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ARTICLE

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Adult male Cuvier's beaked whales (*Ziphius cavirostris*) engage in prolonged bouts of synchronous diving

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Abstract

Studies of the social behavior of Cuvier's beaked whales (*Ziphius cavirostris*) are challenging because of their deep-water habitat usually far from shore and the limited time they spend at the surface. The sociality of these deepest diving mammals is of interest, however, especially for our understanding of how social systems evolve in extreme habitats. High levels of scarring suggest that males compete agonistically for access to females and so we predicted that associations among adult males would be unstable due to competitive exclusion. We tested this prediction by evaluating the diving behavior of animals within social groups off Cape Hatteras, North Carolina, considering diving synchrony a proxy for group membership. Using data from satellite-linked depth-recording tags, we found that adult male–male pairs showed extended periods of synchrony in diving behavior, while all pairs that included an adult male with an individual of another age and/or sex dove synchronously for less than a day. We assessed three hypotheses to explain these surprising results: sexual segregation; extended bouts of male–male competition; and the presence of male alliances. Finally, we considered testable predictions to distinguish among these explanations.

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KEYWORDS
Argos, biologging, Cuvier's beaked whale, diving synchrony, Ziphiidae, *Ziphius cavirostris*

1 | INTRODUCTION

The beaked whales (family Ziphiidae) are the second most speciose family of cetaceans, but little is known about their social structure or mating systems. Their pelagic lifestyle and short surfacing periods present challenges for gathering high resolution longitudinal behavioral data on individuals and their companions. Beaked whales include the deepest diving mammals (Schorr et al., 2014; Shearer et al., 2019; Tyack et al., 2006) and their foraging dives often exceed an hour in duration and are followed by very short periods at the surface, so it is difficult to apply traditional behavioral sampling methods to these animals (Quick et al., 2020).

Despite these difficulties, ongoing photo-identification studies (Baird, 2019) as well as advances in tagging and tracking technology (Baird, 2019; Schorr et al., 2009) have expanded the range of questions that can be posed in these systems. Due to their extreme diving ecology, the beaked whales may indeed be a particularly fruitful group for the study of ecological dynamics of mammalian social structure evolution. Additionally, this speciose family which diverged relatively early among the odontocetes (Geisler et al., 2011) provides both a large sample size within a single clade, as well as phylogenetic distance to clades of other cetaceans for comparison. For example, the Delphinidae can provide useful comparisons as this clade includes taxa with well-studied sociality and both relatively deep-diving species (e.g., pilot whales, *Globicephala* spp.; Aguilar de Soto et al., 2008; Risso's dolphins, *Grampus griseus*; Arranz et al., 2018) and shallow-diving species (e.g., bottlenose dolphins, *Tursiops* spp.; Connor & Krützen, 2015; Frère et al., 2010).

Beaked whale social behavior also has practical importance in terms of the conservation and effective management of these species. Some beaked whales, particularly Cuvier's beaked whales (*Ziphius cavirostris*), are especially susceptible to disturbance from anthropogenic noise, most notably tactical military mid-frequency active sonar systems (DeRuiter et al., 2013; Falcone et al., 2017; Simonis et al., 2020; Southall et al., 2016; Tyack et al., 2011). Several species of beaked whales have mass stranded following exposure to naval training exercises (D'Amico et al., 2009). Social factors might play a role in the response of these species to such stimuli, and the susceptibility to disturbance of individuals within a social group may influence the behavior of others, but to date these connections have not been well studied (Brakes et al., 2019).

The Cuvier's beaked whale is one of the most widely distributed beaked whale, although individual populations often occur in restricted ranges (Baird 2019; Forney et al., 2017; McSweeney et al., 2007; Stanistreet et al., 2017). This species is also the most common of all beaked whale species to mass strand following exposure to tactical sonars (D'Amico et al., 2009). In the present study we investigated social aspects of the diving behavior of Cuvier's beaked whales off Cape Hatteras, North Carolina, where they occur year-round in high densities offshore of the continental shelf break (McLellan et al., 2018; Stanistreet et al., 2017). Previous research on Cuvier's beaked whales in this area using photo-identification and telemetry suggests a high degree of individual residency (Baird et al., 2018; Foley et al., 2018, 2021).

Like most species of beaked whales, Cuvier's beaked whales exhibit sexually dimorphic dentition, with a single pair of tusks erupting only in adult males. These tusks are believed to be used during competitive bouts with other males, and perhaps in sexual displays or other signaling (MacLeod, 1998). Adult males are often extensively scarred, presumably because of high levels of male–male competition (Heyning, 1984; McCann, 1974; Rosso et al., 2011). Mixed age-sex class groups with multiple adult males are not uncommon though (Falcone et al., 2009) and the males are often observed on the outskirts in these groups separated from one another (Baird, 2016). These observations contrast somewhat with studies of Blainville's beaked whales (*Mesoplodon densirostris*), which have similar sexual dimorphism and heavy adult male scarring and appear to exhibit female defense polygyny with one-male units (Baird, 2019; Claridge, 2013; McSweeney et al., 2007; Schorr et al., 2009).

