Received: 16 October 2019 | Accepted: 5 April 2020

DOI: 10.1111/mms.12695

ARTICLE

Marine Mammal Science

Mating patterns of dusky dolphins (*Lagenorhynchus obscurus*) explored using an unmanned aerial vehicle

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Abstract

Few studies have explored the mating patterns of free-ranging cetaceans, largely because of logistical challenges. We used an unmanned aerial vehicle (UAV) to follow and video-record 25 groups of mating dusky dolphins (*Lagenorhynchus obscurus*) near the surface of the water and examine how behavior patterns varied with mating group type. We collected aerial footage of dolphins mating in traditional Isolated Pods and within Integrated Pods and compared differences in the number of mating animals, swimming speed, bearing change, percent time at the surface of the water, female respiration rate, copulatory position rate, and sex-specific mating behaviors. Only the mean number of mating animals and some sex-specific mating behaviors varied significantly between the two mating group types. More dolphins were engaged in mating behaviors in Isolated Pods than Integrated Pods. Males engaged in more interference behaviors in Isolated Pods compared to Integrated Pods. Females performed fewer speed bursts but more rolls on their backs in Integrated Pods compared to

Isolated Pods. Several similarities and differences were found in comparison to boat-based research of the same population of dolphins. We highlight the value of UAVs for noninvasive and accurate collection of cetacean behavioral data.

KEYWORDS

delphinid, drone, dusky dolphin, *Lagenorhynchus obscurus*, mating, sexual behavior

1 | INTRODUCTION

Mating behaviors are challenging to observe in free-swimming cetaceans (whales, dolphins, and porpoises) that spend most of their lives beneath the surface of the water, often avoid humans, and may occur offshore (e.g., Moore & Clarke, 2002). Additionally, mating events are typically brief and opportunistic (Lanyon & Burgess, 2014; Orbach, Keener, Ziltner, Packard, & Würsig, 2019; Schaeff, 2007). Copulation can serve several nonconceptive functions including play, social learning, and the establishment of social bonds (Mann, 2006), which can confound the understanding of mating strategies. However, there are a few populations where local ecological conditions and animal behavior provide conducive environments to observe the mating behaviors of free-swimming cetaceans. For example, harbor porpoises (*Phocoena phocoena*) can be observed mating year-round beneath the Golden Gate Bridge (GGB) in San Francisco, California (Keener, Webber, Szczepaniak, Markowitz, & Orbach, 2018; Orbach et al., 2019). The GGB traverses the narrowest point in the strait, where harbor porpoises congregate daily while following their prey at high tide (Keener et al., 2018; Stern, Keener, Szczepaniak, & Webber, 2017). Despite the typical shy behavior associated with harbor porpoises, males attempting to copulate with females perform rapid, precision-timed, aerial leaps observable from the GGB (Keener et al., 2018). Dusky dolphins (*Lagenorhynchus obscurus*) can also be observed mating regularly off Kaikoura, New Zealand, likely because of the local ecological conditions. The Kaikoura Canyon, one of the most productive canyons worldwide, reaches 1,200 m deep and is within 500 m of shore (Boyd, LaRoche, Gall, Frew, & McKay, 1999; Würsig, Dupray, & Weir, 2007). The local population of dusky dolphins feed on the mesopelagic prey of the deep scattering layer that migrates nightly towards the surface (Benoit-Bird, Würsig, & McFadden, 2004; Benoit-Bird, Dahood, & Würsig, 2009). Foraging is rarely observed in the daytime off Kaikoura (Markowitz, 2004, 2012), when the dolphins move inshore to socialize and rest (Würsig et al., 1997, 2007).

The Kaikoura population consists of ~2,000 dusky dolphins present at any given time, from a national New Zealand population estimate of ~12,000 dolphins (Markowitz, 2004); however, recent data suggest that the Kaikoura population[1] may be larger (Orbach et al., 2018). Dusky dolphins are gregarious animals with a highly fluid fission-fusion social structure and group sizes ranging from 2 to over 1,000 animals (Orbach et al., 2018; Würsig et al., 1997). The mating patterns of male and female dusky dolphins have been described using boat-based videos and photographs (Markowitz, Markowitz, & Morton, 2010; Orbach, Packard, Kirchner, & Würsig, 2015a). Male dusky dolphins use both pre- and postcopulatory mating tactics to compete for paternity. They have among the highest reported relative testes sizes in mammals (up to 8.5% of body mass; Van Waerebeek & Read, 1994), indicating investment in postcopulatory sperm competition inside the female's reproductive tract (Kenagy & Trombulak, 1986). Males also engage in exploitative scramble competition and utilize their agility to maintain physical proximity to a female (Orbach et al., 2015a). Copulation peaks in austral summer months and consists of dolphins in a ventrum-to-ventrum position, with the horizontally-positioned and ventrum-down female pushed partly above the surface of the water by the male beneath her (Markowitz et al., 2010; Orbach et al., 2015a; Figure 1).

Small mating groups, defined by multiple attempted copulations or visible erect penises, form in isolation near larger pods of dusky dolphins (Markowitz et al., 2010; Orbach, Packard, & Würsig, 2014; Orbach et al., 2015a). These

