



## Research

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# Deep-diving beaked whales dive together but forage apart

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

## 1. Introduction

For social animals, the benefits from group living may include lower predation risks or increased foraging efficiency [1–3]. However, aggregating may also have costs involving physical interference such as intra-group competition for resources, or sensory interference of the visual, chemical or acoustic cues used to find food or to mediate group coordination [4]. Acoustic signals used for communication often have long durations and low directionality, making them vulnerable to interference from other vocal group members [5,6]. For example, when the acoustic signals of nearby animals overlap in time and frequency, signal interference either for communication, hunting or habitat exploration can result in signal interference either for communication, hunting or habitat exploration [7]. By contrast, the powerful foraging echolocation clicks of many social-living toothed whales, used to identify prey, are short

(10–250  $\mu$ s) and directional [8] and are thus inherently less susceptible to direct acoustic interference, also known as jamming. However, clicks from other animals could reduce the detection of weak echoes returning from prey via direct interference as well as forward and backwards masking, i.e. due to a transiently increased detection threshold for weak echoes that immediately precede or follow a conspecific click [9]. It has been postulated that some bats and dolphins mitigate interference by changing the frequency, amplitude and/or timing of their echolocation signals, or increase their silent periods when animals forage close to each other, known as a jamming avoidance response [10–12]. These strategies differ between species and can be absent or remain undiscovered for others. For example, some bats shift the frequency of their signals when foraging close to conspecifics, while other species of echolocating bats lack any apparent jamming avoidance response [13].

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

The foraging trade-offs imposed by group living may be especially acute for social deep-diving toothed whales such as beaked whales that must capture enough food in physiologically limited dives to compensate the energy expended in reaching their deep prey resources [21,22]. Blainville's and Cuvier's beaked whales (*Mesoplodon densirostris* and *Ziphius cavirostris*, abbreviated hereon as Blainvillés and Cuvier's, respectively) are echolocators that forage in light-limited deep waters and perform highly coordinated foraging dives when associated in small social groups [23], exacerbating the potential impact of acoustic interference and/or competition. Group members of both species show close temporal coordination of their foraging dives and of periods of hunting by echolocation within dives; this coordination has been proposed to increase survival by reducing predation risk from orcas. This is because diving in coordination enables beaked whales to ascend from deep vocal dives in silence and with a random direction, thus surfacing at unpredictable locations some 1 km from their last vocal position and presumably avoiding being detected by orcas [23]. This fitness benefit could be augmented if they additionally gain hunting benefits by foraging in groups, e.g. by cooperative hunting or eavesdropping. Acoustic and/or physical interference resulting from vocal aggregation and competition could be the price to pay for these potential benefits. We expect that for a given prey density, intra-group competition and acoustic interference would reduce the availability of prey for each individual, resulting in a decrease in hunting rates. The decrease should be roughly proportional to the number of members of the social group mainly when beaked whales target prey in patches [24,25]. This expectation assumes that the probability of success of each prey capture attempt is independent of the number of animals.

Here, we analyse the acoustic activity of Blainville's and Cuvier's beaked whales echolocating in groups to understand

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

## 2. Methods

Multi-sensor archival DTAGs [26] were attached to Blainville's (16 deployments on 11 whales) off El Hierro (Canary Islands, Spain) and to Cuvier's (10 whales) in the Ligurian Sea (Italy) during field experiments performed between 2003 and 2018 (table 1). Animals were approached from a small boat and the tags were attached to the dorsum of the whales with suction cups using a long pole for deployment. Pairs of whales were tagged in the same social group on one occasion each in El Hierro and Liguria [23]. DTAGs recorded depth, three-dimensional magnetic field and acceleration (sampling rate of 50 Hz or higher) as well as acoustic data with one or two hydrophones sampling at 96 kHz in 2003 and 192 kHz thereafter [26]. The size and social composition of the groups of tagged whales were visually assessed. Tags detached from the whales after 3–30 h (median 8.6 h) of recording and floated to the surface where they were retrieved with the aid of VHF tracking.