Based on presumed high levels of competition among males, we predicted that multiadult male groups of Cuvier's beaked whales would be relatively unstable, with one male competitively excluding potential challengers. To test this prediction, we examined data from pairs of Cuvier's beaked whales instrumented with satellite-linked depth-recording tags in the same and different groups and used synchrony of diving behavior as a proxy for continued group membership (e.g., Sakai et al., 2011).

2 | METHODS

2.1 | Satellite tag deployment and data validation

We deployed satellite-linked depth-recording SPLASH10-292 tags with the extended-depth-range option (Wildlife Computers, Redmond, WA) on Cuvier's beaked whales off Cape Hatteras, North Carolina, from May to September 2017 (Figure S1). During tagging, we defined a group as all animals in close spatial and temporal proximity at the surface, typically observed surfacing within 100 m of one another.

In addition to producing positions estimated from the Argos satellite system, the satellite-linked tags recorded and transmitted summaries of diving behavior, including beginning and end time, duration, and maximum depth of each dive. The beginning and end of each dive was determined by a conductivity sensor on the tag, which defined submersion events. We programmed the tags to archive only submergences (identified by the conductivity sensor) of greater than 50 m in depth and 33 min in duration (Quick et al., 2019). Periods during which dives did not pass this threshold were recorded as inter-long-dive intervals. We selected these thresholds to focus our data collection on long dives, presumed to be primarily for foraging and which typically last more than 33 min to depths of more than 800 m off Cape Hatteras (Shearer et al., 2019). We validated data using on-board diagnostics of the pressure transducer, a speed filter, and visual inspection of patterns of corrupt and missing data (see supplementary information for details).

In this paper we focus on baseline behavior of animals, though we deployed these tags as part of a large behavioral response study to evaluate the effects of experimental exposure to naval mid-frequency active sonar (3–5 kHz; MFAS). In the present analysis, we truncated tag records to include only data before the first known experimental exposure to MFAS signals. To monitor for incidental exposure to MFAS, the local acoustic environment was recorded continuously throughout the deployment period of all tags using bottom-mounted broad-band acoustic recorders (Hildebrand et al., 2018). A single event of 31 min from distant naval operations (more than 100 km away) was detected during the deployment period of three tags. Given the short duration, considerable distance, and relatively low amplitude of this signal we did not truncate the data further and we assumed the data records analyzed here represent baseline behavior not influenced by responses to MFAS (see supplementary information for details).

2.2 | Photographic identification and sex determination

We attempted to photograph all animals in each group for individual identification and sex determination (Foley et al., 2018). In this population only adult males can be consistently and unambiguously sexed from photographs. Adult females were assigned if sighted with a dependent calf, but are otherwise difficult to differentiate from immature animals of either sex. We classified all individuals with erupted teeth and/or with heavy linear scarring on their heads and bodies as adult males (Baird, 2016; Coomber et al., 2016; Falcone et al., 2009; McSweeney et al., 2007). For this analysis we conservatively assigned all other animals to an age-sex class of "other." This latter class is very unlikely to include any adult males and we do not believe it included any dependent calves, based on their size and behavior. We use the term age-sex class loosely throughout to refer to these two broad demographic categories.

2.3 | Synchrony and null model

We compared each pair of dive records by calculating the time differences and depth differences (see supplementary information for depth analysis) between the nearest events of the same type (both animals starting or both animals ending a dive) to create distributions of time differences for each pair with overlapping data (Figures S10 and S11). In addition, we used a threshold of 60 s for two events (the beginning or end of a long dive) to be considered synchronous, due to the on-board accuracy of the tag. We used this threshold to create timelines of synchrony for pairs tagged in the same group as well as other groups and identify any periods of extended synchrony. Cuvier's beaked whale ventilation (surface) periods are typically short relative to their long dives, but they are often >60 s in duration. For example, in a previous analysis conducted on this population, we estimated the median ventilation duration to be 2.2 min, with slightly longer durations before deep dives (median = 4.0 min) (Shearer et al., 2019). Therefore, a 60 s threshold for synchrony should ensure that most events scored as synchronous would in fact represent times when both animals were at the surface (see supplementary information for details).

We constructed a null model of diving behavior to determine the probability at which synchrony might occur at random using the R programming language (R Core Team, 2019). We generated simulated behavior records for each pair of animals by re-sampling dives and inter-long-dive intervals (Figure S5). We generated a set of random diving behavior for each pair 999 times and calculated the proportion of synchronous beginnings and ends of dives. Finally, we calculated one sided *p*-values (including the real observed value for a total $n = 1,000$) and assessed significance with an alpha of 0.05.