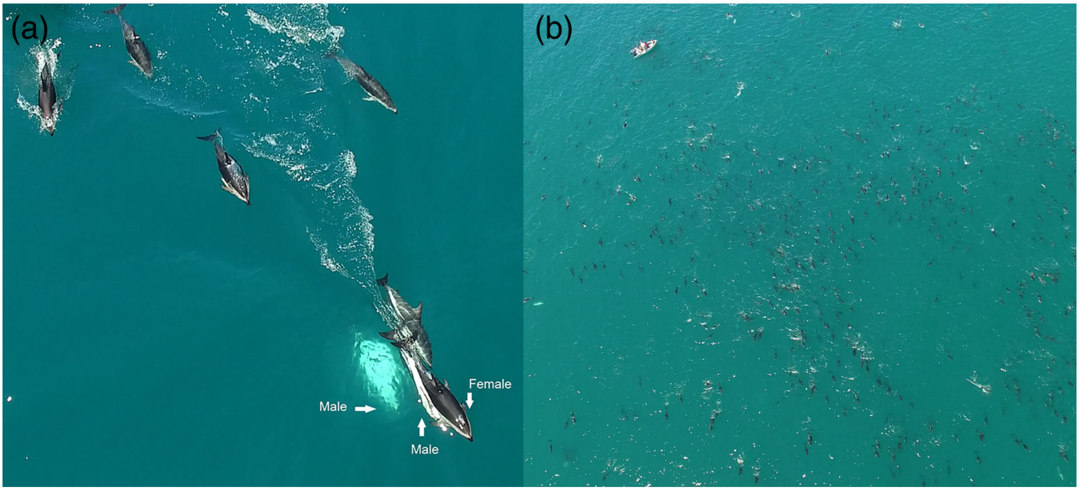

FIGURE 1 Still frame images from videos obtained by an unmanned aerial vehicle showing dusky dolphins in (a) an Isolated Pod with a ventrum-up inverted male pushing a ventrum-down female to the surface of the water in copulatory position. A second male is swimming under the mating pair. The UAV was 10 m altitude above the dolphins, and (b) an Integrated Pod with several hundred dolphins present. The 6 m boat is in the upper left quadrant of the image as a dimension reference. The UAV was 70 m altitude above the dolphins.

mating groups, herein referred to as an "Isolated Pod," typically consist of one female and three males, all within 10 m of each other, and are labile throughout the day but have some spatio-temporal stability (Markowitz et al., 2010; Orbach et al., 2014, 2015a). In addition to these traditional isolated mating groups, dusky dolphins can also be observed in copulatory position within large pods of up to several hundred dolphins, where behaviors appear to be more social than sexual and more passive than in Isolated Pods (Markowitz et al., 2010). We use the term "Integrated Pod" to denote this mating group type, where dolphins mate in subgroups within large pods. In contrast to Isolated Pods, in which dolphins are spatially disjunct from a large pod, dolphins in Integrated Pods occur within large pods. Variations in behaviors across mating group types (i.e., Isolated Pod and Integrated Pod) have not been previously quantified in dolphins. We hypothesized that if sexual interactions have primarily socio-sexual functions within Integrated Pods and primarily procreative functions within Isolated Pods, then overall effort expenditure should be lower in Integrated Pods because of constrained movement with so many dolphins nearby and the ease of fissioning into other nearby subgroups of dolphins.

While boat-based observations off Kaikoura have provided important new insights into dusky dolphin mating behaviors (Markowitz et al., 2010; Orbach et al., 2014, 2015a), fission-fusion societies (Markowitz, 2004; Orbach et al., 2018), and nursery group habitat use (Weir, Deutsch, & Pearson, 2010; Weir, Duprey, & Würsig, 2008), the platform of observation has inherent limitations. For example, the low angle of view from a small (~6 m long) boat can prevent observations of dolphin behaviors slightly below the surface of the water that are visible from a higher vantage point (Smultea et al., 2017). Boats influence the behaviors of dusky dolphins in some contexts (Lundquist, Gemmel, & Würsig, 2012). Dusky dolphins often engage in high speed chases during mating that include several directional changes at tight angles (Markowitz et al., 2010). Restricted boat maneuverability inhibits close pursuit of mating dolphins to accurately gauge their speed of travel. Additionally, there are limitations to focal individual follows. Males are inverted during much of mating chases and are consistently inverted during copulation attempts (Orbach et al., 2015a), and only 52% of the population has distinguishable natural markings on their dorsal fins (Kügler & Orbach, 2014). Consequently, it is typically not possible to track individual males in situ or by photo-identification based on dorsal fin markings, the common technique used for distinguishing individual dusky dolphins (Orbach et al., 2018; Würsig & Jefferson, 1990). However, unmanned aerial vehicles (UAVs) provide a platform of observation that circumvents these limitations and can procure high quality video data for post hoc analyses.

Advances in lightweight UAVs over the past decade have provided the marine mammal research community with a cost-effective and noninvasive way (when performed in accordance with regulations) to monitor cetaceans, including access to coastal regions unreachable by boat or foot. UAVs have become waterproof and more affordable, with longer battery life, larger ranges of travel, and reduced noise production (Christiansen, Rojano-Doñate, Madsen, & Bejder, 2016; Fiori, Doshi, Martinez, Orams, & Bollars-Breen, 2017). While applications of UAVs to cetacean research have typically centered on abundance estimates, photogrammetry, and photo-identification (Durban et al., 2016; Fiori et al., 2017; Koski et al., 2015; Landeo-Yauri, Ramos, Niño-Torres, Castelblanco-Martinez, & Searle, 2019), some recent research efforts have assessed behavioral patterns (Fiori, Martinez, Bader, Orams, & Bollard-Breen, 2019; Nielsen, Sprogis, Bejder, Madsen, & Christiansen, 2019; Torres, Nieukirk, Lemos, & Chandlerm 2018; Weir et al., 2018). Our objective was to assess the behavioral patterns of dusky dolphins in mating groups collected from UAV footage. Unlike previous studies on dusky dolphins that used boats to explore only traditional isolated mating groups (Markowitz, 2004; Markowitz et al., 2010; Orbach et al., 2014, 2015a; Orbach, Rosenthal, & Würsig, 2015b), we also followed mating dolphins within large pods to understand how behavioral patterns vary with mating group types. Specifically, we determined the (1) number of mating animals, (2) speeds of travel, (3) bearing changes, (4) percent time at the surface of the water, (5) respiration rates of females, (6) copulatory position rates, and (7) frequencies of male- and female-specific mating behaviors in two disparate mating group types. We predicted that speed of travel, bearing change, rate of copulatory position, and frequencies of sex-specific mating behaviors would be higher in Isolated Pods than Integrated Pods if Isolated Pods form for procreative purposes because these actions that require comparatively more effort have the potential high yield reward of insemination. In contrast, we predicted that the number of mating animals, percent time at the surface, and respiration rate of females would be lower in Isolated Pods than Integrated Pods if Integrated Pods form for social purposes and lack the potential high yield reward of insemination.