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

Trains of frequency-modulated usual echolocation clicks emitted by tagged whales were interspersed by fast series of unmodulated clicks (buzzes) associated with prey capture attempts [28,31,32]. Buzzes were defined as non-frequency-modulated click trains with an ICI < 100 ms [28]. Foraging buzzes can be readily distinguished from social sounds like

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

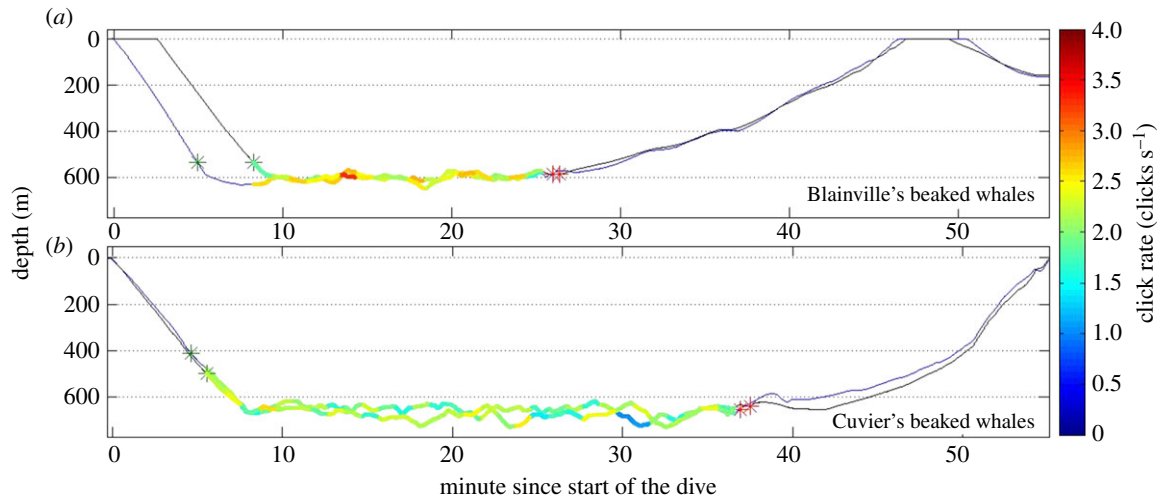
species	individual (sex)	tag deployment	group size	no. of foraging dives
Blainvillés beaked whale	MdH1 (♂)	Md03_284a	5	5
		Md05_294b	3	4
		Md08_137a	4	5
	MdH6 (♂)	Md05_277a	5	3
		Md08_136a	4	2
	MdH15 (I)	Md03_298a	2	2
	MdH22 (♀)	Md04_287a	5	4
		Md05_294a	3	1
		Md08_289a	6	7
	MdH43 (♀)	Md05_285a	3	4
	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	1	
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

whistles (which are tonal sounds produced rarely by Blainville's and not yet found in Cuvier's) and rasps, which consist of frequency-modulated click trains with median ICI of 5 ms [33].

