measurements were calibrated
104 using a ‘moving quantile’ zero-offset correction method (details in Luque & Fried 2011),
105 and each dive event was classified using a dive threshold of 1 m. Behavioural aerobic
106 dive limit (bADL) was estimated by following the method provided in Kooyman &
107 Kooyman (1995). Dive duration with the minimum post-dive duration was identified by
108 fitting a spline regression with segmented relationship in post-dive durations
109 (“segmented” package in R). We applied Burger’s (1991) method for other diving
110 seabirds to develop the allometric relationship between maximum dive depth and body
111 mass averaged across individuals using data from published studies (values from other
112 literatures was used for some species when body mass was not presented in the
113 references) as the estimated slope of the \log_{10} - \log_{10} linear regression. As there are intra-
114 specific variations in dive depth in seabirds (Halsey *et al.* 2006) and sample sizes varied
115 among studies, we further tested whether absolute maximum dive depth is related to
116 sample size, by using the residual of absolute maximum dive depth on body mass against

117 number of individuals used in each study. We tested for normality and homoscedasticity
118 prior to the analysis and data were transformed if necessary. To analyse the relationship
119 between dive duration (s) and dive depth (m) in Manx Shearwaters, we used linear mixed
120 models with individual as a random effect to include multiple dives per individual. Model
121 selection was based on minimising Akaike's information criterion (AIC) and we
122 calculated Δ AIC relative to the null model (intercept-only). Unless otherwise stated,
123 means \pm 1 SD are presented.

124

125 **Results**

126 We deployed loggers on 18 birds in 2009 (5 males, 11 females, 2 unknown), 9 in 2010 (4
127 males, 4 females, 1 unknown), and 10 in 2011 (8 males, 2 females). Corrupted data from
128 4 TDRs (1 male in 2009, 2 males and 1 female in 2011) were discarded. Mean
129 deployment period (duration of device attachment) was 3.8 ± 1.2 days (range 2-10). The
130 median recorded foraging trip was 1 day (interquartile range 1-3, range 1-8) after which
131 tracked parents fed chicks a meal with a mean mass of 48.1 ± 20.7 g, and 56 g for parents
132 carrying devices $<1\%$ body mass (Gray & Hamer 2001). In total we recorded 3,329 dives
133 during 122 bird-days from 33 deployments: 1,209 dives in 53 days from 17 birds in 2009,
134 733 dives in 28 days from 9 birds in 2010; and 1,387 dives in 41 days from 7 birds in
135 2011. One female was tracked in both 2009 and 2010 so the first deployment was
136 excluded. Mean mass of tracked males (419.3 ± 23.5 g) and females (419.3 ± 31.8 g) was
137 similar ($t_{27} = 0.001$, $P = 0.99$), and mean dive depth and dive frequency per day did not
138 differ between sexes (mean dive depth: male = 34.4 ± 9.4 m, female = 31.0 ± 6.9 m,
139 pooled = 32.7 ± 8.2 m, $t_{27} = 1.33$, $P = 0.19$; dive frequency: male = 256.6 ± 130.5 dives
140 day^{-1} , female = 184.6 ± 156.9 dives day^{-1} , pooled = 219.3 ± 146.8 dives day^{-1} , $t_{27} = 1.11$,

141 $P = 0.28$). There was a clear diurnal pattern to diving behaviour (Fig. 1a, b), showing that
142 diving activities in this species occurred during the daytime between 04:00 - 19:00 GMT
143 ($n = 3,329$). Dive duration increased with dive depth ($\Delta AIC = - 5477$, GLMM: Estimate =
144 1.55 ± 0.01 s, Fig. 1c). Maximum dive depth across individuals averaged 31.0 ± 9.9 m
145 (range: 9.6 - 54.9m), while the maximum individual dive duration averaged 46.2 ± 16.0 s
146 (range: 23 – 84 s). To determine the relationship between surface-pause duration and dive
147 duration, we related each dive time to the shortest succeeding surface time needed for that
148 dive time, and found a break point identified by fitting a spline regression (30.02 ± 14.51
149 (95 % CI) s; Fig. 2). Surface times rose steeply for dives longer than 30 s ($y = 9.45 \times$
150 1.04^x , $P < 0.0001$) ;. Approximately 10 % of dives exceeded the behavioural ADL (Fig.
151 1d).