2.4 | Pairwise horizontal distance

Argos positions for this study site and species are too imprecise to determine group membership, as errors routinely range from several to tens or hundreds of kilometers (see supplementary information for details). We did, however, test whether our best estimates of pairwise distances were smaller for synchronously diving animals than asynchronous pairs. We used a continuous-time state-space model implemented in the R package *foieGras* to estimate locations, which incorporates the error-ellipses calculated in the Kalman filtered Argos positions (Jonsen & Patterson, 2020). We used the location quality classes to exclude class Z, which represents invalid positions. Model estimated locations were calculated at 6 hr intervals and distances between each pair were calculated from the WGS84 longitude and latitude using the haversine formula. We tested for significant differences in median pairwise distances among synchronously and nonsynchronously diving pairs using an asymptotic Wilcoxon-Mann–Whitney test implemented in the R package *coin* (Hothorn et al., 2008). In all analyses, we only considered pairs for which transmitted data overlapped for more than a day ($n = 21$ pairs).

2.5 | Data accessibility and reproducibility

All analyses were conducted using R version 3.6.2 (R Core Team, 2019). Data and scripts to reproduce these analyses and figures are available at https://github.com/williamcioffi/zc_sync (dx.doi.org/10.5281/zenodo.4542749).

3 | RESULTS

3.1 | Satellite tag deployment and data validation

During nine sightings of groups of Cuvier's beaked whales we deployed tags on nine adult males and five animals of another age and/or sex (Table 1). On four occasions we tagged 2–3 individuals in the same group (A, D, F, I; Table 1).

TABLE 1 Deployment information for each satellite-linked depth-recording tag. Tag records were truncated if the tags malfunctioned (see supplementary information for details) and immediately prior to any experimental treatments. AM = adult male, Other = other age and/or sex (likely not adult male).

Tag ID	Sex	Group	Group size	Deploy date	Truncation date	Days of dive data	Reason for truncation
54	AM	A	6–7	May 10, 2017	May 28, 2017	17.6	last status message
55	AM	A	6–7	May 10, 2017	May 17, 2017	6.3	unknown onboard failure
56	AM	A	6–7	May 10, 2017	June 27, 2017	47.5	last status message[a]
57	Other	B	2	May 16, 2017	June 14, 2017	28.7	pressure transducer failure[a]
58	Other	C	1	May 16, 2017	June 23, 2017	37.8	last status message[a]
60	AM	D	3	August 17, 2017	August 22, 2017	4.9	experimental treatment
61	Other	D	3	August 17, 2017	August 22, 2017	4.9	experimental treatment
62	Other	E	3	August 17, 2017	August 22, 2017	4.9	experimental treatment
63	AM	F	4	August 20, 2017	August 22, 2017	2.0	experimental treatment
64	Other	F	4	August 20, 2017	August 22, 2017	2.0	experimental treatment
66	AM	H	3–4	September 4, 2017	September 12, 2017	7.9	experimental treatment
67	AM	I	6–8	September 4, 2017	September 12, 2017	7.8	experimental treatment[b]
68	AM	I	6–8	September 4, 2017	September 12, 2017	7.8	experimental treatment

[a] A low amplitude incidental MFAS sonar event was recorded on June 6, 2017 while these tags were recording data (see supplementary information for details).

[b] Tag 67 experienced pressure transducer drift shortly after deployment and so was excluded from the depth analysis (see supplementary information for details) but was retained in other analyses.

A single tag was truncated to less than a day of data due to an experimental treatment and therefore was excluded from the present analysis. After filtering and truncation, the median length of behavior data collection was 7.8 days (*n* = 13, range = 2–47.5). Three of the thirteen tags had a single period of missing data each ranging from 7.7 to 12.6 hr.

3.2 | Synchrony

All the adult male Cuvier's beaked whale pairs tagged within the same group showed high levels of synchrony for days to weeks, while the pairs consisting of one adult male and one animal of another age and/or sex showed very low levels of synchrony (Figures 1, S6, S10, S11).

Three adult males tagged together in group A (tags 54, 55, and 56) were all highly synchronous for 6.3 days until tag 55 suffered an unknown onboard failure and its data were truncated. The two remaining tags from this group continued to show synchronous dives for 17.6 days at which point tag 54 ceased transmitting (Figure 1). In this group 76%–89% of events were within 60 s of each other. Photographs obtained in subsequent sightings three weeks after deployment demonstrated that 55 had separated from 54 and 56 (see supplementary information for details), but the exact time of separation was unknown due to the tag failure. The two adult males tagged together in group I (tags 67 and 68), dove synchronously for 4.7 days before becoming asynchronous (Figure 1). In group I, 46% of events were within 60 s of each overall, and 86% during the first 4.7 days of deployment.

In addition, we observed continuous stretches during which every dive event for a particular pair was within 60 s of each other. For groups A and I, maximum duration of uninterrupted synchronous events was 36.9 and 34.2 hr, respectively (Figure 1).