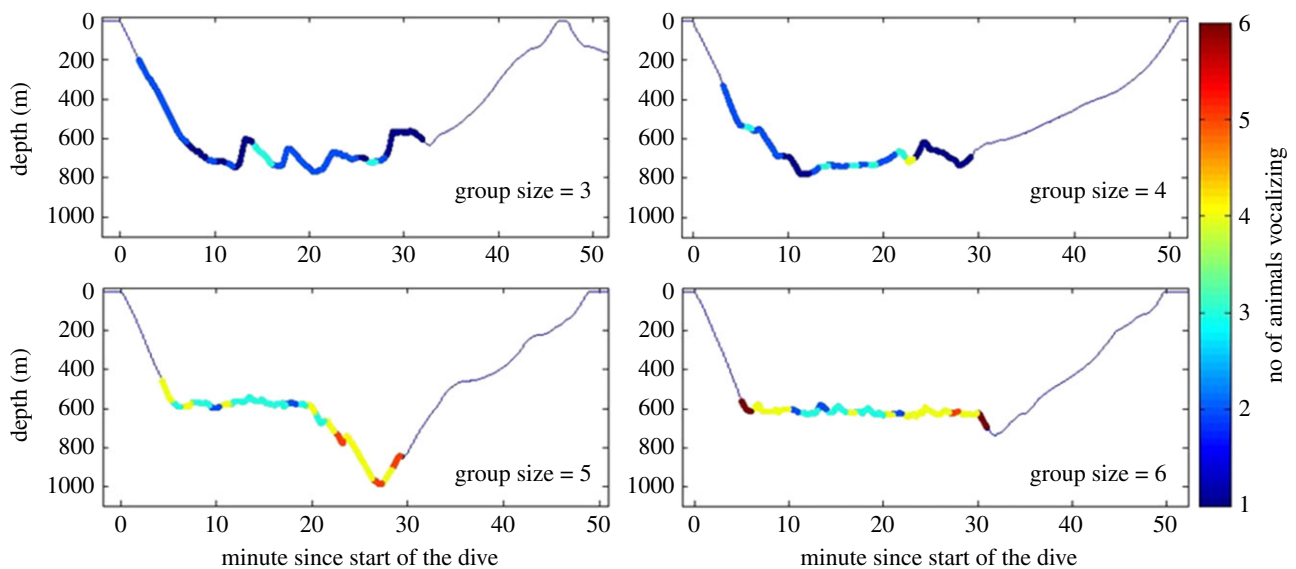
We constructed predictive models to assess the influence of group size on click and buzz rates of the tagged whales, i.e. the total number of clicks or buzzes in the vocal phase of each dive divided by the duration of the vocal phase. These models also allow us to determine if periods of silence are increased as an anti-jamming response, via a reduction in click rates per dive. Since our data contained multiple observations per individual, generalized estimation equations (GEEs) were fitted in R [34–37] with package *geepack* [38] using foraging dive as the sampling unit and tag deployment as the clustering factor. Click and buzz rates per foraging dive were the response variables in separate models with group size as the predictor variable. Although the dependent variables were rates, which are usually Poisson-distributed, the counts of clicks and buzzes were large and thus were fitted with an identity link function (Gaussian family). We used an auto-regressive correlation structure (AR1) in which the expected correlation between observations (values per dive) within each cluster (tag ID)

decreased as observations become further apart in time [39]. Although the group size of Cuvier's ranged 1–5, the dataset was dominated by groups of 4–5 individuals (table 1). Because of this, foraging dives performed by the less frequent groups of 1–3 animals were pooled. A non-parametric Kolmogorov–Smirnov test [40] was then used to check whether click and buzz rates in the dives performed by the smaller groups fit the same distribution as in dives performed by larger groups.

Vocalizing animals in a group of foraging beaked whales at a given time might be less than the actual group size, and individuals might potentially respond to jamming from a nearby animal by either silencing or increasing their acoustic output [12,41]. To test for these tactics, a Pearson correlation test was performed to evaluate the relationship between group size and the mean rate of clicks (i.e. clicks/sec) from untagged animals recorded by the tag for each minute of the vocal phase of the tagged whale. The rate was quantified by dividing the number of clicks from untagged whales received at the tag during the vocal phase by the duration of this phase. This analysis was limited to a subset of recordings with the lowest ambient noise, i.e. without sounds from other marine mammal species or boat traffic



**Figure 1.** Coordinated dives of two pairs of tagged whales (Blainville's (a) and Cuvier's (b)) 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. (Online version in colour.)



