

1 **Deep-diving beaked whales dive together but forage apart.**

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23

24 Abstract

25 Echolocating animals that forage in social groups can potentially benefit from eavesdropping on
26 other group members, cooperative foraging or social defence, but may also face problems of
27 acoustic interference and intra-group competition for prey. Here, we investigated these potential
28 trade-offs of sociality for extreme deep-diving Blainville's and Cuvier's beaked whales. These
29 species perform highly synchronous group dives as a presumed predator-avoidance behaviour, but
30 the benefits and costs of this on foraging have not been investigated. We showed that group
31 members could hear their companions for a median of at least 91% of the vocal foraging phase of
32 their dives. This enabled whales to coordinate their mean travel direction despite differing
33 individual headings as they pursued prey on a minute-by-minute basis. While beaked whales
34 coordinated their echolocation-based foraging periods tightly, individual click and buzz rates were
35 both independent of the number of whales in the group. Thus, their foraging performance was not
36 affected by intra-group competition or interference from group members, and they did not seem to
37 capitalize directly on eavesdropping on the echoes produced by the echolocation clicks of their
38 companions. We concluded that the close diving and vocal synchronization of beaked whale groups
39 that quantitatively reduces predation risk has little impact on foraging performance.

40

41 **Keywords:** beaked whales, collective behaviour, acoustic interference, eavesdropping, cooperative
42 foraging

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46

47 **Introduction**

48 For social animals, the benefits from group-living may include lower predation risks or increased
49 foraging efficiency [1–3]. However, aggregating may also have costs involving physical
50 interference such as intra-group competition for resources, or sensory interference of the visual,
51 chemical or acoustic cues used to find food or to mediate group coordination [4]. Acoustic signals
52 used for communication often have long durations and low directionality, making them vulnerable
53 to interference from other vocal group members [5,6]. For example, when the acoustic signals of
54 nearby animals overlap in time and frequency, signal interference either for communication,
55 hunting or habitat exploration can result in signal interference either for communication, hunting
56 or habitat exploration [7]. In contrast, the powerful foraging echolocation clicks of many social-
57 living toothed whales, used to identify prey, are short (10-250 μ s) and directional [8], and are thus
58 inherently less susceptible to direct acoustic interference, also known as jamming. However, clicks
59 from other animals could reduce the detection of weak echoes returning from prey via direct
60 interference as well as forward and backwards masking, i.e., due to a transiently increased detection
61 threshold for weak echoes that immediately precede or follow a conspecific click [9]. It has been
62 postulated that some bats and dolphins mitigate interference by changing the frequency, amplitude
63 and/or timing of their echolocation signals, or increase their silent periods when animals forage
64 close to each other, known as a jamming avoidance response [10–12]. These strategies differ
65 between species and can be absent or remain undiscovered for others. For example, some bats shift
66 the frequency of their signals when foraging close to conspecifics, while other species of
67 echolocating bats lack any apparent jamming avoidance response [13].

68

69 Despite the potential for interference, echolocating within a group can have benefits if the group is
70 herding prey in a cooperative manner [14] or if foraging individuals can eavesdrop and interpret
71 the acoustic cues produced by conspecifics [15]. Of particular value for eavesdropping may be
72 rapid click sequences, called buzzes, which appear to be produced by all echolocating animals
73 when approaching prey [16,17]. Some echolocating bats are attracted by conspecific buzzes in
74 laboratory experiments suggesting eavesdropping [18]. Eavesdropping has also been suggested for
75 wild foraging orcas (*Orcinus orca*) and bottlenose dolphins (*Tursiops truncatus*) [19,20].

76

77 The foraging trade-offs imposed by group living may be especially acute for social deep-diving
78 toothed whales such as beaked whales that must capture enough food in physiologically-limited
79 dives to compensate the energy expended in reaching their deep prey resources [21,22]. Blainville's
80 and Cuvier's beaked whales (*Mesoplodon densirostris* and *Ziphius cavirostris*, abbreviated hereon
81 as Blainville's and Cuvier's, respectively) are echolocators that forage in light-limited deep waters
82 and perform highly-coordinated foraging dives when associated in small social groups [23],
83 exacerbating the potential impact of acoustic interference and/or competition. Group members of
84 both species show close temporal coordination of their foraging dives and of periods of hunting by
85 echolocation within dives; this coordination has been proposed to increase survival by reducing
86 predation risk from orcas. This is because diving in coordination enables beaked whales to ascend
87 from deep vocal dives in silence and with a random direction, thus surfacing at unpredictable
88 locations some 1 km from their last vocal position and presumably avoiding being detected by
89 orcas [23]. This fitness benefit could be augmented if they additionally gain hunting benefits by
90 foraging in groups, e.g. by cooperative hunting or eavesdropping. Acoustic and/or physical
91 interference resulting from vocal aggregation and competition could be the price to pay for these
92 potential benefits. We expect that for a given prey density, intra-group competition and acoustic