2 | METHODS

We collected aerial videos of dusky dolphins in mating groups off Kaikoura, New Zealand (42°30′S, 173°32′E) during December 2017. The study area is an open-ocean embayment of ~100 km^2, extending from the Kaikoura Peninsula in the north to Haumuri Bluffs in the south, a distance of about 20 km. Groups of mating dusky dolphins were detected visually by researchers in a 6 m rigid-hulled inflatable boat with a single 80 hp 4-stroke outboard engine. The horizon was systematically scanned for leaping dolphins, as simultaneous leaps among dolphins are most prevalent in mating groups (Markowitz et al., 2010; Orbach et al., 2015a). Once a mating group was found, we manually launched a Phantom 4 (DJI Innovations, Shenzhen, China) 4-rotor helicopter (1.38 kg; diameter: 35 cm engine-to-engine). The vertical take-off and landing UAV was equipped with a built-in camera (FOV 94° 20 mm) fitted with a polarized filter and DJI Li-Po batteries. The UAV was flown directly above the mating group and was maintained at a minimum height of 10 m above sea level or up to 50 m, as per permit regulations. The area covered by the frame at 10 m altitude was 22.5 × 12 m (when the camera angle was 90° to the water surface). The maximum flight time was 20 min, and flights only occurred in conducive visual meteorological conditions (Civil Aviation Authority of New Zealand, 2018) when wind speeds were below 10 knots. An iPad Air (Apple, A1474) was used to directly monitor dolphin activity and as a means to maintain the UAV centered over the focal animals. When mating behaviors were observed (Table 1), we launched the UAV to 10 m altitude. If all dolphins in frame were engaged in mating behaviors or pursued the presumed female, and the group was at least 200 m apart from a large pod of dolphins (>200 dolphins), the group was deemed an Isolated Pod. In contrast, if only a subset of dolphins in frame were engaged in mating behaviors or pursued the presumed female, and the mating animals were within 200 m of a large pod of dolphins (>200 dolphins), the group was deemed an Integrated Pod. Follows of the mating groups ended when mating behaviors ceased, the group dove and was lost or potentially confused with other dolphins in the area,

TABLE 1 Ethogram and count of mating behavior types exhibited by male or female dusky dolphins (modified from Orbach et al., 2015a).

Behavior type	Sex	Number of events	Description
Inverted swim	Male	1,261	Male swims in a ventrum-up body position (not under a dyad in copulatory position).
Push female to surface	Male	297	Inverted male pushes female up vertically while swimming ventrum-to-ventrum with her such that her dorsal region is above the surface of the water.
Reorientation leap	Male	156	Male leaps vertically out of the water and reenters head-first nearby. His whole body clears the surface of the water and no loud splash is generated.
Swim under leaping female	Male	73	Male swims inverted below a leaping female.
Swim under mating pair	Male	156	Male swims inverted below and within one body-width of a dyad in a copulatory position.
Interference	Male	57	Male moves in a manner resulting in separation of a dyad in copulatory position (e.g., blocking the direction of swimming).
Tail slap	Female	326	Female raises her tail out of the water and strikes it against the surface of the water with force, creating a noisy splash.
Direction change	Female	256	Female quickly moves nonlinearly through the water, abruptly switching direction one or more times, with each change at $<90^{\circ}$ angle.
Extreme directional change	Female	331	Female quickly moves nonlinearly through the water, abruptly switching direction one or more times, with each change $>90^{\circ}$ angle
Body roll	Female	476	Female rotates her body along her longitudinal axis (e.g., rolls onto her back).
Shallow dive	Female	347	Female swims slightly below the surface of the water (still visible) following a minimal or nonexistent peduncle arch
Reorientation leap	Female	130	Female leaps vertically out of the water and reenters head-first nearby. Her whole body clears the surface of the water and no loud splash is generated.
Speed burst	Female	87	Female moves horizontally and at high speed at the surface of the water with minimal changes in direction.
Spy hop	Female	12	Female is positioned vertically in the water with her eyes and rostrum above the surface.

the UAV battery reached 30% remaining capacity, a second vessel approached within 300 m of the dolphins, or the Beaufort Scale was >3.

Videos collected from the UAV were viewed and transcribed using Windows Media Player (v.12.0.7601.17514). The video playback was slowed down by as much as 10× the original speed to extract data. Analyses of each video terminated when mating behaviors (Table 1) were no longer exhibited or the video ended.

2.1 | Number of mating animals, swimming speed, and bearing change

Time stamps, altitude, and GPS (global positioning system) coordinates were extracted from the video files using the subtitle function in DJI GO that overlays the metadata on the flight video. Specifically, the latitude, longitude, visible number of mating animals, and their group composition were recorded with instantaneous sampling every 30 s. The number of mating animals was recorded as the number of dolphins engaged in mating activities that were visible at or near the surface of the water, and is a conservative estimate because dolphins below the surface were excluded from the count. The overall group size was not counted because Integrated Pods could contain several hundred dolphins. When a dolphin was partly out of the frame of view but sufficiently within frame to confirm its presence, it was included in the number of mating animals count. This decision was implemented because these animals were consistently observed engaged in mating behaviors in the next few frames of the videos. The drone was flown centered above the (presumed) focal female dolphin to provide a standardized measure of distance between consecutive data points. Females were identified in the videos by their ventrum-down positioning with inverted dolphins swimming beneath them (Orbach et al., 2014, 2015a). As only one dolphin was observed in this female body positioning at any given time in any of the videos prior to a dive (which could confuse individual identities), it was assumed there was only one female per video, regardless of mating group type.

Swimming speed (kilometers/hour) was calculated in Microsoft Excel (2013) by dividing the distance between two consecutive dolphin locations by time (30 s sample interval). The distance was subtracted between successive data points. The bearing of the dolphin group (between 0° and 359°) and the bearing change (difference between two consecutive bearings of a group) were calculated in Microsoft Excel (2013). Bearing measurements were calculated relative to the preceding group movement, with the drone turning in synchrony with the presumed female. For each group follow, the mean (± *SD*) was calculated for the number of mating animals, swimming speed, and bearing change, and compared between Isolated Pods and Integrated Pods.