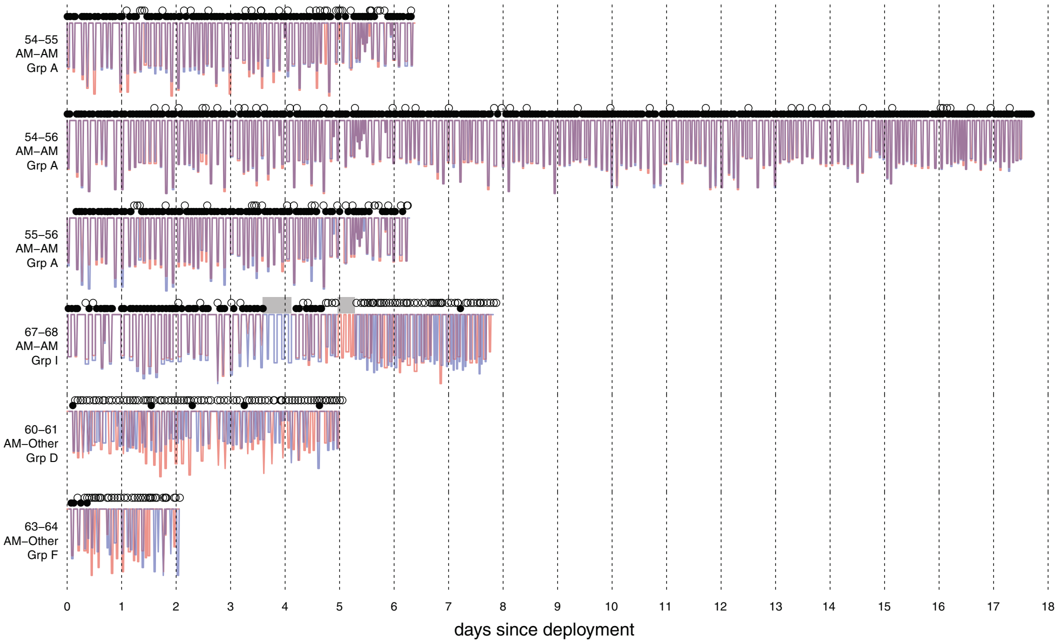

FIGURE 1 Pseudo-dive profiles based on behavior data summaries for pairs tagged in the same group (A, I, D, F) measured from deployment. Profiles are indicated by a blue line for one animal and a red line for the other, purple appears where profiles closely overlap. Filled circles indicate events which are synchronous to within 60 s; open circles indicate asynchronous events. Gray blocks indicate periods of missing data. Only dives over 33 min in duration were recorded. Inter-dive intervals are indicated at zero depth, though they include all dives under 33 min in addition to any time spent at the surface. Only a general shape of each dive is indicated (for details on shape calculation, see Wildlife Computers, Inc., 2017, p. 10). Numbers in *y*-axis labels indicate tag ID pairs, AM = adult male, other = other age and/or sex. For a enlarged view of the first four days see Figure S6. For pairs tagged in different groups see Figures S7–S9.

Pairs of whales tagged in group D and F were both comprised of an adult male and a whale of another age and/or sex. These pairs were observed to be in the same group at the time of tagging but did not remain synchronous for more than a few dives ($\ll$1 day) after tag deployment. Overall, only 5% and 10% of beginning and ends of dives were within 60 s, respectively (Figure 1). Among pairs that were not tagged in the same group, but for which we had more than one day of temporally overlapping data, only 1%–6% of events occurred within 60 s of each other (Figures S7–S9).

3.3 | Null model

We used a null model to test if pairs of tagged whales were significantly more synchronous than expected by chance over the course of the study (Figure 2). The median proportion of events <60 s apart ranged from 0.0% to 2.1% in the random simulations (n pairs = 21, simulations = 999 each). All pairs of adult males tagged in the same group were significantly more synchronous than random (in all cases, p = .001). Both pairs consisting of a single adult male with an animal of another age and/or sex tagged in the same group were also significantly more synchronous than expected by chance (tags 60 and 61, p = .022; tags 63 and 64, p = .003), though as noted above the absolute size of the effect was small and most of these synchronous effects occurred in the first dives of the records. Interestingly, one pair tagged in different groups was also significantly more synchronous than expected by chance (tags 60 and 62, p = .003). Again, this effect was small; only 6% of events were within 60 s of each other and were concentrated