93 interference would reduce the availability of prey for each individual, resulting in a decrease in
94 hunting rates. The decrease should be roughly proportional to the number of members of the social
95 group mainly when beaked whales target prey in patches [24,25]. This expectation assumes that
96 the probability of success of each prey capture attempt is independent of the number of animals.

97

98 Here we analyse the acoustic activity of Blainville's and Cuvier's beaked whales echolocating in
99 groups to understand how these animals may experience and manage the above trade-offs of group
100 foraging. For both species we used suction-cup attached multi-sensor tags to record their individual
101 sound production and movements throughout foraging dives to test the null hypothesis that beaked
102 whale foraging performance is unaffected by group size. We specifically tested the following
103 predictions: i) if beaked whales experience intra-group foraging competition, individual buzz rates
104 will tend to decrease in larger groups; ii) if acoustic interference from vocalizations of other group
105 members causes jamming or masking, individual click rates would change with increasing group
106 size to compensate [12]; iii) if beaked whales benefit from eavesdropping on the vocalizations of
107 other group members, individual click rates would reduce with increasing group size as animals
108 take advantage of shared information, while individual buzz rates would increase due to the
109 expanded detectability of prey items through eavesdropping.

110

111 **Methods**

112 Multi-sensor archival DTAGs [26] were attached to Blainville's (16 deployments on 11 whales)
113 off El Hierro (Canary Islands, Spain) and to Cuvier's (10 whales) in the Ligurian Sea (Italy) during
114 field experiments performed between 2003 and 2018 (Table 1). Animals were approached from a
115 small boat and the tags were attached to the dorsum of the whales with suction cups using a long

116 pole for deployment. Pairs of whales were tagged in the same social group on one occasion each
117 in El Hierro and Liguria [23]. DTAGs recorded depth, 3D magnetic field and acceleration
118 (sampling rate of 50 Hz or higher) as well as acoustic data with one or two hydrophones sampling
119 at 96 kHz in 2003 and 192 kHz thereafter [26]. The size and social composition of the groups of
120 tagged whales were visually assessed. Tags detached from the whales after 3 to 30 hrs (median 8.6
121 hrs) of recording and floated to the surface where they were retrieved with the aid of VHF tracking.

122

123 Tag data were analysed using custom software [27] for MATLAB v7 (MathWorks). A supervised
124 click detector [28] was used to locate echolocation clicks and thereby identify foraging dives.
125 Clicks produced by tagged whales were typically identifiable in the sound recordings by the
126 presence of low frequencies that were absent in clicks from untagged whales [29]. Foraging dives
127 were divided into phases of silent descent and ascent, and vocal foraging based on the presence of
128 clicks. Click trains from untagged whales were identified regularly in the recordings when ambient
129 noise was low. To quantify clicking activity from conspecifics the vocal phase of the tagged animal
130 was divided into minutes, and for each minute the maximum number of concurrently detected click
131 trains was noted representing the minimum number of animals vocalizing at the same time. To
132 verify the identification of clicks from tagged whales, we used the inter-click-interval (ICI) and
133 angle of arrival (AoA) of the clicks at the stereo tags [28,30]. The AoA and ICI of clicks produced
134 by the tagged whale showed little and smooth variations. Conversely, click trains from untagged
135 whales show wider variations in the AoA within a short time period [29], as well as highly variable,
136 and generally lower, received levels, due to the varying direction and aspect of untagged whales
137 relative to the tag [28,30].

138

139 Trains of frequency modulated usual echolocation clicks emitted by tagged whales were
140 interspersed by fast series of unmodulated clicks (buzzes) associated with prey capture attempts
141 [28,31,32]. Buzzes were defined as non-frequency modulated click trains with an ICI <100 ms
142 [28]. Foraging buzzes can be readily distinguished from social sounds like whistles (which are
143 tonal sounds produced rarely by Blainville's and not yet found in Cuvier's) and rasps, which consist
144 of frequency modulated click trains with median ICI of 5 ms [33].