**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. (Online version in colour.)

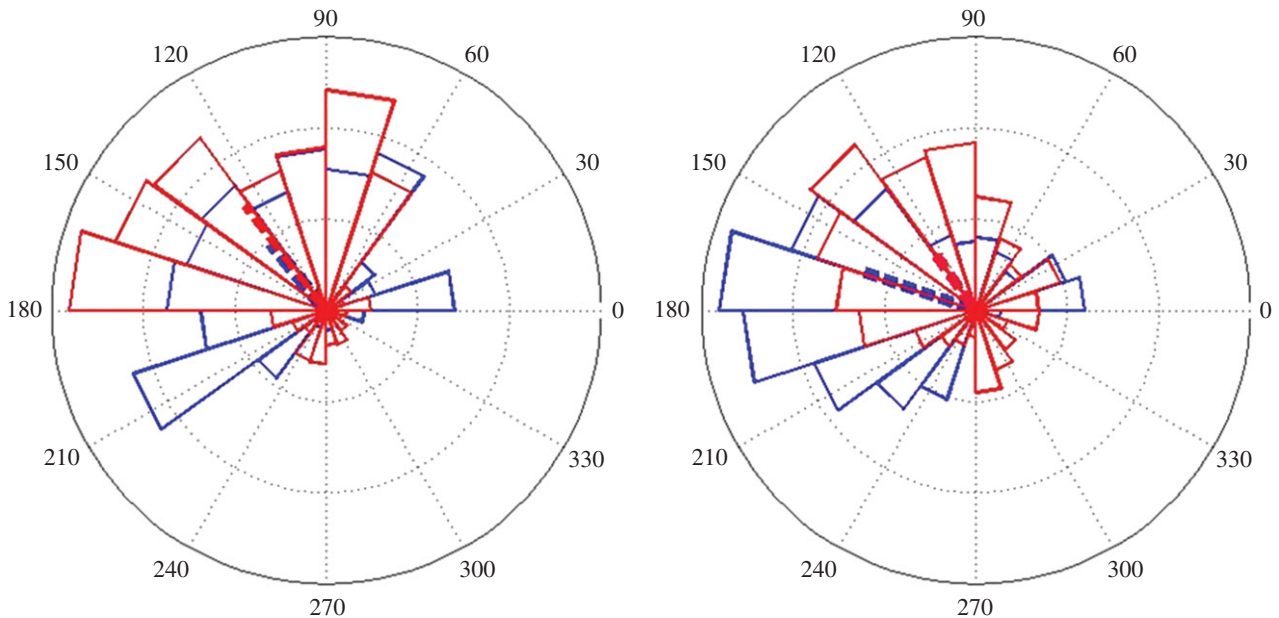
noise, and low noise from water flow over the tag due to the tag being located forward on the body of the whale. Also, we computed (i) the amount of time-tagged whales were silent (i.e. the sum of pauses in clicking greater than 1 s long), and (ii) the apparent source levels (ASLs) of tagged whale clicks, and if these were influenced by the number of other vocalizing animals during each minute of the vocal phase of all dives with low ambient noise. The tag position behind the head precludes measurement of the spectral characteristics or intensity of the forward-directed clicks [29]. However, the intensity of clicks from the tagged animal as recorded by the tag (the ASL) provides a relative measure of on-axis level [32]. We measured ASL by the first highpass filtering the sound data to remove noise at low frequencies (5 kHz, 4-pole Butterworth filter) and then calculating the root mean squared (RMS) level of each filtered click over a 1.4 ms window aligned to the start of the click waveform [28]. To test the relationships between minute-averaged animal counts and pauses and ASL, we used GEEs as described above, using the dive as the clustering factor and the tagged whale and minutes within foraging dive as the sampling unit. Although spectral adjustments are another potential response to jamming, these cannot be reliably measured in data from

either the tagged animal or other nearby whales except in rare cases when conspecifics are echolocating directly towards the tag [28].

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

To examine if the whales tagged in the same social group travelled in the same average direction during their synchronized dives, we plotted the heading of the two tagged whales, computed from the magnetometer in the tag, while producing each





**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 (*a*) and two Cuvier's (*b*) 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. (Online version in colour.)

click using the CircStat toolbox [42] for MATLAB. We also calculated the average headings of each whale in the pair for the full duration of their vocal foraging phase. To test if whales coordinated their heading on a finer timescale, we compared the average travel directions of the two tagged whales of the pair within each coincident minute of the vocal phase using a Pearson correlation test.

