

Assessing the dynamics of common dolphin (*Delphinus delphis*) mother-calf pairs along the south coast of Portugal using unmanned aerial vehicles

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Funding information

AIMM - Associação para a Investigação do Meio Marinho; Fundação para a Ciência e a Tecnologia, Grant/Award Numbers: Programa Investigador FCT 2013, SFRH/BD/134156/2017, UID/MAR/04292/2019

Abstract

Maternal grouping dynamics involve trade-offs between: (1) infant protection from predation (predation hypothesis), (2) infant protection from male harassment (infant safety hypothesis), and (3) reducing scramble competition for prey resources (foraging-type scramble competition hypothesis). Using unmanned aerial vehicles, we assessed grouping dynamics in common dolphin (*Delphinus delphis*) groups containing mother-calf pairs to address these hypotheses. We analyzed social aspects and structural group elements using generalized additive mixed models and modeled group formation using multinomial generalized estimating equations. Calf proportion was higher in very compact groups and in groups of 10–20 individuals but decreased in larger groups. The frequency of socio-sexual behaviors increased in larger groups and decreased in groups with higher calf proportion. Calf distance to its nearest neighbor decreased with increasing group size and cohesion. With a higher proportion of calves, scatter (versus parallel) formation was less frequent. A calf's nearest neighbor was most

often (55.4%) a nonmother. Calves showed a preference for being in the front center of the group. These results offer strong support for the predation and infant safety hypotheses and partial support for the foraging-type scramble competition hypothesis. This work provides insight into the adaptive function of maternal strategies in a small delphinid.

KEYWORDS

cetacean, delphinids, foraging, infant safety, mother-calf pairs, nursery groups, predation, scramble competition, social strategies, unmanned aerial vehicles

1 | INTRODUCTION

In social animals, grouping dynamics reflect different social, ecological, and environmental pressures (Bond et al., 2019; Castro et al., 2020; Clutton-Brock, 1974). For groups with females and their infants, social strategies are crucial to protect vulnerable young (Pusey & Packer, 1994), provide them with social learning and bond-formation opportunities (Gibson & Mann, 2008), and accommodate the needs of the mother, such as foraging (Whitehead, 1996). Three of the most important trade-offs for mothers are between the protection of their infant from predation (predation hypothesis), shielding infants from male harassment (infant safety hypothesis; Otali & Gilchrist, 2006), and the reduction of scramble competition with respect to prey resources foraging-type scramble competition (Agrell et al., 1998; Gowans et al., 2007; Hamel & Côté, 2007; Pearson, 2011). Mammals with flexible grouping dynamics, such as cetaceans, may display different strategies to balance these factors (Gowans et al., 2007; Mann et al., 2000; Weir et al., 2010). The predation, infant safety, and foraging-type scramble competition hypotheses are not mutually exclusive and can help explain these observed variations in grouping patterns due to socio-ecological variables (Fanucci-Kiss, 2015; Gibson & Mann, 2008).

1.1 | Predation Hypothesis (H1): The function of maternal grouping strategies is to protect the young from predation

Due to the small size and limited motor skills of infants, mothers and their offspring incur high predation risk (Mann et al., 2000). This influences maternal and grouping strategies (Lewis & Pusey, 1997). In cetaceans, different predation counterstrategies include large group sizes (Heithaus, 2001), central positioning within the group (Leatherwood, 1977 in Shane et al., 1986), and increased cohesiveness (Sucunza et al., 2015). One maternal strategy offering predator protection to mothers and calves is the formation of nursery groups (Gowans et al., 2007). These groups are primarily composed of mother-calf pairs and have been documented in dusky dolphins (*Lagenorhynchus obscurus*; Würsig & Würsig, 1980), common bottlenose dolphins (*Tursiops truncatus*; Wells et al., 1987), Indo-Pacific humpback dolphins (*Sousa chinensis*; Karczmarski, 1999), and common dolphins (*Delphinus delphis*; Stockin, 2008). Nursery groups ensure calf safety since they are generally larger and more cohesive than adult groups (Liu et al., 2021; Lunardi & Ferreira, 2014). In addition, they may attract less attention from predators than, for example, mating groups because they behave more inconspicuously (Srinivasan & Markowitz, 2010) and tend to prefer habitats with decreased predation risk such as shallow waters (Weir et al., 2008).

1.2 | Infant Safety Hypothesis (H2): The function of maternal grouping strategies is to protect the young from harassment by male conspecifics

Maternal strategies are also influenced by the need to shield the young from agonistic interactions with male conspecifics (Agrell et al., 1998), known as the infant safety hypothesis (Otalí & Gilchrist, 2006). Two types of male-perpetrated harassment compromise the safety of females with dependent offspring: sexual coercion (Sundaresan et al., 2007) and infanticide (Hrdy, 1979; Palombit, 2015). Sexual coercion has been observed in marine tucuxi dolphins (*Sotalia guianensis*; Nery & Simão, 2009) and dusky dolphins (Markowitz et al., 2010; Weir et al., 2010). Infanticide has been reported in bottlenose dolphins (Patterson et al., 1998), humpback dolphins (Zheng et al., 2016), orcas (*Orcinus orca*; Towers et al., 2018) and Amazon river dolphins (*Inia geoffrensis*; da Silva et al., 2021). To reduce the exposure to male harassment, females with dependent calves aggregate in nursery groups (Fury et al., 2013; Gibson & Mann, 2008; Weir et al., 2010). Spatial separation from sexually mature males also protects mothers and calves from aggression (Martin & da Silva, 2004), which is why nursery groups may seek refuge in habitats seldomly sought out by males, such as shallow waters (Fury et al., 2013; Weir et al., 2008).