145

146 We constructed predictive models to assess the influence of group size on click and buzz rates of
147 the tagged whales, i.e., total number of clicks or buzzes in the vocal phase of each dive divided by
148 the duration of the vocal phase. These models also allow us to determine if periods of silence are
149 increased as an anti-jamming response, via a reduction in click rates per dive. Since our data
150 contained multiple observations per individual, Generalised Estimation Equations (GEEs) were
151 fitted in R [35–38] with package `geepack` [39] using foraging dive as the sampling unit and tag
152 deployment as the clustering factor. Click and buzz rates per foraging dive were the response
153 variables in separate models with group size as the predictor variable. Although the dependent
154 variables were rates, which are usually Poisson-distributed, the counts of clicks and buzzes were
155 large and thus were fitted with an identity link function (Gaussian family). We used an auto-
156 regressive correlation structure (AR1) in which the expected correlation between observations
157 (values per dive) within each cluster (Tag ID) decreased as observations become further apart in
158 time [40]. Although the group size of Cuvier's ranged 1-5 the dataset was dominated by groups of
159 4-5 individuals (Table 1). Because of this, foraging dives performed by the less frequent groups of
160 1-3 animals were pooled. A non-parametric Kolmogorov-Smirnov test [41] was then used to check
161 whether click and buzz rates in the dives performed by the smaller groups fit the same distribution
162 as in dives performed by larger groups.

163 Vocalising animals in a group of foraging beaked whales at a given time might be less than the
164 actual group size, and individuals might potentially respond to jamming from a nearby animal by
165 either silencing or increasing their acoustic output [12,43]. To test for these tactics, a Pearson
166 correlation test was performed to evaluate the relationship between group size and the mean rate
167 of clicks (i.e., clicks/sec) from untagged animals recorded by the tag for each minute of the vocal
168 phase of the tagged whale. The rate was quantified by dividing the number of clicks from untagged
169 whales received at the tag during the vocal phase by the duration of this phase. This analysis was
170 limited to a subset of recordings with the lowest ambient noise, i.e. without sounds from other
171 marine mammal species or boat traffic noise, and low noise from water flow over the tag due to
172 the tag being located forward on the body of the whale. Also, we computed (i) the amount of time
173 tagged whales were silent (i.e., the sum of pauses in clicking >1 s long), and (ii) the apparent source
174 levels (ASLs) of tagged whale clicks, and if these were influenced by the number of other
175 vocalizing animals during each minute of the vocal phase of all dives with low ambient noise. The
176 tag position behind the head precludes measurement of the spectral characteristics or intensity of
177 the forward-directed clicks [29]. However, the intensity of clicks from the tagged animal as
178 recorded by the tag, (the ASL), provides a relative measure of on-axis level [44]. We measured
179 ASL by first highpass filtering the sound data to remove noise at low frequencies (5 kHz, 4-pole
180 Butterworth filter) and then calculating the root mean squared (RMS) level of each filtered click
181 over a 1.4 ms window aligned to the start of the click waveform [28]. To test the relationships
182 between minute-averaged animal counts and pauses and ASL we used GEEs as described above,
183 using the dive as the clustering factor and the tagged whale and minutes within foraging dive as
184 the sampling unit. Although spectral adjustments are another potential response to jamming, these
185 cannot be reliably measured in data from either the tagged animal nor other nearby whales except
186 in rare cases when conspecifics are echolocating directly towards the tag [28].

187 In the two instances when pairs of whales were tagged in the same social group, the independence
188 of the click rates of the pair was investigated. These data, previously analysed by Aguilar de Soto
189 *et al.* [23] consisted on highly-synchronized dive profiles and vocal periods. The independence of
190 the click rates of the pairs was tested by comparing the time-paired minute average ICI sequences
191 of the two whales with a Pearson correlation test. This involved calculating the average ICI per
192 coincident minute of clicking, i.e. starting from the first second when both animals were
193 simultaneously echolocating until the earliest end of clicking of the two tagged whales ($n = 17$ and
194 31 coincident minutes in Blainville's and Cuvier's, respectively). The minute averaging interval
195 was chosen to reduce potential serial correlation in the ICI. Buzzes and pauses in clicking were
196 removed from this analysis by selecting ICIs between 0.1 and 1 s.

197

198 To examine if the whales tagged in the same social group travelled in the same average direction
199 during their synchronized dives, we plotted the heading of the two tagged whales, computed from
200 the magnetometer in the tag, while producing each click using the CircStat toolbox [42] for
201 MATLAB. We also calculated the average headings of each whale in the pair for the full duration
202 of their vocal foraging phase. To test if whales coordinated their heading on a finer time scale, we
203 compared the average travel directions of the two tagged whales of the pair within each coincident
204 minute of the vocal phase using a Pearson correlation test.