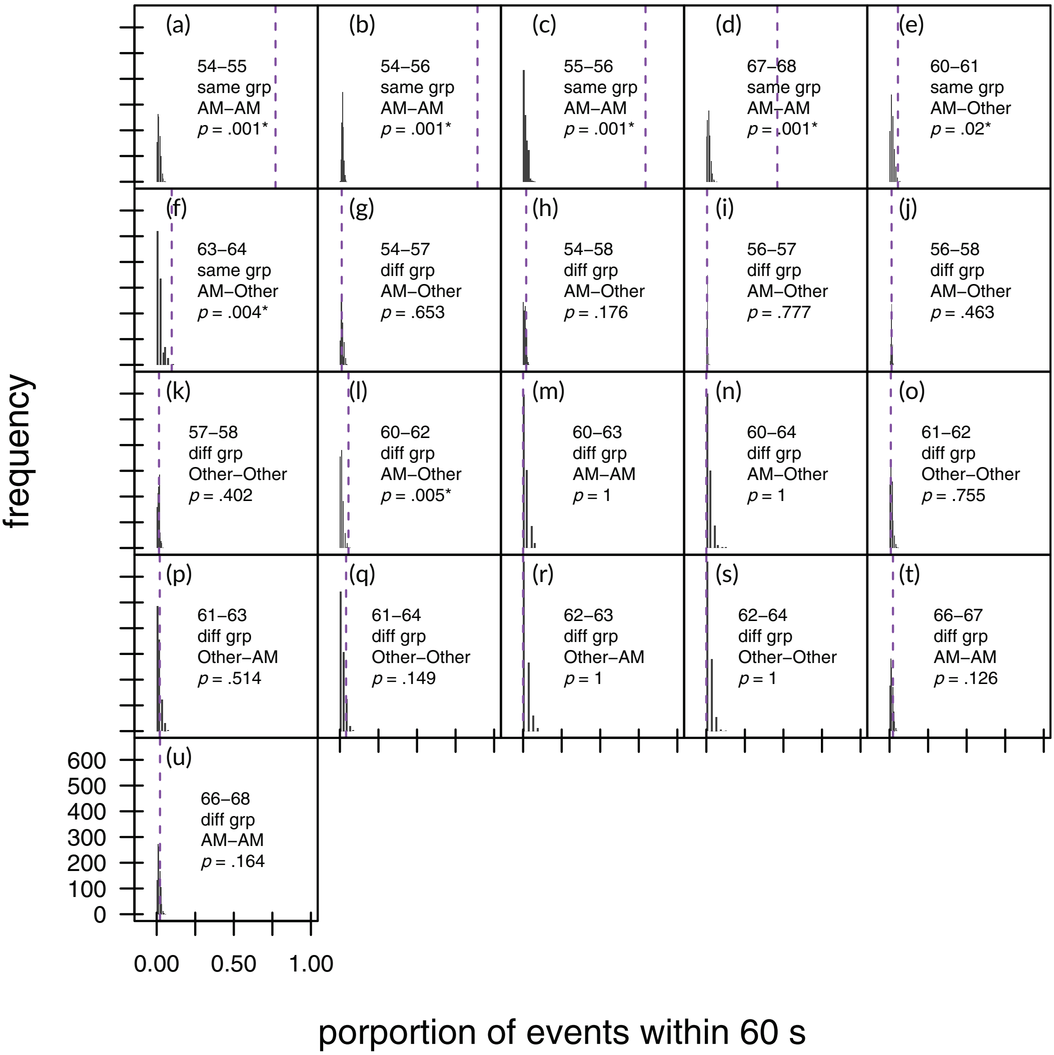

FIGURE 2 Null model results for all pairs of tags for which the deployments overlapped in time for more than one day. Gray histograms show null distributions of the simulated proportion of dive and surface period events within 60 s of each other (999 simulations per pairs). Observed proportion for each pair shown with a broken purple line. All plots are drawn at the same scale. Number codes indicate specific pairs, Same grp = animals were initially tagged initially in the same group (a–f), diff grp = animals were initially tagged in separate groups (g–u), AM = adult male, Other = other age and/or sex, but not adult male, * = significant (alpha = 0.05).

during the first day of the data record. These animals were tagged on the same day in the same general area (~7 km apart), so this could possibly represent a brief period of synchronous behavior after we ceased to observe these animals directly from the tagging vessel.

3.4 | Pairwise horizontal distance

The estimated positions of individuals in synchronous pairs tagged in the same group were closer together than other pairs (Wilcoxon-Mann–Whitney test, z = 2.76, p = .006). These positions did not provide enough