### 3. Results

Tagged whales occurred in groups ranging 2–6 animals (Blainville's) and 1–5 (Cuvier's) (table 1). Blainville's performed foraging dives that lasted on average  $49.4 \pm 6.5$  min with vocal periods lasting a mean  $24.2 \pm 5$  min, while Cuvier's dives lasted  $59.3 \pm 10.5$  min during which they were vocal  $33.9 \pm 7$  min.

The two pairs of whales tagged simultaneously in the same social group demonstrated highly coordinated dives [23] (figure 1, electronic supplementary material, figure S1). Tags carried by each whale received clicks produced by the other tagged animal of the pair in 100% of the coincident vocal minutes when both tagged whales were clicking (figure 1). The stereo tags recorded click trains of at least one other beaked whale (most probably a group member) during a median 91% of the vocal time of the tagged whales, within the subsampled low-noise dives (electronic supplementary material, figure S2). As the detection probability of clicks from untagged whales is likely well less than 1 [43], the minimum number of whales counted for each group acoustically was similar to, but generally underestimated the group size estimated visually in the field (figures 2 and electronic supplementary material, figure S2). A similar assessment could not be performed for Cuvier's beaked whales tagged in Liguria due to the higher ambient noise level in this area of the Mediterranean Sea.

The average headings of the two whales of each pair during the vocal phase of their synchronized dives were very similar ( $129^\circ$  and  $128^\circ$  for the two Blainville's and  $161^\circ$  and  $126^\circ$  for the two Cuvier's figure 3). However, despite

the similarity of overall dive swimming direction, there was no evidence of the correlation between the average per-minute headings of the tagged whales (Pearson correlation,  $R^2=0.04$  and  $0.08$  and  $p$ -values= $0.47$  and  $0.11$  for Blainville's and Cuvier's, respectively).

Despite the large potential for eavesdropping or interference, we found no evidence that individual acoustic activity was influenced by group size or by the acoustic behaviour of other group members (electronic supplementary material, table S1). Click rates averaged  $2.41 \pm 0.41$  clicks/s for Blainville's and  $1.54 \pm 0.44$  clicks/s for Cuvier's. Individual buzz rates averaged  $1.1 \pm 0.34$  buzzes/min for Blainville's and  $0.52 \pm 0.37$  buzzes/min for Cuvier's. No evidence of differences in the distribution of click and buzz rates of Cuvier's between small and larger groups was found ( $p$ -values for the K-S tests greater than 0.5). Also, the rate of clicks from untagged whales recorded at the tags showed no significant relationship with group size for the analysed Blainville's dives (Pearson correlation test:  $R^2=0.12$ ,  $p$ -value = 0.08).

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

### 4. Discussion

Deep-diving animals that live in groups face an apparent trade-off: if they stay close during dives to maintain social contact, competition and interference in hunting seem inevitable. Conversely, if they separate to hunt efficiently, they

risk losing the group and the benefits of sociality, such as reduced predation risk [23]. Allaying predation risk may be an especially strong evolutionary driver of the behaviour of Cuvier's (and most probably also Blainville's) beaked whales, given their strong responses to orca sounds and naval sonar [44–46]. Here, we tested the hypotheses that echolocating beaked whales foraging with echolocation in highly coordinated groups may incur costs of aggregation due to intra-group competition for prey or interference of their echolocation signals, or may benefit from the proximity of group members through eavesdropping on their echolocation clicks and buzzes. Interference and eavesdropping seem particularly likely given the potential aggregation of their prey: in the mesopelagic realm, small fauna found in scattering layers can form patches some 20 to 150 m wide and beaked whales may target these small organisms in addition to larger predatory fauna also preying on these aggregations [24,25,47].