2.2 | Percent time at the surface

To determine the likelihood of capturing mating behaviors from a UAV platform, we calculated the percent time dolphins in mating groups were detected at the surface. We subtracted the durations of all group dive intervals (seconds) from the total duration of the mating group encounter, and converted these values to percentages (Laake, Calambokidis, Osmek, & Rugh, 1997). A group dive was defined as the moment that no dolphins were visible at the surface of the water until the first dolphin resurfaced. The mean (± *SD*) percent time at the surface was then calculated for each group follow.

2.3 | Respiration rates of females

Breaths were tallied each time the (presumed) focal female was at the surface and her blowhole was observed to open and close and/or a puff of exhaled spray was observed emanating from her blowhole. Each female was tracked individually throughout the video sequence. If all dolphins dove out of view, the dolphin that resumed female behaviors and body positioning upon resurfacing was assumed to be the same individual. We tallied the number of breaths from a female when she was pushed to the surface by a male swimming inverted beneath her, and the number of breaths when she was not pushed to the surface, as this could provide insights on breathing patterns. For example, opportunistic breaths taken by females when pushed to the surface by males could result in fewer breaths taken when not pushed to the surface. To calculate each female's respiration rate, the number of breaths per video was tallied and divided by the duration of the video sequence. The mean (± *SD*) respiration rate of females was then calculated for all group follows.

2.4 | Copulatory positions

Copulation in dusky dolphins occurs in a ventrum-to-ventrum body position, with the male inverted beneath the female, and their ventrums in physical contact (Markowitz et al., 2010; Orbach et al., 2015a; Figure 1). The number of occurrences of copulatory positions was counted in each group follow, and rate was calculated by dividing total count by duration of the follow. Multiple copulatory positions within one follow were counted as independent samples.

2.5 | Frequencies of male- and female-specific mating behaviors

Males were distinguished from females based on viewing their anal-urogenital slits or everted penis and/or body positioning during copulation events (males ventrum-up and females ventrum-down; Markowitz et al., 2010; Orbach et al., 2014, 2015a; Figure 1). We acknowledge the possibility of misclassification of sex and potential skew of the data when apparent sex was determined by behavior only. During individual tracking of dolphins, each behavior was tallied using ad libitum sampling. Behavior categories were developed based on previous observations of dusky dolphin mating groups off Kaikoura (Orbach et al., 2015a). The videos were carefully assessed for detection of novel mating behaviors. Behaviors were divided into five male-specific and six female-specific categories (Table 1). It was not possible to track each dolphin continuously as they frequently dove out of view or were momentarily out of the video frame. A new tally of behaviors was started each time a dolphin surfaced from a deep dive or moved into frame. To mitigate potential pseudoreplication bias, we tallied behaviors by sex rather than by individual. Therefore, the tally for all males would be the same whether one male performed the majority of behaviors or a few males performed equal numbers of behaviors, and the individual identity of the dolphin was irrelevant. Total number of behavioral events was calculated by adding the tally of each behavior type. Frequency of occurrence (number of events per second) of each behavior type observed at the surface was then calculated for all Isolated Pod and Integrated Pod videos.

2.6 | Statistical analysis

We tested whether the mean number of mating animals, mean swimming speed, mean bearing change, mean percent time at surface, mean respiration rate of females, mean rate of occurrence of copulatory position, and frequency of male- and female-specific mating behaviors varied between Isolated Pods and Integrated Pods using the statistical program R (v.3.4.0; R Core Team, 2019). Nonparametric Mann-Whitney U tests for independent samples were used for assessments of continuous variables, as data did not meet assumptions of a normal distribution. Log-likelihood ratio tests and binomial z score post hoc tests were used to assess categorical behavior type data using Excel (2013). The binomial z score decision rule was based on the critical value 1.96. One female behavior type, “Head ups,” was excluded from the statistical analysis because of a low minimum expected value (<5).

3 | RESULTS

Forty-three videos collected from the UAV were analyzed, representing 25 mating groups (18 Isolated Pods and 7 Integrated Pods). Consecutive videos were recorded for some groups when mating behaviors persisted. The shortest mating group interaction was 134 s and the longest was 1,010 s.

3.1 | Number of mating animals

The mean number of mating animals was 5.32 dolphins (SD = ±2.25, median = 4), with a minimum of 3 and maximum of 11 dolphins. The number of mating animals was smaller in Integrated Pods (mean ± SD = 4.13 ± 2.03, median = 3.5) compared to Isolated Pods (mean ± SD = 5.8 ± 2.19, median = 6, W = 37, p = .026; Figure 2a).