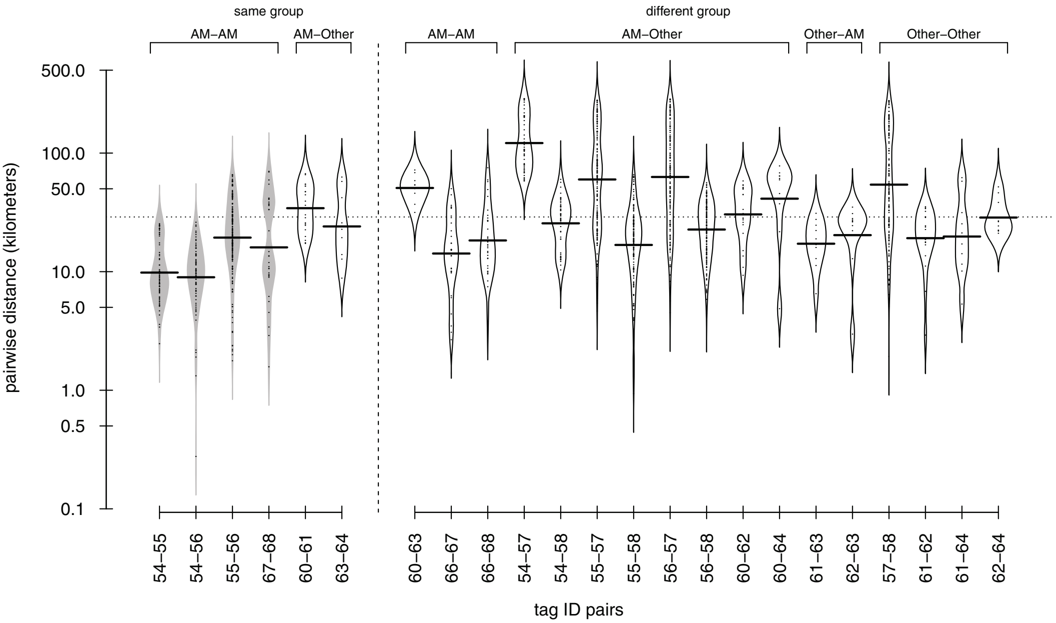

FIGURE 3 Pairwise horizontal distance distributions for all pairs of tags for which the deployments overlapped in time for more than one day. Shading indicates pairs of individuals which were synchronous. Brackets above indicate age-sex class if animals were initially tagged in the same or different groups. The broken horizontal line is the grand mean, horizontal black lines are pair means, and dots indicate individual data points. Figure constructed using R package *beanplot* (Kampstra, 2008). AM = adult male, Other = other age and/or sex, but likely not adult male.

spatial resolution to determine group membership with certainty (Figure 3; see supplementary information for details).

4 | DISCUSSION

All pairs of adult male Cuvier's beaked whales tagged in the same group displayed continuous periods of synchrony in foraging dives that lasted from days to weeks (Figure 1). This finding contrasts with our prediction that groups including multiple adult males would be unstable due to high levels of male–male competition. Cuvier's beaked whales typically engage in multiple, relatively short, shallow dives between long foraging dives, which we recorded simply as bouts, and therefore we were unable to investigate the synchrony of these nonforaging dives. We also did not tag multiple adult females in the same group, so were unable to test for synchrony among adult females or make inferences about the duration of female–female bonds. Our sample size is limited (two groups with multiadult male deployments and two groups with adult male-other deployments out of nine groups), but the consistency and magnitude of the effect were large (Figure 2). Therefore, we interpret this result as an indication that adult males may spend longer durations with other adult males, more closely synchronizing their behavior, than they do with animals of another age and/or sex.

4.1 | Synchrony as a proxy for group membership

We found that synchronously-diving animals tended to be in closer spatial proximity than asynchronous pairs (Figure 3), but the substantial error in Argos-derived positions prevents us from diagnosing group membership based on position alone. Individuals in some species do appear to coordinate movements even when separated by kilometers (e.g., sperm whales, *Physeter macrocephalus*, Christal & Whitehead, 1997; Whitehead, 2016; false killer whales, *Pseudorca crassidens*, Baird, 2016; Baird et al., 2008, 2010). Indeed, we often observe concentrations of Cuvier's beaked whales in the same general area scattered amongst discrete clusters (groups) all within several kilometers of one another. Simple spatial autocorrelation could be driving the similar pairwise distances we found for synchronous pairs if animals tagged in the same area are likely to persist on a nearby resource for some time or are otherwise coordinated at distance. Higher resolution positional measurements will be required to test this further. Nevertheless, due to the very high levels of synchrony (many events over days occurring within 60 s of each other), we conclude that our synchrony observations represent animals that are in close spatial proximity at the surface. While the 60 s threshold is somewhat conservative, the distributions of time differences between events (Figures S10–S11) show that more lenient thresholds would not change our interpretation. Indeed, the synchrony we observe appears to be largely binary—either animals are highly synchronous, or they are not synchronous at all. This is also evidenced by stretches of uninterrupted synchrony which can be seen in Figure 1. These data are consistent with the supposition that high levels of synchrony correspond to group membership. This conclusion is further supported by recent observations we have made over multiple resightings of synchronous animals instrumented with telemetry tags and confirmed to be in the same surface groups visually (unpublished data). Finally, evidence from another population of this species has shown similar group synchrony including during shallow dives observed in animals instrumented with higher resolution telemetry tags (Aguilar de Soto et al., 2020; Alcázar-Treviño et al., 2021).

4.2 | General explanations for group synchrony

Synchrony may be beneficial in cooperative foraging (e.g., Benoit-Bird & Au, 2009; Parks et al., 2014). There is some evidence, however, that Cuvier's beaked whales that surface in groups may separate while foraging at depth, before rejoining during ascent (Aguilar de Soto et al. 2020; Alcázar-Treviño et al., 2021; see also sperm whales; Watkins et al., 1985; Irvine et al., 2017). Even if animals do not coordinate prey-capture attempts, maintenance of synchrony in diving pattern may be beneficial if individuals use eavesdropping to find areas of high prey availability (e.g., Barclay, 1982; Gannon et al., 2005; Götz et al., 2006).