We found no evidence that individual prey encounter rates (indicated by buzz rates) within dives were affected by group size, suggesting that on average there is little intra-group competition for foraging resources in social groups of beaked whales. Gregarious animals display a number of behaviour strategies to mitigate intra-group competition for food, e.g. sheep in large aggregations form subgroups to exploit different sub-patches of vegetation [48], and individual bees specialize in extracting pollen from different types of flowers around their colony [49]. Social mammals targeting a deep-water niche similar to beaked whales employ different strategies. Long- (*Globicephala melas*) and short-finned (*G. macrorhynchus*) pilot whales [30,50] might reduce intra-group competition for prey by diving asynchronously and emitting calls to maintain acoustic contact between diving and surface group members [6,30]. Although these calls can provide cues to acoustic-guided predators, the strong cohesion of their large social groups enables pilot whales to perform mobbing responses against predators [51]. Our data suggest that the behavioural tactic employed by beaked whales to reduce intra-group competition for prey is that group members diving in tight coordination spread out when foraging at depth. However, they then reunite to ascend together, avoiding the need to vocalize near the surface where they are more vulnerable to predator attacks [23]. This behaviour might have co-evolved with small group sizes so that individuals can swim close enough to each other to coordinate their movements during dives, but sufficiently apart to find unexploited prey patches.

As expected for efficient independent foraging, we revealed that group members swim in directions which are uncorrelated on a short timescale while diving together. Nonetheless, they maintain a similar average heading over the full dive presumably to facilitate reunion during the ascent [23]. While relative heading could only be measured directly in the two instances when animals were tagged in the same group, the usually continuous changing angles-of-arrival of clicks from group members recorded by all stereo tags supports this interpretation of independent movement [29]. Moreover, visual observations of groups of beaked whales regularly surfacing together after long dives affirms that overall swimming direction of group members is tightly coordinated during dives. Such coordination must be mediated by the near-continuous reception of the echolocation clicks of other group members, implying that foraging

clicks have a secondary communicative function, acting as acoustic beacons of the relative position of animals while foraging.

The near-continuous inter-audibility of vocal group members is a consequence of beaked whales diving together and coordinating the vocal phase of their dives [23]. However, the regular detection of one or more close group member throughout the foraging periods of the tagged whales raises the possibility that their echolocation signals might negatively interfere or alternatively that whales might beneficially eavesdrop on the echo returns of clicks from conspecifics. We found no evidence of jamming compensating behaviours: click rates of tagged whales were not affected by group size either for Blainvillés or Cuvier's. This was also supported by the two pairs of whales tagged in the same social group. The individual click rates of these whales averaged over intervals of 1 min showed no correlation between pair members. Moreover, whales tagged singly in groups did not extend their silent periods (pauses in clicking) nor adjust the source level of their clicks when more conspecifics were audible as would be expected to enhance eavesdropping or combat jamming. Thus, we posit that acoustic interference does not constrain biosonar-mediated foraging in these species, and echolocation production is not detectably influenced by information-sharing, even if we cannot dismiss that whales might use the information provided by the acoustic activity of other group members. Instead, individual click rates in beaked whales have been observed to correlate with the movement patterns of the whales and may be influenced by prey distribution [25,32].

The absence of compensatory behaviours in beaked whales contrasts with the 'anti-jamming' response proposed for bats where silent periods of individuals are increased when conspecifics are very close [12]. However, these taxa are subject to highly divergent ecological and physiological constraints. Echolocating animals that pause click production lose information on prey location and thus risk reducing their foraging efficiency [52]. While bats can hunt continuously for an entire night, the rate and duration of breath-hold foraging dives of beaked whales are physiologically limited. This results in a stereotyped behaviour that affords them only 20–30 min of foraging time every hour or 1.5 h on average [22,53]. It seems reasonable to hypothesize that these whales cannot afford to use silence as a strategy against jamming.