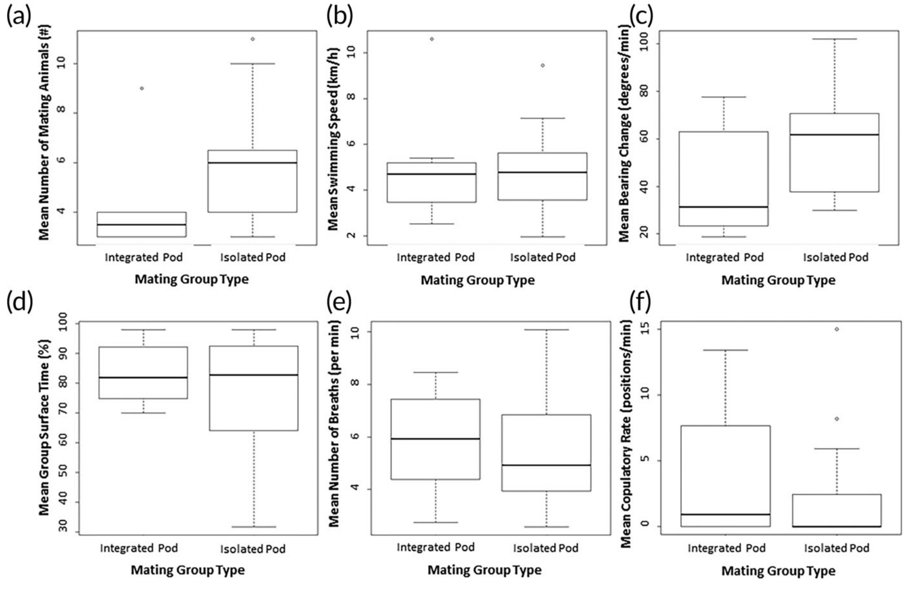

FIGURE 2 Boxplot showing differences in dusky dolphins exhibiting mating behaviors in Integrated Pods and Isolated Pods for mean (a) number of mating animals, (b) swimming speed (kilometers/hour), (c) bearing change (degrees/minute), (d) surface time (percent), (e) female breathing rate (breaths/minute), and (f) copulatory position rate (positions/minute). Boxes represent first and third quartiles, solid horizontal lines inside boxes represent medians, whiskers above and below boxes show 10th and 90th percentiles, and open circles represent outliers.

3.2 | Speed of travel and bearing change

The mean swimming speed was 5.02 km/h (*SD* = ±2.71, median = 4.7 km/hr) for Integrated Pods and 4.79 km/hr (*SD* = ±1.82, median = 4.8 km/hr) for Isolated Pods ($W = 63$, $p = 1$; Figure 2b). The mean bearing change was 42.93°/min (*SD* = ±25.38, median = 31.3°/min) for Integrated Pods and 57.90°/min (*SD* = ±20.39, median = 61.8°/min) for Isolated Pods ($W = 38$, $p = .1409$; Figure 2c).

3.3 | Percent time at the surface of the water

The mean percent surface time for Integrated Pods was 83.27% (*SD* = ±10.19, median = 81.97%) and the mean percent surface time for Isolated Pods was 77.42% (*SD* = ±17.49, median = 82.81%, $W = 90$, $p = .6358$; Figure 2d).

3.4 | Respiration rates of females

The mean respiration rates (breaths/minute) for focal female dolphins were 5.83 in Integrated Pods (*SD* = ±1.97, median = 5.92) and 5.36 in Isolated Pods (*SD* = ±2.05, median = 4.92, $W = 95$, $p = .4688$; Figure 2e). Females took a total of 383 breaths when pushed to the surface of the water by males swimming inverted beneath them, and 960 breaths when they were not pushed to the surface.

3.5 | Copulatory position

Ventrum-to-ventrum copulatory positions were recorded 22 times in Integrated Pods for a mean rate of 0.38 ($SD = \pm 0.55$) positions/min, and 33 times in Isolated Pods for a mean rate of 0.20 ($SD = \pm 0.38$) positions/min ($W = 92$, $p = .5168$; Figure 2f).

3.6 | Sex-specific mating behaviors

Frequencies of male- and female-specific mating behaviors differed across mating group types (log-likelihood ratio test: $G^2_{male} = 38.59$, $df = 5$, $p = .001$; $G^2_{female} = 22.78$, $df = 6$, $p = .001$; Figure 3). Males engaged in significantly more interference behaviors in Isolated Pods compared to Integrated Pods than expected by chance (binomial z score post-hoc test: $z = 4.99$). Females performed fewer speed bursts in Integrated Pods compared to Isolated Pods than expected by chance ($z = -2.47$). In contrast, females performed significantly more rolls on their backs and sides in

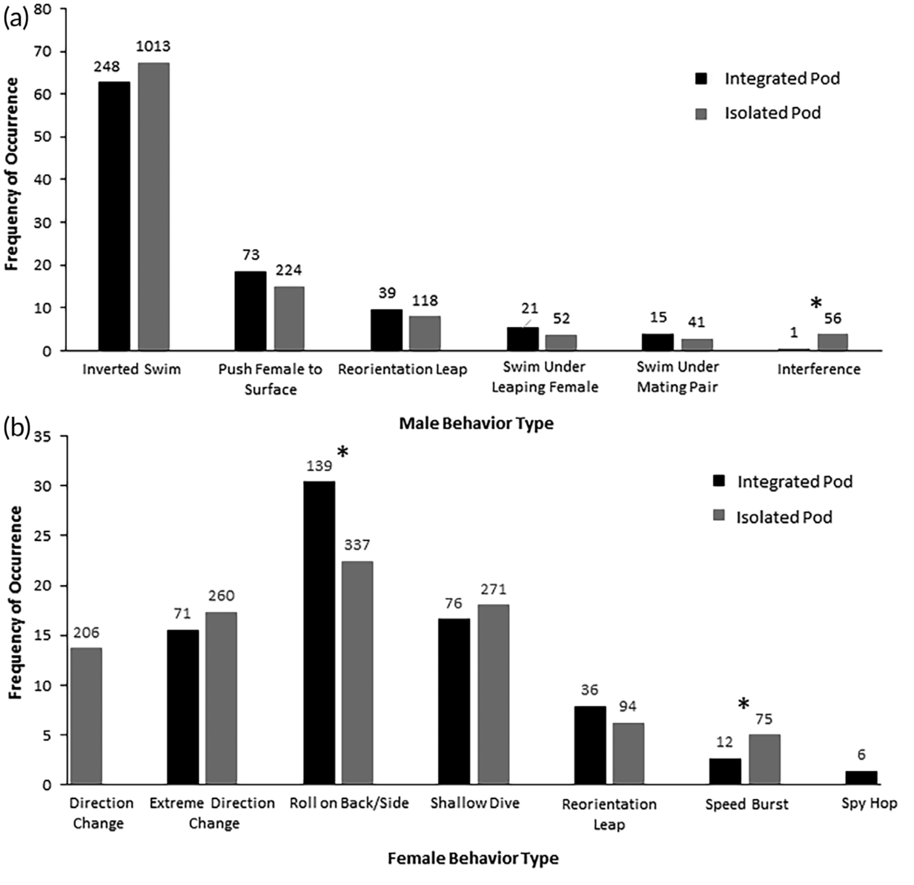

FIGURE 3 Frequency of occurrence of mating behavior types exhibited by (a) male and (b) female dusky dolphins in Integrated Pods and Isolated Pods off Kaikoura, New Zealand. Occurrences in Integrated Pods are in black and occurrences in Isolated Pods are in grey. The number of occurrences of each behavior type is above the boxes. Log-likelihood ratio tests and binomial z score post-hoc tests were used to assess differences between categorical behavior types. Behavior types that occurred at significantly different frequency between Integrated Pods and Isolated Pods are demarcated with an * symbol.