1.3 | Foraging-Type Scramble Competition Hypothesis (H3): The function of maternal grouping strategies is to reduce scramble competition for prey resources for the mother

Due to the increased energy expenditure and demands of motherhood, females with dependent offspring are especially susceptible to the effects of scramble competition with respect to prey resources (foraging-type scramble competition) (Pearson, 2011). Since dolphins are highly gregarious animals living in environments with temporally and spatially unpredictable prey (Gowans et al., 2007) they are subject to intraspecific foraging-type scramble competition (Díaz López & Shirai, 2008; Vermeulen et al., 2015). To minimize this feeding competition, cetacean societies adapt different strategies such as sex- and/or age-dependent resource partitioning (Basso et al., 2021; Riccialdelli et al., 2013; Young & Cockcroft, 1994). This dietary specialization is particularly important for dolphin mothers due to lactation-induced energetic increases (Rechsteiner et al., 2013; Reddy et al., 1991). During cooperative feeding, larger males pose considerable competition to females accompanied by a calf (Ball et al., 2017). Thus, dolphin mothers can meet their increased energetic demands and avoid competition by targeting different prey and/or selecting different foraging grounds, for instance by splitting off into nursery groups (Bernard & Hohn, 1989; Cañadas & Hammond, 2008; Young & Cockcroft, 1994). Another factor contributing to a heightened vulnerability to scramble competition for mothers is their elevated locomotion cost resulting from “infant carrying” (Noren, 2008) and, to reduce this, dolphin mothers benefit from being less gregarious (Pearson, 2011).

1.4 | Study aims

Common dolphins are highly gregarious animals that live in large groups with complex social strategies (Ball et al., 2017; Castro et al., 2022; Gowans et al., 2007; Neumann, 2001a). The formation of nursery groups (Mason, 2016; Neumann, 2001b; Stockin, 2008) and sophisticated maternal strategies (Schaffar-Delaney, 2004) have been documented in this species. However, little is known about the adaptive functions of the spatial relationships of common dolphin mother-calf pairs. This is partially due to the limitations of boat-based observations, such as the difficulty of assessing group configuration and interindividual distances from a low-vantage, horizontal point of view (Weir et al., 2018). The use of unmanned aerial vehicles (UAVs) can circumvent these restrictions by providing an aerial perspective of these spatial components, granting novel insights into this topic (Weir et al., 2018). UAVs are an emerging tool that facilitate certain aspects of cetacean research due to their affordability, flexibility, and low impact (Castro et al., 2021; Orbach et al., 2020).

The aim of this study was to investigate maternal strategies of common dolphins in the south of Portugal from the perspective of the calves by using a UAV as a platform of observation. Common dolphins in this region are potentially subject to all three pressures explained in the above hypotheses. This is evidenced by the formation of large nursery groups (Castro et al., 2022), and their preference for unpredictably available food resources (e.g., sardines, *Sardina pilchardus*; Silva, 1999). Further, multiple shark species which can predate on dolphins occur in the study area (Coelho et al., 2005, Correia, 2009) and occasional shark bites are recorded (Castro et al., 2022). Thus, we developed the following questions to test if/how the predation, infant safety, and foraging-type scramble competition hypotheses explain common dolphin mother-calf behavior. We specifically sought to determine: (1) How does the proportion of calves in a group vary according to group size, group cohesion, and month (addressing H1, H2, H3)? (2) How is the occurrence of socio-sexual events affected by the proportion of calves and group size (addressing H2)? (3) How does the distance of the calf to the mother (addressing H1, H2) and to the nearest neighbor (addressing H1, H3) vary with group size and structure (formation, calf position and nearest neighbor type) and socio-sexual events? (4) How is group formation related to group cohesion and proportion of calves in the group (addressing H1, H3)? We also report descriptive information on common dolphin behaviors and social organization (i.e., suckling behavior, nearest neighbor type and calf position within the group).

2 | METHODS

2.1 | Study site and surveys

Our work was conducted in the Algarve, Portugal, between Cape St. Vicente (37°1.35'N, 8°59.81'W) and Olhão (37°1.56'N, 7°50.54'W). Visual surveys to find common dolphin groups were conducted during the spring, summer, and autumn months of 2016, 2017, and 2019 using a 7 m RHIB with 4-stroke 135 hp outboard engine. Tracks of the surveys and GPS positions of common dolphins were recorded with a Garmin echoMAP 42dv (Figure 1). Surveys were conducted in coastal waters not more than 25 nautical miles (nmi) from shore and were carried out at an average speed of 12 knots, sea state conditions of Beaufort 0–3, swells not higher than 1.5 m, good visibility (>5 km) and no precipitation.

Only groups with calves (animals $\leq \frac{1}{2}$ the length of an adult, traveling alongside an adult; Castro et al., 2020) present were sampled. Nursery groups were considered as groups with one calf per three or fewer noncalves

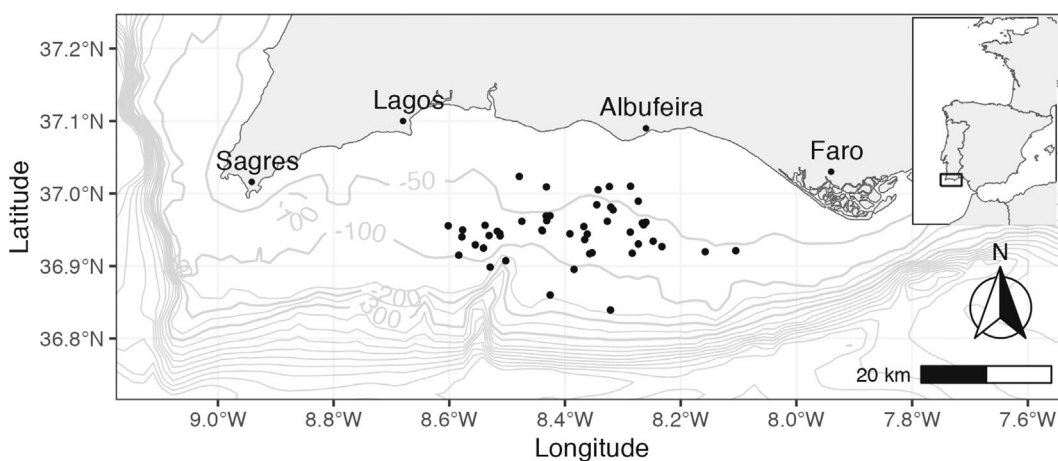


FIGURE 1 Map of the study area in southern Portugal with bathymetric lines in meters. Black dots represent common dolphin (*Delphinus delphis*) sightings sampled with the unmanned aerial vehicle (UAV; $n = 49$).