205

206 **Results**

207 Tagged whales occurred in groups ranging 2-6 animals (Blainville's) and 1-5 (Cuvier's) (Table 1).

208 Blainville's performed foraging dives that lasted on average 49.4 ± 6.5 min with vocal periods

209 lasting a mean 24.2 ± 5 min, while Cuvier's dives lasted 59.3 ± 10.5 min during which they were
210 vocal 33.9 ± 7 mins.

211

212 The two pairs of whales tagged simultaneously in the same social group demonstrated highly
213 coordinated dives [45] (Figure 1, Figure S1). Tags carried by each whale received clicks produced
214 by the other tagged animal of the pair in 100% of the coincident vocal minutes when both tagged
215 whales were clicking (Figure 1). The stereo tags recorded click trains of at least one other beaked
216 whale (most probably a group member) during a median 91% of the vocal time of the tagged
217 whales, within the subsampled low-noise dives (Figure S2). As the detection probability of clicks
218 from untagged whales is likely well less than 1 [46], the minimum number of whales counted for
219 each group acoustically was similar to, but generally under-estimated the group size estimated
220 visually in the field (Figures 2 and S2). A similar assessment could not be performed for Cuvier's
221 beaked whales tagged in Liguria due to the higher ambient noise level in this area of the
222 Mediterranean Sea.

223

224 The average headings of the two whales of each pair during the vocal phase of their synchronized
225 dives were very similar (129° and 128° for the two Blainville's and 161° and 126° for the two
226 Cuvier's Figure 3). However, despite the similarity of overall dive swimming direction, there was
227 no evidence of correlation between the average per-minute headings of the tagged whales (Pearson
228 correlation, $R^2 = 0.04$ and 0.08 and p -values = 0.47 and 0.11 for Blainville's and Cuvier's,
229 respectively).

230 Despite the large potential for eavesdropping or interference, we found no evidence that individual
231 acoustic activity was influenced by group size or by the acoustic behaviour of other group members
232 (Table S1). Click rates averaged 2.41 ± 0.41 clicks/s for Blainville's and 1.54 ± 0.44 clicks/s for

233 Cuvier's. Individual buzz rates averaged 1.1 ± 0.34 buzzes/min for Blainville's and 0.52 ± 0.37
234 buzzes/min for Cuvier's. No evidence of differences in the distribution of click and buzz rates of
235 Cuvier's between small and larger groups was found (p-values for the K-S tests > 0.5). Also, the
236 rate of clicks from untagged whales recorded at the tags showed no significant relationship with
237 group size for the analysed Blainville's dives (Pearson correlation test: $R^2 = 0.12$, p-value = 0.08).

238

239 In addition to the dive-averaged click and buzz rates of individuals being uninfluenced by group
240 size, whales within a group clicked at independent rates throughout the dive. Data from the two
241 pairs of whales tagged simultaneously in the same social group showed no correlation in the
242 minute-averaged ICI of the paired animals for either species ($R^2 = 0.002$ and p-value = 0.17 for
243 Blainville's and $R^2 = 0.04$ and p-value = 0.57 for Cuvier's), albeit within the limitations of the
244 small sample size. The number of nearby conspecifics detected by each tag did not influence the
245 apparent source level of the clicks of tagged whales nor the amount of time tagged whales were
246 silent during the vocal phase of the dives (Table S2).

247

248 **Discussion**

249 Deep-diving animals that live in groups face an apparent trade-off: if they stay close during dives
250 to maintain social contact, competition and interference in hunting seem inevitable. Conversely, if
251 they separate to hunt efficiently, they risk losing the group and the benefits of sociality, such as
252 reduced predation risk [45]. Allaying predation risk may be an especially strong evolutionary driver
253 of the behaviour of Cuvier's (and most probably also Blainville's) beaked whales, given their strong
254 responses to orca sounds and naval sonar [47–49]. Here we tested the hypotheses that echolocating
255 beaked whales foraging with echolocation in highly coordinated groups may incur costs of

256 aggregation due to intra-group competition for prey or interference of their echolocation signals,
257 or may benefit from the proximity of group members through eavesdropping on their echolocation
258 clicks and buzzes. Interference and eavesdropping seem particularly likely given the potential
259 aggregation of their prey: in the mesopelagic realm small fauna found in scattering layers can form
260 patches some 20 to 150 m wide and beaked whales may target these small organisms in addition
261 to larger predatory fauna also preying on these aggregations [24,25,50].