Integrated Pods compared to Isolated Pods than expected by chance ($z = 3.22$). All other frequencies of male and female behaviors were not found to differ significantly between mating group types.

4 | DISCUSSION

Our results do not appear to support the hypothesis that sexual interactions have primarily socio-sexual functions within Integrated Pods and primarily procreative functions within Isolated Pods of dusky dolphins. In contrast, we found that proxies of effort expenditure do not appear to be indicative of why dusky dolphins engage in sexual behaviors in very different mating group types. Whether and how the behaviors observed serve to produce offspring, enhance social learning, help develop dominance hierarchies, convey pleasure, or some other unidentified purpose, we found that dusky dolphins showed few differences in swimming and behavioral patterns in Isolated Pods and Integrated Pods. Questions remain regarding why mating is often observed in Isolated Pods and Integrated Pods but not in other subgroup types. The answer might relate to a female's state of estrus, accessibility, or monopolization potential. Future studies that directly measure the energetic investments of sexual behaviors may also provide insights into their function in different contexts.

We predicted that there would be more mating animals in Integrated Pods compared to Isolated Pods. However, we found the opposite pattern. Integrated Pods might have had fewer mating animals because dolphins were gradually fusing into a larger group that could subsequently separate into an Isolated Pod. While it remains unclear how isolated mating groups of dolphins form, one possibility is that they begin within Integrated Pods and gradually move away as mating chases become more vigorous and the need for less constrained 3-dimensional space increases. The mean number of mating animals was five dolphins (irrespective of mating group type) and comprised of four adult males and one adult female; this is consistent with findings obtained from boat-based platforms (Orbach et al., 2014, 2015b), highlighting that our instantaneous sampling approach to determine the number of mating animals provided an accurate estimate. Although slightly fewer than the previous prediction of seven mating animals per encounter in this population, our range of observed number of mating animals (3–11) is congruent with the predicted range (4–11) based on ecological and social tradeoffs associated with mating group formation (Orbach et al., 2014). With more or fewer mating dolphins, the costs of remaining outweigh the benefits of departing to join other mating animals (Orbach et al., 2014).

It was surprising that we did not find differences in speeds of travel between the two mating group types, as females in Isolated Pods used bursts of speed more often than did females in Integrated Pods. The instantaneous sampling approach for speed calculations could potentially underestimate the actual speed of travel if brief and frequent direction changes occurred within the 30 s sampling interval. It was not surprising, however, that speed bursts occurred more frequently in Isolated Pods than Integrated Pods, as speed bursts require open spaces for fast paced “slicing” at the surface of the water that would be obstructed by other dolphins in Integrated Pods. The higher than expected occurrence of body rolls by females in Integrated Pods compared to Isolated Pods could also reflect limited space constraints for maneuverability within an Integrated Pod. The action of rolling over, which can misalign the genitals of females and males in copulatory position, is less energetically expensive and requires less physical space than many other mating behavior types exhibited by females (Orbach et al., 2015a). The mean swimming speed of dolphins in mating groups obtained by UAV (4.9 km/hr) was similar between mating group types to those obtained by boat-based platform (5.1 km/hr, Orbach et al., 2014) and to those obtained by UAV in nursery groups (4.65 km/hr; Weir et al., 2018). While nursery groups swim continuously at a slow rate, mating groups have interval swimming speeds, consisting of fast chases interspersed with relatively stagnant movement during copulation attempts and ventrum-to-ventrum swimming.

The mean bearing change obtained by UAV (53.7°) appears to have been similar between mating group types. This bearing change reflects the linearity of movement and suggests that dolphins frequently changed directions when mating. The mean bearing change obtained by UAV was higher than that obtained during boat-based follows

(35.9°; Markowitz et al., 2010). As the UAV had a tighter turning radius and higher maneuverability than boats travelling at minimal wake when near dolphin groups, we postulate that data obtained by UAVs can more accurately reflect mating group travel patterns in addition to being noninvasive to dolphin groups and unlikely to disrupt social interactions.

Dusky dolphins in mating groups spent a median of 82% of the time at the surface of the water, regardless of the mating group type. As the relative frequency of reorientation leaps for both sexes (during which dolphins dove) appear to be similar in Integrated Pods and Isolated Pods, the percent surface times are congruent. Calculations of surface time obtained by UAV footage was low compared to the 91% surface time estimates obtained during boat-based follows (Orbach et al., 2015a). This difference could reflect varied accuracy in determining if a dolphin was deep diving or just below the surface of the water, which was exceptionally discernable with the UAV platform of observation. UAV-based research on mating patterns is feasible and valuable for other small cetacean species that remain near the surface of the water while mating.

The mean respiration rate of mating female dusky dolphins (5.5 breaths/min) was much higher than females in nursery groups also obtained by UAV (2.8 breaths/min; Weir et al., 2018), and dusky dolphins tagged with biologgers (2.1 breaths/min; Pearson et al., 2017). Mating activity is rigorous and may require more breaths to replenish oxygen supplies. Future research may be able to directly ascertain differences in energy expenditure over time in different contexts without using proxies. The higher breathing rate of females in mating groups compared to other groups may also reflect that females were pushed above the surface of the water by inverted males during 40% of breaths, which may have been an opportunistic occasion for additional breaths. Ideally, individual follows of a female could be performed over long durations to confirm that breathing rates are context specific. However, there are still many data acquisition challenges to overcome as current multisensor biologgers that attach via suction cup typically detach from dusky dolphins after 67 min (Pearson et al., 2017), boat based observations may overlook respirations with no evident breath, and drone battery life constrains lengthy focal follows to about 20 consecutive minutes. Unlike biologger data, however, video footage can also provide a context for behavior as the activity states of animals can be monitored (e.g., resting, traveling, feeding). This, in turn, will allow for future research that assesses if breathing rates are correlated with fluke beats and if they vary with the number of mating animals.