(Weir et al., 2008). Once the group was found, focal follows (Weir et al., 2018) were conducted using a multirotor (quadcopter) VTOL UAV (DJI Phantom 2 and 4; 35 cm diameter, 1 kg and 1.38 kg, respectively, with plastic propellers; <http://www.dji.com>); with an attached GoPro HERO4 camera. A radio antenna system installed on the UAV allowed live-streaming the video during flight guaranteeing that the UAV was centered over the focal animals. Flight time was limited by battery capacity to 25 min, although the actual flight time was shorter. When necessary, the drone was retrieved and relaunched again during the same focal follow. The UAV was launched and retrieved manually from the bow of the vessel, oriented downwind and with the engine in neutral. Once the UAV was launched and during sampling, the research vessel maintained a distance of 30–100 m from the group and the UAV maintained a minimum altitude of 20 m. Distance and altitude were a compromise between being able to visually follow the group and minimizing the potential impacts of the vessel and the UAV on the animals' behavior (more details in Castro et al., 2021). An attempt to fly the UAV as centered as possible above the focal group was made to provide a standardized measure of distance between consecutive data points.

All sampling was conducted with no other boats present within a 1 nmi radius, sea state of ≤ 3 on the Beaufort scale, < 0.5 m swell, visibility ≥ 5 km, and skyline clear of clouds. To prevent group resampling, the research vessel traveled ≥ 1 nmi and/or transited ≥ 1 hr in the opposite direction of the previously sampled group.

Data were not collected live during the UAV flight. Instead, all video analyses were done post-hoc after excluding samples in which the group was not sufficiently visible (e.g., due to UAV height or sun glare). The videos were analyzed using VLC media player (version 3.0.16; <https://www.videolan.org/vlc/>) and the software Meazure (version 2.0.1; <https://meazure.en.softonic.com/>). Moreover, all video analyses were done by the same observer (J.C.) to avoid bias. Focal follow data were collected in sampling intervals of 30 s. Every 30 s the video was paused to record the following data: (1) group size (an individual was considered as part of the group according to a combination of the 10-m chain rule (Smolker et al., 1992), coordinated activity (Mann, 1999) and presence in the frame), (2) number of calves, (3) group formation (Table 1), and (4) cohesion (Table 1). Further, for each mother-calf (MC) pair, the following data were recorded for every sampling interval: (1) position within the group (Table 1), (2) minimum distance between mother and calf, and (3) minimum distance between the calf and the nearest neighbor that was not the mother. Nearest neighbors were categorized as either a MC pair or a nonmother (i.e., an individual not accompanied by a calf). At each sampling interval, distances between individuals were measured on the computer screen using the average size of an adult common dolphin (2.0 m; Evans, 1994) as reference. This reference value of 2 m for an adult common dolphin was selected due to its appropriateness for the actual size of adults from this population (206.1 cm; A. Marçalo, personal communication, July 28, 2023; data extracted from Marçalo et al., 2018). To allow more precise observations of the data extracted from the video, the playback was slowed down by as much as $10\times$ the original speed.

Additionally, during each sampling interval the following social and behavioral events adapted from Neumann and Orams (2005) and Schneider (1999) were recorded: (1) number of nursing/suckling events where the infant rolls under the mother with rostrum in position of the mammary slits (Weir et al., 2018); (2) leaps where the dolphin jumps, clearing its body partially or totally out of the water; (3) belly-up contact with or without actual intromission; and (4) socio-sexual events: any type of physical contact, individuals chasing one another, including bites and rubbing. Suckling rate was calculated by pooling together the total number of nursing events divided by the total number of minutes of videos analyzed.

As it was not possible to reliably identify and track individuals throughout the video, each frame was analyzed independently from the previous. To obtain the best frame for assessing the variables recorded at each sampling interval, a 10 s buffer was used consisting of the 5 s before and after the respective 30 s time stamp. The focal follow ended when the group was lost for four intervals (2 min) in a row, if the calves left the frame for four intervals in a row, if visibility was impaired due to glare or height of the UAV or if the UAV battery reached 30% remaining capacity.

TABLE 1 Detailed description of group formation, cohesion, and position of mother-calf pairs.

Group formation	
Lone (L)	Single individual
Parallel (P)	Individuals within the group are side by side and perpendicular to the direction of movement
Linear Vertical (LV)	Individuals are in a line or rows aligned with the direction of movement
Pack (PK)	Individuals in a round and tight formation
Scatter (S)	Individuals are randomly distributed and show different headings while remaining in the same unit
Echelon (E)	Individuals are lined up abreast at evenly spaced intervals; wider at the rear and progressively narrower at the head
Group cohesion	
Very Compact (VC)	Most individuals separated by <1 body width
Compact (C)	Most individuals separated by 1 to 5 body widths
Dispersed (D)	Most individuals separated by 5 to 10 body widths
Very Dispersed (VD)	Most individuals separated by >10 body widths
Lone (L)	Single individual
Mother-calf pair position within group	
Front Center (FC)	Position within the front half of the group and in the middle (center of the group surrounded by other individuals)
Front Edge (FE)	Position within the front half of the group and on the peripheral limits of the group
Back Center (BC)	Position within the back half of the group and in the middle
Back Edge (BE)	Position within the back half of the group and on the peripheral limits of the group

This study was conducted under the authorization of the Portuguese Nature Conservation Institute (Instituto da Conservação da Natureza e das Florestas – ICNF; permits AOC/17/2016 and AOC/30/2018). All animal protocols adhered to ICNF standards.

2.2 | Modeling

We used generalized additive mixed models (GAMMs; Wood, 2004, 2011) to assess the effect of (1) group size, cohesion, and month of observation on the proportion of calves; (2) group size and proportion of calves on the number of socio-sexual events observed; (3) group size, cohesion, formation, calf position, nearest neighbor (NN) type, distance to NN, and socio-sexual events on the distance to mother; and (4) group size, cohesion, and NN type on the distance of calf to the NN (Table 2). GAMMs were used to accommodate the nested structure of the data (i.e., correlated observations within the same focal follow) and nonlinear relationships between the response variable and predictors (Zuur et al., 2009). The models were fitted using the *gamm()* function provided by the “mgcv” package (version 1.8–31; Wood, 2012) for R (R Core Team, 2018). Continuous predictors were specified as smooth terms in the models via the *s()* function; the dimension of the basis was set to 5 to avoid the model overfitting and the smoothing basis function was defined as thin plate regression splines. The family distribution and the link function used in each model are specified in Table S1. All models were fitted accounting for individual differences between groups (group ID defined as a random effect). The degree of concurvity (Ramsay et al., 2003), a nonparametric analogue of multicollinearity, was measured using the built-in function provided by the “mgcv” package. Different models were fitted using subsets of the predictors (Table S1) by employing a backward selection process based on the significance of the model terms (i.e., removing the least significant predictor one after the other). The optimal model was selected according to the Akaike information criterion (AIC).