262

263 We found no evidence that individual prey encounter rates (indicated by buzz rates) within dives
264 were affected by group size, suggesting that on average there is little intra-group competition for
265 foraging resources in social groups of beaked whales. Gregarious animals display a number of
266 behaviour strategies to mitigate intra-group competition for food, e.g. sheep in large aggregations
267 form subgroups to exploit different sub-patches of vegetation [51], and individual bees specialize
268 in extracting pollen from different types of flowers around their colony [52]. Social mammals
269 targeting a deep-water niche similar to beaked whales employ different strategies. Long-
270 (*Globicephala melas*) and short-finned (*G. macrorhynchus*) pilot whales [30,53] might reduce
271 intra-group competition for prey by diving asynchronously and emitting calls to maintain acoustic
272 contact between diving and surface group members [6,30]. Although these calls can provide cues
273 to acoustic-guided predators, the strong cohesion of their large social groups enables pilot whales
274 to perform mobbing responses against predators [54]. Our data suggest that the behavioural tactic
275 employed by beaked whales to reduce intra-group competition for prey is that group members
276 diving in tight coordination spread out when foraging at depth. However, they then reunite to
277 ascend together, avoiding the need to vocalise near the surface where they are more vulnerable to
278 predator attacks [23]. This behaviour might have co-evolved with small group sizes so that

279 individuals can swim close enough to each other to coordinate their movements during dives, but
280 sufficiently apart to find unexploited prey patches.

281

282 As expected for efficient independent foraging, we revealed that group members swim in directions
283 which are uncorrelated on a short time scale while diving together. Nonetheless, they maintain a
284 similar average heading over the full dive presumably to facilitate reunion during the ascent [23].

285 While relative heading could only be measured directly in the two instances when animals were
286 tagged in the same group, the usually continuous changing angles-of-arrival of clicks from group
287 members recorded by all stereo tags support this interpretation of independent movement [29].

288 Moreover, visual observations of groups of beaked whales regularly surfacing together after long
289 dives affirms that overall swimming direction of group members is tightly coordinated during
290 dives. Such coordination must be mediated by the near-continuous reception of the echolocation
291 clicks of other group members, implying that foraging clicks have a secondary communicative
292 function, acting as acoustic beacons of the relative position of animals while foraging.

293

294 The near-continuous inter-audibility of vocal group members is a consequence of beaked whales
295 diving together and coordinating the vocal phase of their dives [23]. However, the regular detection
296 of one or more close group member throughout the foraging periods of the tagged whales raises
297 the possibility that their echolocation signals might negatively interfere or alternatively that whales
298 might beneficially eavesdrop on the echo returns of clicks from conspecifics. We found no
299 evidence of jamming compensating behaviours: click rates of tagged whales were not affected by
300 group size either for Blainville's or Cuvier's. This was also supported by the two pairs of whales
301 tagged in the same social group. The individual click rates of these whales averaged over intervals

302 of one minute showed no correlation between pair members. Moreover, whales tagged singly in
303 groups did not extend their silent periods (pauses in clicking) nor adjust the source level of their
304 clicks when more conspecifics were audible as would be expected to enhance eavesdropping or
305 combat jamming. Thus, we posit that acoustic interference does not constrain biosonar-mediated
306 foraging in these species, and echolocation production is not detectably influenced by information-
307 sharing, even if we cannot dismiss that whales might use information provided by the acoustic
308 activity of other group members. Instead, individual click rates in beaked whales have been
309 observed to correlate with the movement patterns of the whales and may be influenced by prey
310 distribution [25,32].

311

312 The absence of compensatory behaviours in beaked whales contrasts with the “anti-jamming”
313 response proposed for bats where silent periods of individuals are increased when conspecifics are
314 very close [12]. However, these taxa are subject to highly divergent ecological and physiological
315 constraints. Echolocating animals that pause click production lose information on prey location
316 and thus risk reducing their foraging efficiency [34]. While bats can hunt continuously for an entire
317 night, the rate and duration of breath-hold foraging dives of beaked whales are physiologically
318 limited. This results in a stereotyped behaviour that affords them only 20-30 minutes of foraging
319 time every hour or 1.5 hours on average [22,55]. It seems reasonable to hypothesise that these
320 whales cannot afford to use silence as a strategy against jamming.