Unlike other male mating behaviors, it is possible that interference events were observed more frequently in Isolated Pods compared to Integrated Pods because of differences in the mean number of mating animals and the perceived increased competition risk when more rivals were present. Variation in the frequency of interference events could reflect inherent differences in the costs of lost copulatory opportunities in the two different mating group types and supports our hypothesis that mating in Isolated Pods and Integrated Pods have separate conceptive and social functions, respectively. Despite our recordings of 56 interference events in Isolated Pods, males do not appear to intimidate their rivals (Markowitz et al., 2010; Orbach et al., 2014) and no events of male-male aggression were observed. Male dusky dolphins do not appear to be able to evict nor exclude their rivals from joining mating groups (Orbach et al., 2015b), and interference appears to be an important behavioral tactic in Isolated Pods. Interestingly, no new mating behavior types were observed by UAV that were not previously described from boat-based observations. This contrasts with Torres et al.'s (2018) finding that novel behaviors of gray whales were detectable by UAVs that were not discernable by boat-based observations. The UAV perspective facilitates observations of dolphin behaviors beneath the surface of the water. As dusky dolphins in Integrated Pods spent marginally more time at the surface of the water than dusky dolphins in Isolated Pods, dusky dolphins may experience more challenges related to group cohesion when diving within a large group. Mating chases at the surface, like speed bursts, may provide females with a criterion to evaluate prospective mates, as similar agility and speed are needed to pursue a potential mate, evade a predator, or capture prey (Markowitz et al., 2010).

Future advancements in UAV technology, especially longer battery life and therefore longer recording times, hold great promise to increase our understanding of the socio-sexual behaviors of dolphins. Compared to boat-based platforms of observation, UAVs can provide a noninvasive tool to observe dolphins and obtain information on the number of mating animals, travel speed, bearing change, percent time at the surface, breathing rate, copulation occurrence rate, and sex-specific frequencies of behavior types. Without UAVs, it would be exceptionally complicated to assess behaviors within Integrated Pods and to track certain individuals continuously. Future research that can overcome the challenge of how to tell individuals apart upon surfacing from dives will yield insights on male-specific mating patterns. For example, although the number of occurrences of copulatory position were similar in both mating group types, it is not known if certain males obtain more copulations than others, if there is laterality in male sexual approaches to a female, and if certain male behavior types are more likely to lead to copulation. Although dusky dolphins perform overt sexual behaviors that can also be observed from boats (Markowitz et al., 2010; Orbach et al., 2014, 2015a), an aerial perspective may be critical to capture mating patterns in cetacean species with more discreet behaviors (e.g., harbor porpoises, *Phocoena phocoena*; Keener et al., 2018; Orbach et al., 2019), and could prevent a potential behavioral response due to boat-based research. We did not detect a behavioral response to the UAV flown at 10 m above dusky dolphins, although not all studies have shown similar trends (Fettermann et al., 2019; Ramos, Maloney, Magnasco, & Reiss, 2018). It seems that the dolphins engaged in active mating were not attentive to a small UAV flown overhead; however, in another behavioral state (e.g., resting, Fettermann et al., 2019), they may be more susceptible to responding and thus activity state should be considered when determining appropriate altitude heights.

ACKNOWLEDGMENTS

All UAV flights were conducted by a certified remote pilot (Lorenzo Fiori, License No. 839465 issued by the Australian Civil Aviation Safety Authority) under Research Permit 55328-MAR issued by the New Zealand Department of Conservation. Strict adherence to the operating rules in the New Zealand Marine Mammals Protection Act 1978, Marine Mammals Protection Regulations 1992, and local dolphin conservation guidelines was maintained at all times. We thank the research branch of the U.S. National Geographic Society for partial funding for this work, as related to an earlier study by B. Würsig. We thank Lindsay Wood, Amélie Paulin, and Yaly Mevorach for their assistance analyzing videos. We thank two anonymous reviewers and Dr. Daryl Boness for their helpful insights. We are indebted to personnel of the New Zealand Department of Conservation for providing and for amending our permit when our colleague and UAV operator Gregory Campbell unexpectedly passed away weeks before field research. We dedicate this work to him in his memory, and we thank Greg for the idea to conduct this research on dusky dolphins with an exciting new technique. Thank you, Greg. The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

Dara Orbach: Conceptualization; data curation; formal analysis; investigation; methodology; writing-original draft. **Jordan Eaton:** Data curation; writing-review and editing. **Lorenzo Fiori:** Investigation; methodology; resources; writing-review and editing. **Sarah Piwetz:** Formal analysis; investigation; methodology; writing-review and editing. **Jody Weir:** Investigation; methodology; resources; writing-review and editing. **Melany Würsig:** Investigation; project administration; writing-review and editing. **Bernd Würsig:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; writing-review and editing.

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ENDNOTE

[1]We use the term "population" as the approximate numbers of animals and not an indicator of cohesive genetic grouping.

REFERENCES

Benoit-Bird, K. J., Würsig, B., & McFadden, C. J. (2004). Dusky dolphin (*Lagenorhynchus obscurus*) foraging in two different habitats: Active acoustic detection of dolphins and their prey. *Marine Mammal Science*, *20*, 215–231.

Benoit-Bird, K. J., Dahood, A. D., & Würsig, B. (2009). Using active acoustics to compare lunar effects on predator–prey behavior in two marine mammal species. *Marine Ecology Progress Series*, *395*, 119–135.

Boyd, P. W., LaRoche, J., Gall, M., Frew, R., & McKay, R. (1999). Phytoplankton dynamics in oceanic waters of south New Zealand. *Journal of Geophysical Research*, *1043*, 13391–13404.