TABLE 2 List of candidate predictors selected based on their potential relevance to estimating the: proportion of calves, socio-sexual events, distance calf to mother, distance calf to nearest neighbor (NN), and formation. The hypotheses addressed in each model are identified as H1 – Predation Hypothesis; H2 – Infant Safety Hypothesis; H3 – Foraging-Type Scramble Competition Hypothesis. MC – mother-calf.

Response variable	Candidate predictors									
	Hypothesis addressed	Group size	Group Cohesion	Month	Proportion of calves	MC position within group	NN type	Distance to NN	Group Formation	Socio-sexual events
Proportion of calves	H1; H2; H3	x	x	x						
Socio-sexual events	H2	x			x					
Distance calf to mother	H1; H2	x	x			x		x	x	x
Distance calf to NN	H1; H3	x	x				x			
Group formation	H1; H3		x		x					

To model group formation, we adopted a nominal multinomial generalized estimating equation (GEE) framework suitable for multilevel responses (Table 2). The nominal multinomial GEE model was fitted considering a baseline category logit model for the marginal probabilities and used a “time-exchangeable” structure of the local odds ratio as recommended for nominal responses (Touloumis, 2015; Touloumis et al., 2013). The least represented category of the group formation was excluded from this analysis to avoid convergence issues in the model (i.e., the formations E corresponding to 4.83% of the observations). A forward model selection process was implemented where the performance of additional candidate predictors was examined using the Wald test applied to the nested models and by checking for multicollinearity issues using the variance inflation factor (VIF). The multinomial-GEEs fitting and the comparison between nested models were implemented using the built-in functions provided by the *multgee* package (Touloumis, 2015), while the multicollinearity issues were assessed using the *performance* package (Lüdtke et al., 2021), both developed for R. The regression coefficients for the multinomial GEEs were expressed as odds ratio (OR): $OR < 1$ indicates that one event reduces the odds of the other event, $OR = 1$ shows that the odds under comparison are equal; while $OR > 1$ suggests that the presence of one event is associated with higher odds of the other (Szumilas, 2010). Model coefficients were displayed using the “*ggplot2*” package (Wickham & Chang, 2014), while the regression tables were formatted with the package “*sjPlot*” (Lüdtke, 2018).

An overview of the response variables, candidate predictors and the hypotheses they address is listed in Table 2.

3 | RESULTS

3.1 | Data description

Data were recorded during 753 30-s sampling intervals in 39 focal follows of common dolphin groups conducted in 2016 (June to October), 2017 (June to September) and 2019 (June to August). An overview of how many videos were collected per year and month, the total used video length, and number of sampling intervals is provided in Table S2. On average, dolphin group size was 21.6 ± 14.95 individuals (range = 1–69, $n = 752$). Just under half (43.6%, $n = 328$) of the groups were classified as nursery groups.

Social events were observed during 541 sampling intervals, occurring at a mean rate of 6.1 ± 4.54 events (range = 1–29) per sampling interval, with 441 observations of socio-sexual events (4.0 ± 2.75 , range = 1–18 per sampling interval). The suckling rate was 0.33 suckling attempts/min. The most observed group formation was parallel (P, 39.54%), followed by linear vertical (LV, 24.93%), pack (PK, 25.20%), scatter (S, 5.50%) and echelon (E, 4.83%). The most observed group cohesion was very dispersed (VD, 53.12%), followed by dispersed (D, 26.03%), compact (C, 16.07%), very compact (VC, 4.65%) and only one observation corresponded to a lone individual (L, 0.13%). The average proportion of calves in the group was 0.2 ± 0.12 ($n = 753$, range = 0–0.5). A total of 2,412 observations of calf positions were recorded, with the majority classified as front center (FC, 35.20%), followed by front edge (FE, 24.96%), back edge (BE, 21.23%), back center (BC, 18.57%), and lone calf (0.04%). The average distance of a calf to the mother was 0.3 ± 0.77 m (range = 0–12.02 m, $n = 2,379$) while average distance of a calf to its nearest neighbor was 3.0 ± 2.77 m (range = 0–29.84 m, $n = 2,412$). Based on 2412 observations of a calf’s NN type, 55.35% were classified as a nonmother.

3.2 | Results of GAMM-based analyses

3.2.1 | Proportion of calves

For the proportion of calves, the selected model included group size as a smoothing function and cohesion and month as categorical variables. This model presented an adjusted R^2 of 0.082 (Table S1), indicating poor

explanatory power. Nevertheless, the GAMM showed a significant effect of group size on the proportion of calves ($F = 3.471$, $p = .006$, $n = 752$). On average, the proportion of calves increased in groups between approximately 10 and 20 individuals and decreased in groups composed of around 20–40 individuals (Figure 2). Comparing between months, only August showed differences statistically significant from the baseline with calves occurring proportionally less than in June ($p = .030$). Regarding group cohesion, the proportion of calves was significantly higher in very compact groups ($p < .001$) compared to the other classes.

3.2.2 | Socio-sexual events

According to the AIC-value, the selected model for the socio-sexual events included group size and the proportion of calves as smoothing functions (Figure 3). All smooths were significant at a $p < .001$ and the model presented an adjusted R^2 of 0.236 with no concurvity issues detected between smooths (concurvity < 0.8).

The frequency of socio-sexual events increased as group size increased (Figure 3). Conversely, socio-sexual events were more frequent in groups with no or lower proportions of calves.