152 To develop an allometric relationship we collected reported averaged maximum dive
153 depths of 14 species (11 *Puffinus* including *Ardenna* and 3 *Calonectris* shearwaters;
154 Table 1, Fig. 3). For presentation purposes, we included *Ardenna* species in the same
155 category as *Puffinus* in this manuscript. The two genera appeared to differ, with
156 *Calonectris* species showing only shallow diving (Fig. 3) compared with the *Puffinus*
157 group. Across all studies (by combining species), residuals of absolute maximum dive
158 depth on body mass increased with sample size (estimate = 0.93 ± 00.37 $t = 2.55$, $R^2 =$
159 0.29 , $P = 0.02$, $N = 13$). Since maximum achievable depths may be missed in small
160 samples we excluded the species with the smallest sample size (Great Shearwaters
161 *Ardenna gravis*, $N = 2$), and found that maximum dive depth then increased with body
162 mass across *Puffinus* species (exponent $\pm SE = 0.59 \pm 0.19$, $R^2 = 0.53$, $t = 3.16$, $P = 0.01$,
163 $N = 11$).

164

165 **Discussion**

166 Manx Shearwater diving behaviour

167 Manx Shearwaters breeding at the world's largest colony have a striking diurnal foraging
168 pattern and dive much deeper than reported dive depth in other groups of
169 *Procellariiformes* (e.g. Dunphy *et al.* 2015). These data provide the first insights into the
170 diving behaviour of the Manx Shearwater based on a large dataset providing detailed
171 information for a *Puffinus* species. The use of high-sampling-rate dive loggers (1 Hz in
172 this study; <10% of median dive duration), as recommended by Wilson *et al.* (1995)
173 captured fine-scale diving behaviour and allowed accurate calculation of dive parameters.
174 As with above-surface movement patterns associated with foraging in Manx Shearwaters
175 (Dean *et al.* 2012), we found that diving behaviour was highly constrained to daylight and
176 twilight hours, strongly suggesting visual pursuit of prey. Diurnal diving is typical of
177 birds dependent on ambient light to forage, such as some albatrosses and prions, though
178 some visual-based predation can occur at night under strong moonlight (Brooke 2004), or
179 at high latitudes when days are too short (Grémillet *et al.* 2005), while some *Pterodroma*
180 species use nocturnal foraging (Rayner *et al.* 2008). The difference could reflect the diet
181 selection or whether or not birds search for prey in flight or sit on the water, which may
182 be more effective at night (Phalan *et al.* 2007). Furthermore, Clupeid fish make diel
183 vertical migrations within the water column in response to ambient light levels (Hays
184 2003), so diving at dawn and dusk might enhance foraging efficiency despite reduced
185 ambient light because prey can be found at shallower depth at those times. In our study,
186 dive frequency peaked in early evening (17:00 - 18:00 GMT), which may reflect a trade-
187 off between increased prey availability and foraging efficiency during low-light
188 conditions (Elliott & Gaston 2015) or perhaps reflecting a strategy to minimise the cost of
189 transporting large food loads to the colony or nocturnal resting at sea. About half of all

190 dives were less than 7 m, consistent with traditional views (Brooke 1990) that Manx
191 Shearwaters rely on pursuit diving for shallow pelagic prey. Nevertheless, all individuals
192 routinely dived much deeper, to a mean maximum depth of 31m with some diving down
193 to nearly 55m. While deep dives were reliably recorded with TDR, foraging related
194 shallow dives may be missed out because we have currently no way to identify uncertain
195 dive events such as bathing, socializing and other non-foraging associated activities from
196 genuine short, shallow dives so shallow dives were excluded from the analyses. Future
197 studies to investigate the role of those dives will allow the nature of shallow dives to be
198 better understood.

199 Sex-specific differences in diving behaviour (dive frequency, depth and duration)
200 have been found in several species of seabird where there is sexual size dimorphism
201 (Quillfeldt *et al.* 2011, Gomez Laich *et al.* 2012), reversed sexual size dimorphism
202 (Lewis *et al.* 2005, Weimerskirch *et al.* 2006), or where the sexes are similar in size
203 (Lewis *et al.* 2002, Pech & Congdon 2006, Elliott *et al.* 2010). Manx Shearwaters show
204 little sexual size dimorphism: <1 mm difference in wing length and bill length, and 1 mm
205 difference in tarsus length between the sexes (Brooke 1990) and the diving profiles of
206 males and females in this study was similar.

207 Similarly, as all telemetric methods can impact behaviour (Phillips *et al.* 2003),
208 for example by reducing provisioning rate or meal sizes (Saether *et al.* 1993), the
209 biologgers in the current study may have impacted where and how birds foraged.
210 Nevertheless, in our study, foraging trip length (median 1 day) and food delivery to chick
211 (48g) were reasonably representative of normal behaviour (56 g for parents carrying
212 devices <1% body mass, Gray & Hamer 2001; 49 g for untagged parents, Hamer & Hill
213 1997). In a comparison of birds with the same or similar devices with control birds , there

214 were no measurable impact of carrying the device on reproductive success, chick-growth
215 rates or foraging trip lengths (Dean *et al.* 2012).