Many species of beaked whales spend very little time at or near the surface and are silent during shallow dives, behavior that has been interpreted as an anti-predator strategy (Aguilar de Soto et al., 2012; Baird, 2019; Baird et al., 2008; Harris et al., 2018; Schorr et al., 2014; Shearer et al., 2019; Tyack et al., 2006). Grouping behavior can impart protection from predators in a variety of ways, including with dilution effects, encounter effects, increased vigilance, or predator inspection, and mobbing or other defensive behavior (reviewed in Connor, 2000). One key function here is how relative detection probability changes with increasing group size. A mathematical model presented in Aguilar de Soto et al. (2018) suggests that detection probability may be decoupled from group size in beaked whales with synchronized dive times and periods of vocalization.

4.3 | Male–male synchrony

The drivers of synchronous group formation above do not, on their own, offer strong explanations for the degree of synchrony we observed amongst adult male Cuvier's beaked whales off Cape Hatteras. Below we consider several hypotheses that are rooted in socio-sexual behavioral theory and, therefore, could explain these observations. Three other possible explanations are segregation among age-sex classes, extended male–male competitive bouts, and the existence of male–male alliances. We do not take a strong position on which of these explanations is most likely and recognize that they may not be mutually exclusive, but we do provide some background and offer specific predictions that could be tested in the field.

4.3.1 | Sex segregation

Perhaps the most basic explanation for our observations of synchrony amongst adult males is that sexual dimorphism drives differences in behavior, including, for example, foraging or antipredator behaviors and this leads to sexual segregation. In Hawai'i, although there have only been 13 pairs of Cuvier's beaked whales sighted where the age-sex class was known, none were pairs of adult males, and no larger groups exclusively composed of adult males have been documented (Baird, 2019). Intraspecific competition and aggression could also directly produce sexual segregation if it is beneficial for females and juveniles to avoid adult males (e.g., in dolphins; Galezo et al. 2018). This explanation assumes that group formation and synchrony are often beneficial, for one or more of the reasons posited above, so that sexual segregation could lead to the pattern we observe here. If this segregation is present, we would predict that there would be differences in male and female activity budgets or habitat usage, and that sightings of groups composed exclusively of adult males would not be uncommon.

4.3.2 | Extended competitive bouts

The linear scarring observed on adult male Cuvier's beaked whales indicates that they interact antagonistically with other adult males (Heyning, 1984; compare Gowans & Rendell 1999). When animals interact in such a manner, they must be in close spatial proximity and, to some degree, coordinate their movements. In some ungulates (e.g., red deer, *Cervus elaphus*, Clutton-Brock & Albon, 1979) males walk side by side in synchrony, known as parallel walks, which has been proposed as a type of contest. Some of these contests are decided by parallel walks alone, with the loser veering off, but others escalate to fighting, especially if the competitors are evenly matched (but see Jennings et al., 2003).

Nevertheless, if such interactions are costly, we expect the contests to be settled quickly in beaked whales. Competition costs might be prohibitively high if contests continue during long foraging dives unless animals take time out during dives and resume later. Even so, additional opportunity costs might arise from especially long contests, because neither the defender nor the challenger would be able to completely restrict access to mates during this period.

If extended competitive bouts are the primary driver of male synchrony, we predict that a significant investment of time will be required for males to switch to new groups after such contests perhaps due to the logistics of aligning in three dimensions and time while diving long and deep. In this case, then the potential costs of staying in a competitive group may be outweighed by the costs of searching for a new group and potentially failing to find one quickly. In addition, males exhibiting this type of synchronous behavior should acquire new scars during synchronous bouts. Finally, we should be able to identify contest winners and losers (the latter being ejected from the group) and, if there are consistent winners, such individuals should have higher long-term reproductive success.

4.3.3 | Male alliances

It is possible that males exhibit alliances or coalitionary behavior in this population, at least over the short term. Male alliances are a prominent feature of the social structure of two species of bottlenose dolphin (*Tursiops* spp.) (Connor & Krützen, 2015; Ermak et al., 2017; Smolker et al., 1992), which engage in synchrony (Connor et al., 2006; McCue et al., 2020), and which also tend to display high levels of male–male aggression, resulting in scars (Scott et al., 2005; Tolley et al., 1995). In general, alliances are useful for acquiring or defending resources from competing individuals or groups. Access to receptive females is usually the most important resource for adult males, as it is the most direct route to increased fitness (Wrangham, 1980). In Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), male alliances engage in herding behavior of reproductive females, which has been proposed as a tactic for coercing mating and for mate guarding (Connor et al., 1996).

Encounter rate may be a key factor in the formation of bottlenose dolphin male alliances, as females are likely to be usurped by competing males if density is high and the operational sex ratio is skewed (Connor & Whitehead, 2005). Ermak et al. (2017) demonstrated a link between density and male alliance complexity in some populations of bottlenose dolphins. Cuvier's beaked whales near Cape Hatteras occur in one of the highest densities (17 animals per 1,000 km^2; McLellan et al. 2018) reported for any ziphiid population, surpassed only by populations of Baird's beaked whales off Japan (40–68 animals per 1,000 km^2; Barlow et al., 2006). These densities are notably high for beaked whales but substantially lower than for some populations of alliance-forming bottlenose dolphins (Ermak et al., 2017).