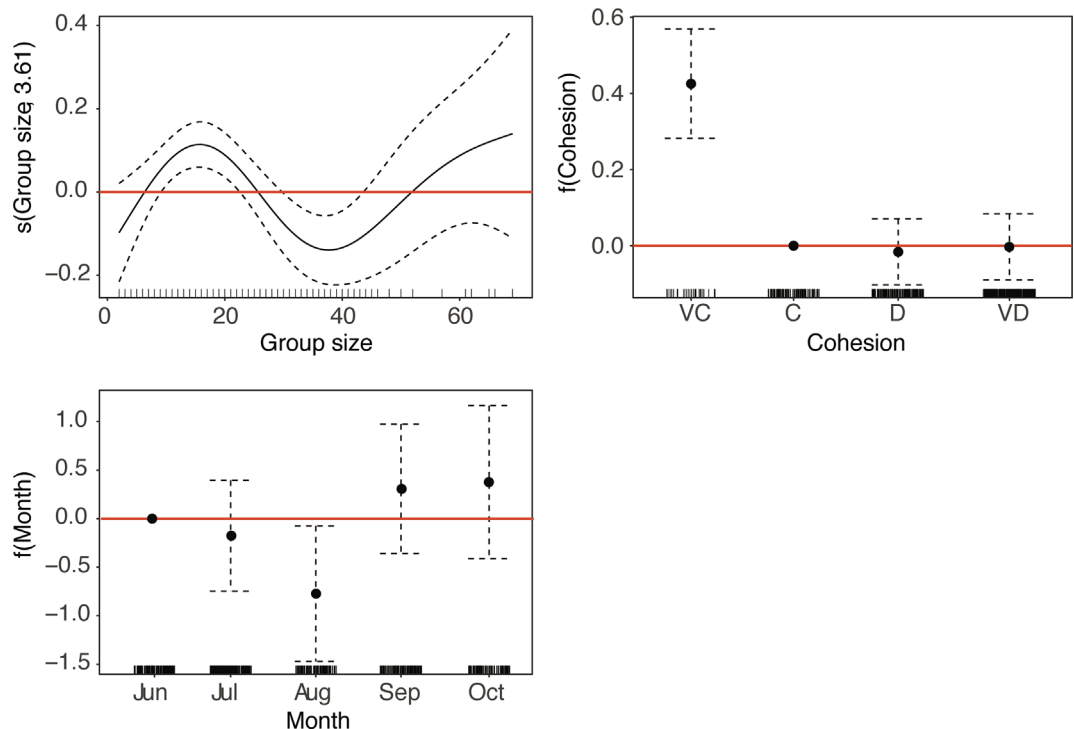


FIGURE 2 Results of the GAMMs for the average proportion of calves as a function of the group size (top left), cohesion (top right; VC – very compact; C – compact; D – dispersed; VD – very dispersed), and month (bottom left). Solid lines represent the estimated smoothing curves from each model and the dashed lines mark the limits of the 95% confidence interval for the mean shape of the effect. Rug plots along the x-axis indicate the distribution of data points. On the y-axis, 0 indicates no effect of the predictor on the estimated response (red line), values > 0 mean a positive correlation, while values < 0 indicate a negative correlation. The y-axis is labeled as $s(\text{predictor name, estimated degrees of freedom})$.

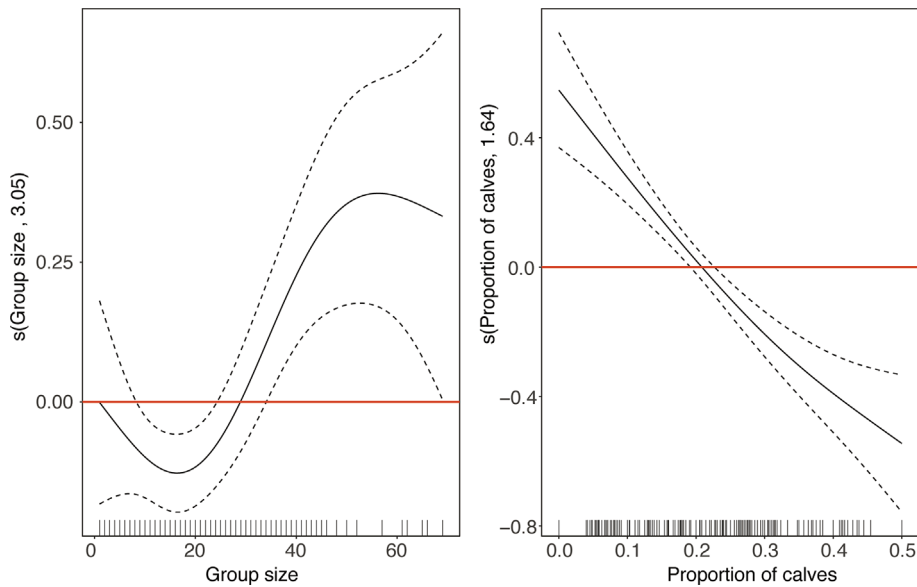


FIGURE 3 Results of the GAMM for the average frequency of socio-sexual events as a function of the group size (left), the proportion of calves in the group (right). Solid lines represent the estimated smoothing curves, and the dashed lines mark the limits of the 95% confidence interval for the mean shape of the effect. Rug plots along the x-axis indicate the distribution of data points. On the y-axis, 0 indicates no effect of the predictor on the estimated response (red line), values >0 mean a positive correlation, while values <0 indicate a negative correlation. The y-axis is labeled as $s(\text{predictor name, estimated degrees of freedom})$.

3.2.3 | Distance of calf to mother

All models developed to describe the distance of a calf to its mother showed issues in the diagnostic plots (i.e., in the quantiles-quantiles plot and patterns in the residuals). The poor fit of the models to the data could also suggest that the predictors considered have low influence on the response variable (Table S1).

3.2.4 | Distance of calf to nearest neighbor

The model selected according to the AIC-value to estimate the distance of calves to the NN included group size and cohesion as predictors (Table S1). The distance to the NN tended to decrease as the group size became larger ($F = 21.1$, $p < .001$, $n = 2,362$) and was greater as the dispersion among the members in the group increased ($p < .001$; Figure 4).