216 Since seabirds are limited by the oxygen they take with them, stored in the
217 respiratory and circulatory systems and muscles, there must be a dive duration (the
218 aerobic dive limit, ADL (but see Butler 2006)) beyond which accumulated blood lactate
219 must subsequently be metabolised during surface recovery (Burger, 2001). Early reports
220 of calculated anaerobic dive limits (cADL) underestimated ADL by about a factor of
221 three (e.g. Croll *et al.* 1992) because they used values for oxygen consumption derived
222 from shallow dive tanks, which overestimated oxygen consumption by a factor of three
223 (Hansen & Ricklefs 2004, Elliott *et al.* 2013). One reason behavioural ADL (bADLs),
224 such as the bADL measured in our study, may be preferable is because they avoid
225 inaccuracies in the measurement of oxygen consumption during diving. Calculated ADL
226 has been reported for several species of diving seabird: 48 s for Brünnich's Guillemot
227 *Uria lomvia* (Croll *et al.* 1992), 78-120 s for Gentoo Penguin *Pygoscelis papua* and 126 s
228 for King Penguin *Aptenodytes patagonicus* (Butler 2001). Estimated bADL was 27-29 s
229 for Imperial Shags *Phalacrocorax atriceps* (Quillfeldt *et al.* 2011) and 240 s for Crozet
230 and Kerguelen Shags *Phalacrocorax melanogenis* and *Phalacrocorax verrucosus*
231 (Tremblay *et al.* 2005, Cook *et al.* 2008), though it seems improbable that there is one
232 order magnitude difference in the bADL among these species, because these three species
233 are closely related (Hackett *et al.* 2008). Rather the inconsistency is likely to reflect
234 ecological or physical differences or is due to a difference in sample sizes. Our estimate
235 for the Manx Shearwater bADL of 30 s, falls within this range and high correlation
236 between dive depth and dive duration suggests that the Manx Shearwaters use their
237 lengthy dives to achieve deeper depth, rather than extending the bottom time of each dive.
238 Only 10 % of dives exceeded 30 s duration, suggesting that Manx Shearwaters rarely dive

239 beyond their aerobic limit, which agrees with the previous report that few dives for most
240 animals exceed their ADL (Butler & Jones 1997). Overwhelmingly most (90%) of
241 Manx Shearwater diving is therefore aerobic, although occasional longer anaerobic dives
242 are also used, perhaps to exploit dense, but mobile and hard-to-find concentrations of
243 prey before they escape or become depleted (Ydenberg & Clark 1989).

244

245 Allometric relationship

246 Maximum dive depth in wing-propelled divers is allometrically related to body mass
247 (Burger 1991), and we found that the relationship across *Puffinus* and *Ardenna*
248 shearwater species was significant after removing the smallest sample. The allometric
249 scaling exponent for dive depth (0.59) in this study was higher than the exponent for dive
250 duration (0.37; Halsey *et al.* 2006). This suggests that *Puffinus* species were using long
251 dive duration to increase their transit times (= deeper depth), rather than to stay longer at
252 the bottom. The high value of the exponent could represent real range in diving behaviour
253 in relation to body size, but the cross-study effect of sample size on apparent maximum
254 dive depths with mass suggests caution. Perhaps because *Puffinus* shearwaters often dive
255 much lesser depth than they are able (as we have shown here for the Manx Shearwater),
256 maximum achievable depths may be missed in small samples making some studies
257 unreliable. Similarly, the due to poorly resolved phylogeny in *puffinus* species (Pyle *et al.*
258 2011), we were unable to account for phylogeny which could be a potential issue.
259 Nevertheless, our results show that dive depth scales with body mass in shearwaters, but
260 that strong conclusions require reliable data.

261

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268 College, Oxford (AS).