High levels of precopulatory competition among males have been assumed for many beaked whale species because of their sexually dimorphic dentition and patterns of acquired scars. For these reasons, which are further supported by observations of one-male social units, female defense polygyny has been proposed as the likely mating system in Blainville's beaked whale (Baird, 2019; Claridge, 2013; McSweeney et al., 2007; Schorr et al., 2009). Male northern bottlenose whales do not have prominent tusks and do not appear to accumulate scars at a high rate, although they can be aggressive towards one another (Gowans & Rendell, 1999). Photo-identification data of northern bottlenose whales suggest that males may maintain relationships over multiple years, while females associate more loosely (Gowans et al., 2001). In contrast, Cuvier's beaked whales do have prominent tusks and males likely compete for access to mates, but they also have relatively larger testes than other Ziphiidae (Dines et al., 2015) and a relatively low degree of sexual size dimorphism (Mead, 1984). These observations suggest that females might mate with multiple males and that postcopulatory competition could occur among males, perhaps favoring mate guarding and, therefore, the formation of alliances (Connor et al., 2000). Note, however, that the few existing photo-identification studies of Cuvier's beaked whale generally suggest a fission-fusion social structure without stable groups (Falcone et al., 2009; Foley et al., 2018; McSweeney et al., 2007; but compare Baird, 2019).

If synchronous bouts among males are reflective of male alliances in this population, we would predict repeated interactions among male pairs, members of which are possibly, but not necessarily, close kin. Putative alliance members should not scar each other at a high rate, especially during cooperative behavior and would be likely to share reproductive success in some way.

A related strategy worth noting that could explain the patterns seen here are leader-follower dynamics like those seen in hamadryas baboons (*Papio hamadryas*, Pines et al., 2011). In this serially polygynous society, the "leader" male of a one-male unit (OMU) may sometimes tolerate a "follower" male. Followers are typically younger and/or prereproductive, but may gain social access to the females in the OMU and thereby be more successful in the future in taking over the OMU or establishing their own OMU. Though there is not strong evidence for these type of long term OMUs in Cuvier's beaked whales, this type of relationship might still be a beneficial strategy for young males over shorter term associations with groups of females. We could support this notion by identifying if there are often age imbalances among synchronous males, assessed perhaps by scaring rates, morphometrics, or molecular age markers.

4.4 | Key questions and future directions

We were unable to test predictions about patterns of synchrony among females and juveniles due to the difficulty in identifying these age-sex classes in the field. Additional photo-identification studies utilizing genetic sex determination from biopsy samples, together with focused tagging efforts on females and juveniles would address these questions. Additionally, our study focused on long dives, but future work should investigate levels of synchrony during shorter dives as well.

Many other important behavioral and demographic parameters remain unknown for this and other populations of Cuvier's beaked whales, including group stability, distribution of kin, interbirth intervals, and seasonality of reproductive behavior. Such information is necessary for testing predictions based on our possible explanations of adult male synchrony and, more broadly, to examine their social structure. Behavioral response studies to disturbance, such as the study that produced the data analyzed here, will benefit from an understanding of the social context of disturbance in individual species and whether this context might mitigate or exacerbate certain types of stimuli. These data will take time to acquire because they require repeated observations of the same individuals over many years. In parallel, some inference can be made for these parameters based on genetic and other molecular evidence, if sufficient biopsy samples are acquired and well-distributed across the population.

Our use of satellite-linked depth-recording tags helped us to overcome some of the challenges of observing a long-diving, pelagic cetacean species for meaningful lengths of time. Further, by deploying multiple tags in the same group we were able to investigate social interactions for weeks at a time. These methods have long been employed in terrestrial systems, and we suggest that such a hybrid approach, pairing traditional behavioral observations and photo-identification with modern sensor packages, may be particularly advantageous for long-diving, pelagic cetaceans. When these approaches are combined with molecular techniques that allow the determination of sex, reproductive state, kin, and population structure, it will be possible to conduct robust tests of social structure in these species.

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AUTHOR CONTRIBUTIONS

William Cioffi: Conceptualization; data curation; formal analysis; investigation; methodology; software; validation; visualization; writing-original draft; writing-review & editing. **Nicola Quick:** Conceptualization; investigation; methodology; writing-review & editing. **Heather Foley:** Conceptualization; data curation; investigation; writing-review & editing. **Danielle Waples:** Conceptualization; data curation; investigation; writing-review & editing. **Zachary Swaim:** Conceptualization; data curation; investigation; project administration; writing-review & editing. **Jeanne Shearer:** Conceptualization; investigation; writing-review & editing. **Daniel Webster:** Conceptualization; data curation; investigation; methodology; resources; writing-review & editing. **Ari Friedlaender:** Conceptualization; writing-review & editing. **Brandon Southall:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; writing-review & editing. **Robin Baird:** Conceptualization; funding acquisition; methodology; project administration; resources; writing-review & editing. **Doug Nowacek:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; writing-review & editing. **Andrew Read:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; writing-review & editing.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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