3.3 | Results of the multinomial GEE analysis

3.3.1 | Formation

The best multinomial-GEE candidate model revealed that group cohesion and the proportion of calves were significant in explaining group formation (Table S3). This model presented low collinearity between variables. When groups were in a pack formation compared to being parallel, very compact groups were more likely to be observed than

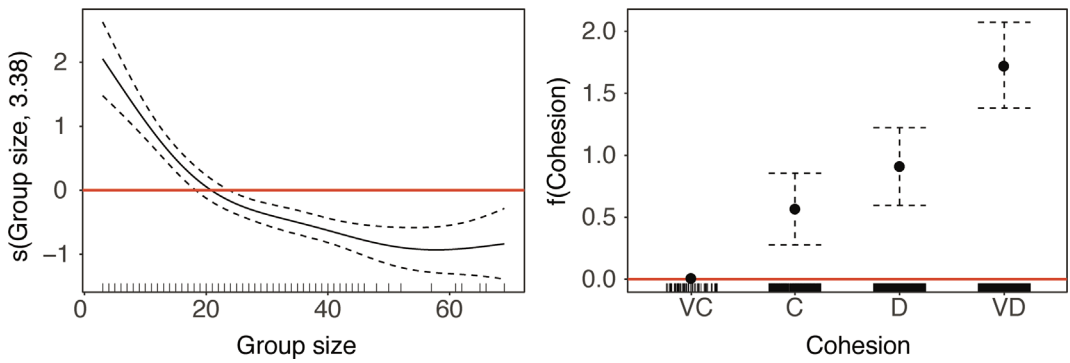


FIGURE 4 Results of the GAMM showing the relationship between the calves' distance to the nearest neighbor (NN) with group size (left) and group cohesion (right; VC – very compact; C – compact; D – dispersed; VD – very dispersed). Solid lines represent the estimated smoothing curves from each model and the dashed lines mark the limits of the 95% confidence interval for the mean shape of the effect. Rug plots along the x-axis indicate the distribution of data points. On the y-axis, 0 indicates no effect of the predictor on the estimated response (red line), values >0 mean a positive correlation, while values <0 indicate a negative correlation. The y-axis is labeled as $s(\text{predictor name, estimated degrees of freedom})$.

compact, dispersed, and very dispersed groups ($p = .031$, $< .001$, and $< .001$, respectively; Figure 5). For the proportion of calves, the largest differences were observed when groups were seen in scatter formation versus parallel (OR = 0, $p < .001$). As the proportion of calves increased in the group, scatter formation was less likely to be observed compared to a parallel formation.

3.4 | Summary

Table 3 summarizes the results of this study, listing the predictions for each hypothesis and highlights which predictions were supported.

4 | DISCUSSION

Mother-calf pairs of common dolphins in the south of Portugal have an important role in shaping the grouping dynamics of this species. Our results provide the strongest support for the predation hypothesis, while also providing strong support for the infant safety hypothesis. Partial support was found for the foraging-type scramble competition hypothesis. The higher proportion of calves in very compact groups, the decreased calf distance to NN in larger groups, the tendency for groups to be organized in a parallel formation and the comparatively higher group cohesiveness in pack formation support the predation hypothesis. The decreased proportion of calves in larger groups (between approximately 20 and 40 individuals) and the decreased frequency of socio-sexual events as the proportion of calves increased support the infant safety hypothesis. Finally, the decrease of calf proportion in group sizes of around 20–40 animals supports the foraging-type scramble competition hypothesis. This is summarized in Table 3.

One limitation of this study was that absolute distances between calves and conspecifics could not be measured through photogrammetry since the UAV footage was recorded at an angle (i.e., not at 90°) to reduce sun glare, and due to inaccuracies with the UAV altimeter. The use of an average value for the size of adult common dolphins

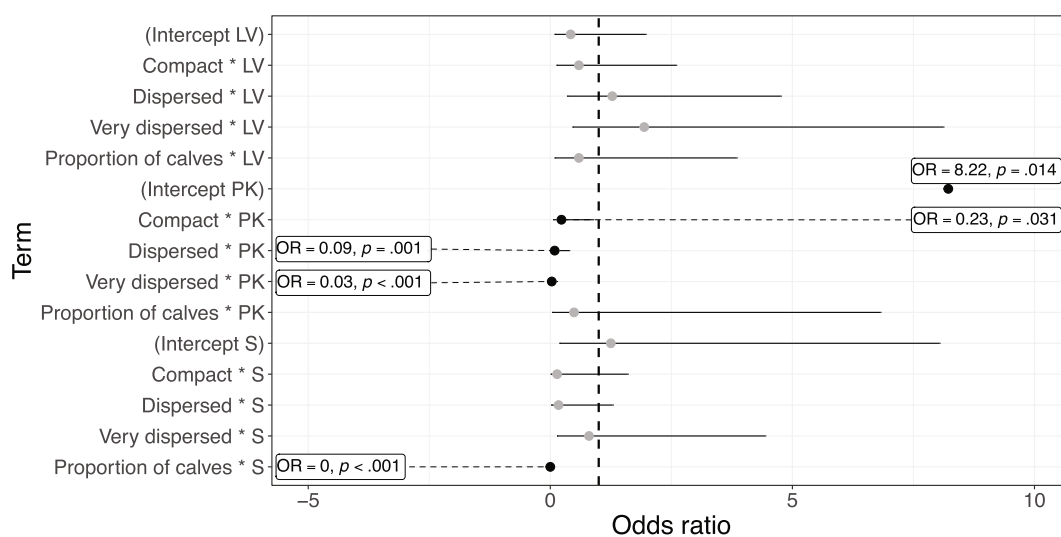


FIGURE 5 Plot with the estimated odds ratio of the marginal model (dots) and respective confidence interval whiskers from the best candidate model for the group formation. Covariates retained are group cohesion (baseline as very compact) and proportion of calves (baseline as lowest proportion). Regression coefficients with significant results from the Wald test are highlighted with black dots. The dark dashed line shows an odds ratio of 1 representing equal likelihood of occurrence. LV - linear vertical; PK - pack; S - scatter; OR - odds ratio.

intended to circumvent this issue. Thus, the results based on distance measurements are as robust as possible within this limitation but need to be viewed with the necessary caution.

4.1 | Proportion of calves

The proportion of calves in common dolphin groups started to decrease when the group size reached approximately 20 animals, providing support for the foraging-type scramble competition and infant safety hypotheses. Although groups with mother-calf pairs tend to be larger than groups without mother-calf pairs (Castro et al., 2022), this is apparently only observed until a certain threshold. This type of reduced gregariousness in mothers may be a response to increased foraging-type scramble competition in larger groups, as documented in bottlenose dolphins (Pearson, 2011) and other social mammals, such as chimpanzees (*Pan troglodytes*; Wrangham, 2000). The higher calf proportion in smaller groups may also function to protect calves from male harassment. As group size increases, there are likely to be more males present, thus increasing the chance of calf-directed aggression (Chapman & Chapman, 2000). In dusky dolphins, nursery groups are smallest and contain fewest infants in the beginning of the calving season, when the calves are youngest (Deutsch, 2008). This period of youngest calf age coincides with the peak of the mating season (Markowitz, 2004). Therefore, the small group sizes of nursery groups during this period may reduce the encounter effect, shielding mothers and calves from male harassment (Weir et al., 2010).