321

322 The lack of influence of group size on click production rate for beaked whales contrasts with
323 observations of the acoustic behaviour of two species of delphinids: orcas and bottlenose dolphins
324 [19,20]. These studies estimated individual click production rate by dividing the number of clicks
325 from the group, detected by nearby drifting hydrophones, by a visual estimate of group size. Click

326 rates in both species were observed to decrease on a per capita basis with increasing group size
327 suggesting that individuals were reducing their click production rates and eavesdropping on echo
328 information returning from clicks produced by group members [19,20]. The contrasting results for
329 the beaked whales studied here might be explained by differences in behaviour and trophic niche.
330 Fish-eating orcas and bottlenose dolphins forage most often in shallow waters [56,57] and
331 sometimes coordinate their hunting [58], while Blainville's and Cuvier's beaked whales dive to
332 mean depths of 800 m [22] and hunt individually. The cacophony of clicks and their surface echoes
333 from echolocating conspecifics in large groups of delphinids might clutter the acoustic scene of
334 these shallow foragers, potentially making it beneficial to reduce individual clicking rates in
335 preference for a scrounging or eavesdropping tactic. In contrast a high resilience to jamming in
336 echolocating dolphins [10] has recently been revealed via low duty cycling of clicking and high
337 directionality in sound transmission and hearing. Alternatively, contrasting observations from
338 delphinids and beaked whales may result from methodological differences in these studies.
339 Animal-borne acoustic tags used here on beaked whales offer a higher confidence when measuring
340 individual click emission rates than do the drifting hydrophones used in the delphinid studies. This
341 is because highly directional clicks may not be detected if they are not orientated towards drifting
342 hydrophones, even when animals are at relatively short distances [59], whereas they are more likely
343 to be recorded on a tag carried by an animal. A further bias may be introduced if animals spread
344 further apart when in larger groups, given that the detectability of animals at larger distances from
345 the hydrophone would be reduced on average. Such an occurrence was found in Blainville's at El
346 Hierro, with a reduction in per capita click rate observed with group size. Given that tag data show
347 that the clicking rates are independent of group size, this means that progressively more clicks from
348 untagged whales are missed at a point receiver as group size increases. This is consistent with
349 acoustic estimation of group size of whales generally underestimating the visual count of whales

350 as observed here, and is likely associated with beaked whales separating and moving independently
351 at depth to hunt [23]. In contrast, correlation between the detection rate of clicks from Blainville's
352 and group size has been observed using an extensive array of deep moored hydrophones. In such a
353 situation clicks have a high probability of being detected in any direction [60] and the probability
354 of missing clicks is low. Such variability in observations when utilising differing methods
355 highlights the importance of considering study design when interpreting results and also is
356 particularly relevant when using passive acoustic monitoring (PAM) for density estimation of
357 echolocating whales [61]. This highlights that an improved understanding of group behaviour and
358 detectability are crucial for appropriate application of acoustic methods for estimating population
359 abundance, particularly when used for the effective management of these iconic megafauna.

360

361 **Conclusion** Blainville's and Cuvier's beaked whales foraging in groups do not modify
362 individual rates of echolocation and prey capture attempts in relation to group size. This indicates
363 that sensory interference or competition from group members is unlikely to occur while hunting.
364 Individuals are also unlikely to benefit from local enhancement directly by sharing information of
365 echo arrivals from conspecific clicks. Tagged whales however, were in acoustic contact with other
366 group members via eavesdropping almost all of their vocal (foraging) time. This presumably aids
367 coordination of the timing and mean direction of their synchronized dives while they separate to
368 hunt independently. Blainville's and Cuvier's beaked whales do not behave as cooperative hunting
369 predators, but more like social foraging herbivores and frugivores such as ungulates and primates
370 that coordinate group movements but forage independently [62,63]. These collective behavioural
371 tactics reduce intra-group competition allowing individuals to maintain foraging efficiency while
372 gaining the social and predation risk abatement benefits of group living [23]. Small group sizes in
373 these species of beaked whales might thus be related to the foraging footprint of the group, as

374 whales keep tightly coordinated during dives but still need to perform prey capture attempts per
375 dive while hunting independently. This in turn suggests dependence upon a reliable foraging niche
376 and sets an upper limit to the number of whales that can efficiently forage simultaneously.

377

378 **Ethics.** Tagging was approved by the University of La Laguna Animal Ethics Committee and
379 authorized by the Canary Islands and Spanish Governments for El Hierro, and by the Woods Hole
380 Animal Ethics Committee (previous affiliation of MJ) for Liguria.