The lack of influence of group size on click production rate for beaked whales contrasts with observations of the acoustic behaviour of two species of delphinids: orcas and bottlenose dolphins [19,20]. These studies estimated individual click production rate by dividing the number of clicks from the group, detected by nearby drifting hydrophones, by a visual estimate of group size. Click rates in both species were observed to decrease on a per capita basis with increasing group size suggesting that individuals were reducing their click production rates and eavesdropping on echo information returning from clicks produced by group members [19,20]. The contrasting results for the beaked whales studied here might be explained by differences in behaviour and trophic niche. Fish-eating orcas and bottlenose dolphins forage most often in shallow waters [54,55] and sometimes coordinate their hunting [56], while Blainville's and Cuvier's beaked whales dive to mean depths of 800 m [22] and hunt individually. The cacophony of clicks and their surface echoes from echolocating conspecifics in large groups of

delphinids might clutter the acoustic scene of these shallow foragers, potentially making it beneficial to reduce individual clicking rates in preference for a scrounging or eavesdropping tactic. By contrast, a high resilience to jamming in echolocating dolphins [10] has recently been revealed via low duty cycling of clicking and high directionality in sound transmission and hearing. Alternatively, contrasting observations from delphinids and beaked whales may result from methodological differences in these studies. Animal-borne acoustic tags used here on beaked whales offer a higher confidence when measuring individual click emission rates than do the drifting hydrophones used in the delphinid studies. This is because highly directional clicks may not be detected if they are not orientated towards drifting hydrophones, even when animals are at relatively short distances [57], whereas they are more likely to be recorded on a tag carried by an animal. A further bias may be introduced if animals spread further apart when in larger groups, given that the detectability of animals at larger distances from the hydrophone would be reduced on average. Such an occurrence was found in Blainvillés at El Hierro, with a reduction in per capita click rate observed with group size. Given that tag data show that the clicking rates are independent of group size, this means that progressively more clicks from untagged whales are missed at a point receiver as group size increases. This is consistent with an acoustic estimation of a group size of whales generally underestimating the visual count of whales as observed here and is likely associated with beaked whales separating and moving independently at depth to hunt [23]. By contrast, the correlation between the detection rate of clicks from Blainville's and group size has been observed using an extensive array of deep moored hydrophones. In such a situation clicks have a high probability of being detected in any direction [58] and the probability of missing clicks is low. Such variability in observations when using differing methods highlights the importance of considering study design when interpreting results and also is particularly relevant when using passive acoustic monitoring (PAM) for density estimation of echolocating whales [59]. This highlights that an improved understanding of group behaviour and detectability is crucial for appropriate application of acoustic methods for estimating population abundance, particularly when used for the effective management of these iconic megafauna.

## 5. Conclusion

Blainville's and Cuvier's beaked whales foraging in groups do not modify individual rates of echolocation and prey capture attempts in relation to group size. This indicates that sensory interference or competition from group members is unlikely to occur while hunting. Individuals are also unlikely to benefit from local enhancement directly by sharing information of echo arrivals from conspecific clicks. Tagged whales however, were in acoustic contact with other group

members via eavesdropping almost all of their vocal (foraging) time. This presumably aids coordination of the timing and mean direction of their synchronized dives while they separate to hunt independently. Blainville's and Cuvier's beaked whales do not behave as cooperative hunting predators, but more like social foraging herbivores and frugivores such as ungulates and primates that coordinate group movements but forage independently [60,61]. These collective behavioural tactics reduce intra-group competition allowing individuals to maintain foraging efficiency while gaining the social and predation risk abatement benefits of group living [23]. Small group sizes in these species of beaked whales might thus be related to the foraging footprint of the group, as whales keep tightly coordinated during dives but still need to perform prey capture attempts per dive while hunting independently. This in turn suggests dependence upon a reliable foraging niche and sets an upper limit to the number of whales that can efficiently forage simultaneously.

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

**Data accessibility.** Datasets basing the analyses of this paper are available in the electronic supplementary material, tables S3–S5 of the electronic supplementary material and per-minute datasets can be accessed from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.gqnk98sm0> [62].

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