The proportion of calves in common dolphin groups was significantly greater in very compact groups versus all other cohesions, providing support for the predation hypothesis. The most common group cohesion overall was very dispersed while very compact was least common, clearly indicating that mother-calf pairs prefer a very cohesive group structure. This is consistent with results for mother-calf pairs in other delphinids, including dusky (Markowitz, 2004) and Guiana (*Sotalia guianensis*) dolphins (Lunardi & Ferreira, 2014), as well as for groups with offspring in different mammalian taxa, e.g., common elands, *Taurotragus oryx* (Underwood, 1981) and blue

TABLE 3 Hypotheses and predictions regarding the dynamics of common dolphin mother-calf (MC) pairs along the south coast of Portugal. Each heading is labeled with the number of the corresponding section of the results. The predictions supported by this study are indicated by a check mark.

Predation Hypothesis (H1): The function of maternal grouping strategies is to protect the young from predation.
3.2.1 Proportion of calves predictions
(1) The proportion of calves increases as the group size increases. (2) The proportion of calves is higher in very compact groups than in very dispersed groups. (✓)
3.2.3 Distance of calf to mother predictions
(1) The distance of a calf to its mother increases as the group size increases. (2) The distance of a calf to its mother is greater in very compact groups than in very dispersed groups. (3) The distance of a calf to its mother is greater if the pair is located in the center than at the edge of the group. (4) The distance of a calf to its mother is greater if the nearest neighbor (NN) type is a MC pair. (5) The distance of a calf to its mother increases with a decreasing distance to the NN. (6) The distance of a calf to its mother increases in pack formation
3.2.4 Distance of calf to NN predictions
(1) The distance of a calf to its NN decreases with increasing group size. (✓)
3.3.1 Group formation predictions
(1) A parallel group formation is most common in groups with a high proportion of calves. (✓) (2) A pack group formation is most common in more cohesive groups. (✓)
Infant Safety Hypothesis (H2): The function of maternal grouping strategies is to protect the young from harassment by male conspecifics.
3.2.1 Proportion of calves predictions
(1) The proportion of calves decreases with an increasing group size. (✓) (2) The proportion of calves is greater in very dispersed groups than in very compact groups.
3.2.2 Socio-sexual events predictions
(1) The number of socio-sexual events increases as group size increases. (✓) (2) The number of socio-sexual events decreases with an increasing proportion of calves in the group. (✓)
3.2.3 Distance of calf to mother predictions
(1) The distance of a calf to its mother decreases with increasing group size. (2) The distance of a calf to its mother is greater in very dispersed than in very compact groups. (3) The distance of a calf to its mother is smaller when the NN is a nonmother than when it is another MC pair. (4) The distance of a calf to its mother increases with an increasing distance to the NN. (5) The distance of a calf to its mother decreases with an increasing number of socio-sexual events.
3.2.4 Distance of calf to NN predictions
(1) The distance of a calf to its NN increases with increasing group size. (2) The distance of a calf to its NN is smaller when the NN is another MC pair than when the NN is a nonmother.
Foraging-Type Scramble Competition Hypothesis (H3): The function of maternal grouping strategies is to reduce scramble competition for prey resources for the mother.
3.2.1 Proportion of calves predictions
(1) The proportion of calves decreases as group size increases. (✓) (2) The proportion of calves is higher in very dispersed groups than in very compact groups.
3.2.4 Distance of calf to NN predictions
(1) The distance of a calf to its NN increases as group size increases. (2) The distance of a calf to its NN is greater when the NN is a nonmother than when the NN is another MC pair.

wildebeest, *Connochaetes taurinus* (Lewis & Pusey, 1997). This decreased interindividual proximity provides increased predator protection (Iranzo et al., 2018; Sucunza et al., 2015) and care for the calves (Markowitz, 2004).

Additionally, our study revealed that calf proportion was significantly smaller in August versus June. This variation may have been influenced by factors that were not considered in this study. For instance, groups containing calves are relatively more frequent in warmer waters (Stockin, 2008), therefore calf proportion may be influenced by temporal fluctuations in sea surface temperature. Additionally, mother-calf pairs are particularly susceptible to disturbances by tourism-based vessel presence, as evidenced by decreased calf survival in bottlenose dolphins (*Tursiops* sp.; Bejder, 2005; Currey et al., 2009). Thus, the observed lower calf proportion might have been caused by a temporary displacement of mother-calf pairs from the study area due to the heightened presence of dolphin watching vessels in August compared to June.

4.2 | Socio-sexual events

As the proportion of calves increased, the number of socio-sexual events decreased, supporting the infant safety hypothesis. Females with calves associate with other mother-calf pairs to avoid being harassed by males looking for mating opportunities (Weir et al., 2008) and are typically less sociable than males (Pearson, 2011). Hence, a decrease of socio-sexual display with an increase of calf proportion was expected. Group living and female gregariousness can serve as a strategy to reduce infanticide risk (Palombit, 2015) via the dilution effect, increased vigilance and/or increased defense against males (Gibson & Mann, 2008; Palombit, 2015; Weir et al., 2008).

The frequency of socio-sexual events increased with increasing group size. It is possible that the larger the group, the more diverse it is with respect to age-sex class distribution, thus creating more opportunities for social and mating events. For example, in bottlenose dolphins, social events tend to increase in larger groups, providing the opportunity for calves to develop their social skills (Gibson & Mann, 2008).