381 **Data availability.** Datasets basing the analyses of this paper are available in the Tables S3-S5 of
382 the electronic supplementary material and per-minute datasets can be accessed at Dryad:
383 <https://doi.org/10.5061/dryad.gqnk98sm0>

384

385 **Author contributions.** NAS, MJ, PA, PTM and JAT collected the data. All authors analysed the
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407

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581

582 **Table 1.** Number of foraging dives analysed for each tag deployment along with visually observed
 583 group size. Deployments are codified by two letters indicating the species followed by the tagging
 584 year and Julian day and a letter indicating the tagging order of the day. Tagged whales are classified
 585 as: adult male (♂), adult female (♀) or indeterminate (I) which are adults or sub-adults of unknown
 586 sex. Most Blainville's are identified by their photo-ID catalogue code (<http://www.cetabase.info>).
 587 Some individuals were tagged more than once throughout the study.

Species	Individual (sex)	Tag deployment	Group size	# foraging dives
Blainville's	MdH1 (♂)	Md03_284a	5	5

beaked whale		Md05_294b	3	4
		Md08_137a	4	5
	MdH6 (♂)	Md05_277a	5	3
		Md08_136a	4	2
	MdH15 (I)	Md03_298a	2	2
	MdH22 (♀)	Md04_287a	5	4
		Md05_294a	3	1
		Md08_289a	6	7
	MdH43 (♀)	Md05_285a	3	4
	MdH74 (♂)	Md08_142a	4	1
	MdHC1 (♂)	Md08_148a	2	2
		Md10_146a (I)	3	1
		Md10_163a (♂)	3	6
		Md17_168a (♂)	6	2
		MdH23 (♀)	Md18_297b	6
Total	11	16		50
Cuvier's beaked whale		Zc03_263a (I)	4	7
		Zc04_160a (♂)	3	2
		Zc04_161a (I)	5	3
		Zc04_161b (I)	5	8
		Zc04_175a (I)	1	3
		Zc04_179a (I)	4	2
		Zc05_167a (♂)	5	3
		Zc05_170a (I)	4	5
		Zc06_204a (I)	4	2
		Zc06_205a (I)	4	4
Total	10			39

588

589

590 **Figure 1.** Coordinated dives of two pairs of tagged whales (Blainville's above and Cuvier's below)

591 coloured by individual click rate. The start and end of the vocal phase of each animal are marked

592 with asterisks (*), and the coincident vocal phase for each whale is shown as a thick line coloured

593 by its click rate.

594

595 **Figure 2.** Examples of foraging dive profiles of tagged Blainville's beaked whales within social

596 groups of 3-6 animals. The vocal phase of each dive is shown as a thick line coloured by the

597 estimated number of animals vocalizing at the same time (including the tagged whale) measured

598 as the maximum number of simultaneous click trains per minute received at the tag. Group size
599 estimated visually in the field is indicated for each dive.

600

601 **Figure 3.** Circular histograms of the headings of pairs of tagged whales in a dive while emitting
602 searching clicks (whale with tag A in red, and whale with tag B in blue) of two Blainville's (left)
603 and two Cuvier's (right) beaked whales tagged in the same group. The dashed lines represent the
604 average heading for each animal during the foraging dive and the line length is inversely
605 proportional to the angular spread of each distribution.

606

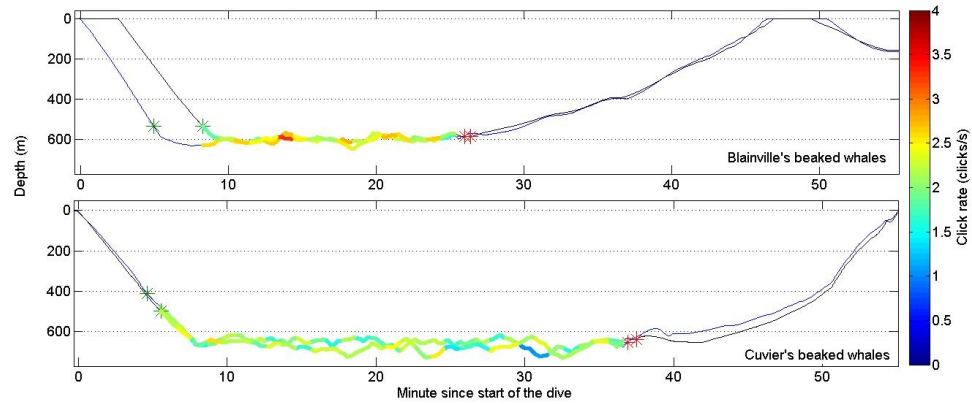


Figure 1. Coordinated dives of two pairs of tagged whales (Blainville's above and Cuvier's below) coloured by individual click rate. The start and end of the vocal phase of each animal are marked with asterisks (*), and the coincident vocal phase for each whale is shown as a thick line coloured by its click rate.