SPECIES	Binary	N	mass	Max depth (m)	Ave. Max depth (m)	Ave. depth (m)	Ave. Max duration (g)	Ave. duration (g)	Method	Reference
Barolo shearwater	<i>Puffinus baroli</i>	6	174.1	23.1	14.8	-	-	-	MDG	Neves et al., 2012
Flesh-footed shearwater	<i>P. carneipes</i>	23	632	28.7	13.6	-	-	-	MDG	Taylor, 2008
Black-vented shearwater	<i>P. opisthomelas</i>	18	406	52	21	-	-	-	MDG	Keitt et al., 2000
Yelkouan shearwaters	<i>P. yelkouan</i>	10	500	30.2	25.7	17.8	-	-	TDR	Peron et al., 2013
Audubon's shearwater	<i>P. Iherminier</i>	7	168	35	15	-	-	-	MDG	Burger, 2001
Manx shearwater	<i>P. puffinus</i>	36	421	55	33.06	9.6	46.22	13.49	TDR	This study
Hutton's shearwater	<i>P. huttoni</i>	13	380	36.6	23	-	-	-	MDG	Taylor, 2008
Balearic shearwater	<i>P. mauretanicus</i>	18	500	28.04	16.35	-	-	-	TDR	Meier et al., 2015
Balearic shearwater	<i>P. mauretanicus</i>	3	500	26	-	5.6	66	17.6	DL	Aguilar et al., 2003
Great shearwater	<i>Ardenna gravis</i>	2	864	18.9	14.9	3	6.9	31	TDR	Ronconi et al., 2010
Fluttering shearwater	<i>A. gavia</i>	1	148	29.4*	-	-	-	-	MDG	Taylor, 2008

Sooty shearwater	<i>A. griseus</i>	9	850	69.9	48	15.9	-	-	TDR	Shaffer et al., 2009
Sooty shearwater	<i>A. griseus</i>	20	850	68.2	-	12.5	-	-	TDR	Shaffer et al., 2006
Sooty shearwater	<i>A. griseus</i>	16	850	92.9	42.7	-	-	-	MDG	Taylor, 2008
Sooty shearwater	<i>A. griseus</i>	10	847	55.1	-	6.93	-	39.73	TDR	Dunphy et al., 2015
Sooty shearwater	<i>A. griseus</i>	35	850	67	-	38.7	-	11.5	MDG	Weimerskirch and Sagar, 1996
Short-tailed shearwaters	<i>A. tenuirostris</i>	22	588	70.6	35.5	-	12	-	MDG	Weimerskirch and Cherel, 1998
Flesh footed shearwater	<i>A. carneipes</i>	3	700	66.5	44.1	3.2	-	-	TDR	Rayner et al., 2011
Wedge-tailed shearwaters	<i>A. pacificus</i>	19	426	66	13	-	-	-	MDG	Burger, 2001
Cory's shearwater	<i>C. borealis</i>	22	770	9.8	7.35	1.95	3.95	24.5	TDR	Paiva et al., 2010
Streaked shearwaters	<i>C. leucomelas</i>	14	513	6	2.53	1.06	4.43	8.64	TDR	Matsumoto et al., 2012
Scopoli's shearwaters	<i>C. diomedea</i>	10	657	5.4	4.45	1.8	7.95	11.7	TDR	Grémillet et al., 2014

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270

271 Table 1. Raw data used in this study on sample size, body mass, dive depth and duration in shearwater species.

272 Note: N = number of individuals, Max depth = absolute maximum dive depth, Ave Max depth = maximum dive depth averaged across individuals, Ave depth = mean depth,
273 Ave. Max duration = maximum dive duration averaged across individuals, Ave duration = mean duration. Method: MDG = maximum depth gage, TDR = temperature-depth
274 recorders, DL = combined depth sensor and depth logger. * indicates median value.

275 **Figure legends**

276 Figure 1. (a) Number of dives and (b) mean dive depths (04:00 - 19:00) as a function of
277 hour of day;(c) relationship between dive depth (m) and dive duration (s); (d) Frequency
278 of dive durations (s) in the Manx Shearwater. Dashed line indicates the behavioural ADL
279 (30 s).

280

281 Figure 2. Dive duration and the shortest succeeding surface pause duration in a given dive
282 duration in the Manx Shearwater. The black solid line represents the segmented
283 regression line with an identified breakpoint (30 s) on dive duration and the two vertical
284 grey broken lines are 95 % confidence intervals (15.69-44.34 s).

285

286 Figure 3. Average maximum dive depth (m) against body mass (g). Grey dots indicate
287 *Puffinus* and *Ardenna* species ($N = 11$) and black dots indicate *Calonectris* ($N = 3$). Black
288 square indicates the smallest sample (Great Shearwater, *Ardenna gravis*; $N = 2$) which
289 was excluded from the analysis. The line is the linear regression for *Puffinus* and *Ardenna*
290 species after removing the smallest samples ($N = 11$). Closed grey dot indicates the value
291 of the Manx Shearwater.

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