4.3 | Distance of calf to mother

None of the parameters we tested affected the distance of a calf to its mother. Thus, we propose that the distance between mother and calf was influenced by environmental and/or ecological factors not considered in this study. For instance, turbid waters can offer predator protection (Constantine, 2019; Derville et al., 2016), which could allow common dolphin mother-calf pairs to loosen predation counterstrategies (i.e. increasing the distance between them). Conversely, with impaired visual contact in turbid waters, bottlenose dolphins rely more heavily on tactile stimuli, which implies a decreased interindividual distance in low visibility scenarios (Paulos et al., 2008). The calf's health condition can also influence its distance to the mother, with frequent contact being a sign of poor health and calf separations indicating high vigor (Mann & Watson-Capps, 2005). Calf age is another factor that was not considered in this study but is known to influence distance to the mother (i.e., distance increases as calves age; Mann & Smuts, 1999). Due to quality limitations of the imagery, we were not able to distinguish between calves and newborns (i.e., by assessing the presence of fetal folds). Since all calves considered in this study were $\leq \frac{1}{2}$ the length of an adult, maximum calf size would be 125 cm, based on the maximum recorded size for common dolphins in Portugal (Silva & Sequeira, 2003). Therefore, we assume that all calves of this study were ≤ 1 year old (Murphy & Rogan, 2006).

4.4 | Distance of calf to nearest neighbor

The distance of a calf to its NN decreased with an increasing group cohesiveness and size. Because cohesion is a measure of interindividual proximity, a correlation with distance to the NN was expected. Conversely, a decreased distance to the NN in larger groups is opposite to what would be predicted by the foraging-type scramble

competition hypothesis. Since competition increases as a group grows, increased spacing between individuals would be expected to reduce competition (Di Fiore, 2003). Yet, tighter spacing between individuals in bigger groups has been reported in multiple ungulate species (e.g., Michelena et al., 2008; Morton, 1993). This effect may arise due to social attraction where gregarious animals actively seek the proximity of conspecifics (Febrer et al., 2006). In ungulates an increased NN proximity also serves as protection for calves, where they extend their resting period, resuming to follow their mothers later when other conspecifics are close-by (Green, 1992). Because larger groups are more easily detected by predators (Bertram, 1978), common dolphin mother-calf pairs might reduce NN distance as a precautionary measure, suggesting support for the predation hypothesis.

4.5 | Formation

Spatial formation was significantly affected by group cohesion and proportion of calves. Groups in pack formation were significantly more often very compact (versus other group cohesions) than groups in other formations. Further, with an increasing calf proportion, groups were more organized, with scatter formation occurring significantly less than parallel formation. Overall, common dolphins were most frequently observed in parallel formation. Parallel formation has been described as the most common formation in nursery groups (Srinivasan & Markowitz, 2010), possibly functioning to increase search efficiency for predators and other potential threats, as well as prey (Norris & Dohl, 1980; Würsig, 1986).

Mother-calf pairs were most often positioned in the front center of the group. This is consistent with previous studies reporting that vulnerable members are herded to central locations (McBride & Hebb, 1948; Norris & Dohl, 1980) since individuals on the margins of a group are more vulnerable to predation than interior animals (selfish herd theory; Hamilton, 1971). Taken together, our results regarding group formation and mother-calf pair spatial positioning support the predation hypothesis.

4.6 | Further implications

This study revealed that mother-calf pair dynamics in common dolphins are most strongly influenced by predation. However, the extent of predation pressure exerted on common dolphins in the Algarve remains unclear. It is possible that even if predation risk is low in the Algarve, common dolphins may still exhibit antipredation strategies driven by the ecology of fear (Srinivasan, 2019; Würsig et al., 2008). Additionally, another pressure that may act similarly to predation by evoking similar counterstrategies is the presence of bottlenose dolphins (Koper & Plön, 2016). Both species occur frequently in our study area (Castro, 2010) and the displacement of entire groups, as well as the violent harassment of a neonate common dolphin by bottlenose dolphins have been recorded (unpublished data). These observations in addition to other reports of interspecific aggression off the Iberian Peninsula (Methion & Díaz López, 2021) suggest that not only predation may drive mother-calf dynamics in common dolphins, but also, potentially, the presence of bottlenose dolphins.

4.7 | Conclusions

Our results revealed a high presence of nursery groups in the south of Portugal, corroborating previous studies that this region is of great importance to common dolphins, particularly as a nursery and breeding area (Castro et al., 2020). Nursery groups play an important role in the social dynamics of common dolphins, providing protection to calves from potential threats such as predators, interspecific harassment, and male conspecifics, thus providing the strongest support for the predation and infant safety hypotheses. Future work should consider the influence of

calf age and behavioral state on mother-calf strategies. In the south of Portugal, marine tourism targets common dolphins and these activities have increased in recent years (Castro et al., 2020). In these areas of high anthropogenic pressure, we recommend consideration of this factor when assessing mother-calf dynamics.

The use of an UAV allowed us to examine common dolphin mother-calf behaviors that would be difficult to observe through other methods, providing new insights into their complex social lives. From this new and different perspective, we conducted a fine-scale analysis of dolphin behavior while also quantifying cryptic behaviors which are difficult to study in most cetaceans, such as suckling. Importantly, this type of methodology is likely to cause little to no disturbance on the behavior of common dolphins (Castro et al., 2021). We recommend that future UAV studies consider other parameters such as respiration rate, swimming speed, calf laterality and calf age.

ACKNOWLEDGMENTS

The authors would like to thank all AIMM volunteers who participated in the data collection and particularly to the research assistants Selma Bajraktarevic, Laura van Zonneveld, Henry Harper, and Guilherme Estrela. We further would like to thank Dr. Randall Wells and Dr. Daryl J. Boness for their comments and reviews and the two anonymous reviewers for their contributions to improve this article. This work was supported by the Associação para a Investigação do Meio Marinho (AIMM) and by the Fundação para a Ciência e a Tecnologia (FCT), through Programa Investigador FCT 2013 granted to Rui Rosa. The FCT also supported this study through (1) the strategic project UID/MAR/04292/2019 granted to MARE and (2) the PhD grant to J.C. (SFRH/BD/134156/2017). Sampling was conducted under the Instituto da Conservação da Natureza e das Florestas (ICNF) permits AOC/17/2016 and AOC/30/2018.

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DATA ACCESSIBILITY

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How to cite this article: Castro, J., Cid, A., Quirin, A., Matos, F. L., Rosa, R., & Pearson, H. C. (2024). Assessing the dynamics of common dolphin (*Delphinus delphis*) mother-calf pairs along the south coast of Portugal using unmanned aerial vehicles. *Marine Mammal Science*, e13115. <https://doi.org/10.1111/mms.13115>