482x204mm (72 x 72 DPI)

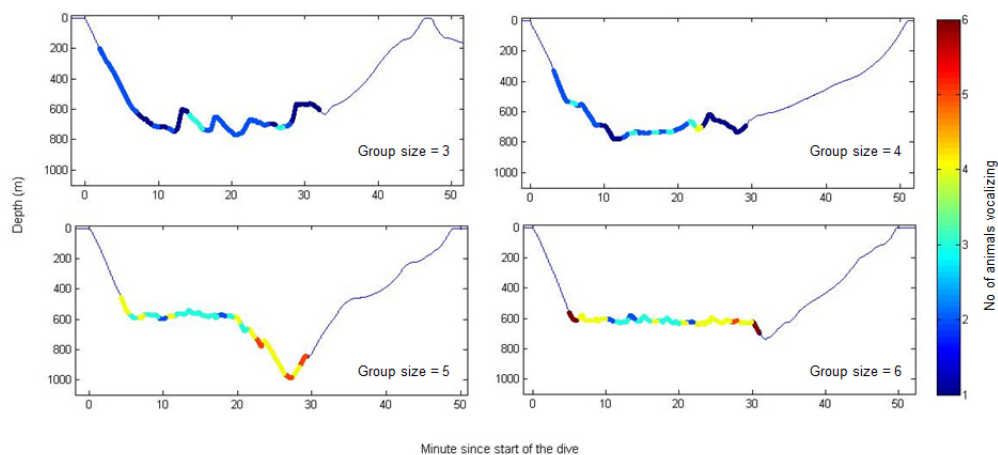


Figure 2. Examples of foraging dive profiles of tagged Blainville's beaked whales within social groups of 3-6 animals. The vocal phase of each dive is shown as a thick line coloured by the estimated number of animals vocalizing at the same time (including the tagged whale) measured as the maximum number of simultaneous click trains per minute received at the tag. Group size estimated visually in the field is indicated for each dive.

330x153mm (72 x 72 DPI)

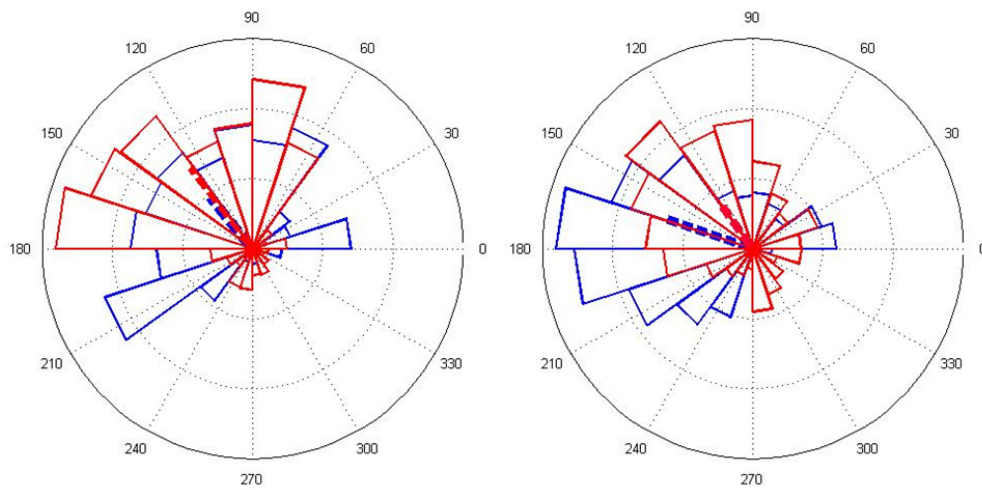


Figure 3. Circular histograms of the headings of pairs of tagged whales in a dive while emitting searching clicks (whale with tag A in red, and whale with tag B in blue) of two Blainville's (left) and two Cuvier's (right) beaked whales tagged in the same group. The dashed lines represent the average heading for each animal during the foraging dive and the line length is inversely proportional to the angular spread of each distribution.

340x201mm (72 x 72 DPI)