Christiansen, F., Rojano-Doñate, L., Madsen, P. T., & Bejder, L. (2016). Noise levels of multi-rotor unmanned aerial vehicles with implications for potential underwater impacts on marine mammals. *Frontiers in Marine Science*, *3*, 277.

Civil Aviation Authority of New Zealand. (2018). *Part 101 CAA Consolidation 2018*.

Durban, J. W., Moore, M. J., Chiang, G., Hickmott, L. S., Bocconcelli, A., Howes, G., … LeRoi, D. J. (2016). Photogrammetry of blue whales with an unmanned hexacopter. *Marine Mammal Science*, *32*, 1510–1515.

Fettermann, T., Fiori, L., Bader, M., Doshi, A., Breen, D., Stockin, K. A., & Bollard, B. (2019). Behaviour reactions of bottlenose dolphins (*Tursiops truncatus*) to multirotor Unmanned Aerial Vehicles (UAVs). *Scientific Reports*, *9*(1), 8558.

Fiori, L., Doshi, A., Martinez, E., Orams, M. B., & Bollard-Breen, B. (2017). The use of unmanned aerial systems in marine mammal research. *Remote Sensing*, *9*, 543.

Fiori, L., Martinez, E., Bader, M. K. F., Orams, M. B., & Bollard-Breen, B. (2019). Insights into the use of an unmanned aerial vehicle (UAV) to investigate the behavior of humpback whales (*Megaptera novaeangliae*) in Vava'u, Kingdom of Tonga. *Marine Mammal Science*, *36*, 209–223.

Keener, W., Webber, M. A., Szczepaniak, I. D., Markowitz, T. M., & Orbach, D. N. (2018). The sex life of harbor porpoises: Male lateralized and aerial behavior. *Aquatic Mammals*, *44*, 620–632.

Kenagy, G. J., & Trombulak, S. C. (1986). Size and function of mammalian testes in relation to body size. *Journal of Mammalogy*, *67*, 1–22.

Koski, W. R., Gamage, G., Davis, A. R., Mathews, T., LeBlanc, B., & Ferguson, S. H. (2015). Evaluation of UAS for photographic re-identification of bowhead whales, *Balaena mysticetus*. *Journal of Unmanned Vehicle Systems*, *3*, 22–29.

Kügler, A., & Orbach, D. N. (2014). Sources of notch and scar patterns on the dorsal fins of dusky dolphins (*Lagenorhynchus obscurus*). *Aquatic Mammals*, *40*, 152–165.

Laake, J. L., Calambokidis, J., Osmek, S. D., & Rugh, D. J. (1997). Probability of detecting harbor porpoise from aerial surveys: Estimating *g*(0). *Journal of Wildlife Management*, *61*, 63–75.

Landeo-Yauri, S., Ramos, E. A., Niño-Torres, C., Castelblanco-Martínez, N., & Searle, L. (2019). Using small drones to photo-identify Antillean manatees: A novel method for monitoring an endangered marine mammal in the Caribbean Sea. *Endangered Species Research*, *41*, 79–90.

Lanyon, J. M., & Burgess, E. A. (2014). Methods to examine reproductive biology in free-ranging, fully-marine mammals. In W. V. Holt, J. L. Brown, & P. Comizzoli (Eds.), *Reproductive sciences in animal conservation: Progress and prospects* (pp. 241–274). New York, NY: Springer.

Lundquist, D., Gemmell, N. J., & Würsig, B. (2012). Behavioural responses of dusky dolphin groups (*Lagenorhynchus obscurus*) to tour vessels off Kaikoura, New Zealand. *PLoS ONE*, *7*(7), e41969.

Mann, J. (2006). Establishing trust: Socio-sexual behaviour and the development of male-male bonds among Indian Ocean bottlenose dolphins. In V. Sommer & P. L. Vasey (Eds.), *Homosexual behaviour in animals: An evolutionary perspective* (pp. 107–130). Cambridge, UK: Cambridge University Press.

Markowitz, T. (2004). *Social organization of the New Zealand dusky dolphin* (Doctoral dissertation). College Station, TX: Texas A&M University.

Markowitz, W. J. (2012). *Comparative socioecology of the dusky dolphin* (Lagenorhynchus obscurus) *in New Zealand* (Doctoral dissertation). Palmerston North, New Zealand: Massey University.

Markowitz, T. M., Markowitz, W. J., & Morton, L. M. (2010). Mating habits of New Zealand dusky dolphins. In B. Würsig & M. Würsig (Eds.), *The dusky dolphin: Master acrobat off different shores* (pp. 151–176). Amsterdam, The Netherlands: Elsevier/Academic Press.

Moore, S., & Clarke, J. T. (2002). Potential impact of offshore human activities on gray whales (*Eschrichtius robustus*). *Journal of Cetacean Research and Management*, *4*, 19–25.

Nielsen, M. L., Sprogis, K. R., Bejder, L., Madsen, P. T., & Christiansen, F. (2019). Behavioural development in southern right whale calves. *Marine Ecology Progress Series*, *629*, 219–234.

Orbach, D. N., Keener, W., Ziltener, A., Packard, J., & Würsig, B. (2019). Testes size, vaginal complexity, and behavior in toothed whales (odontocetes): Arms race or tradeoff model for dusky dolphins (*Lagenorhynchus obscurus*), harbor porpoises (*Phocoena phocoena*), and bottlenose dolphins (*Tursiops* spp.)? *Journal of Comparative Psychology*, *133*, 359–372.

Orbach, D. N., Packard, J. M., Kirchner, T., & Würsig, B. (2015a). Evasive behaviours of female dusky dolphins (*Lagenorhynchus obscurus*) during exploitative scramble competition. *Behaviour*, *152*, 1953–1977.

Orbach, D. N., Packard, J. M., & Würsig, B. (2014). Mating group size in dusky dolphins (*Lagenorhynchus obscurus*): Costs and benefits of scramble competition. *Ethology*, *120*, 804–815.

Orbach, D. N., Pearson, H. C., Beier-Engelhaupt, A., Deutsch, S., Srinivasan, M., Weir, J. S., … Würsig, B. (2018). Long-term assessment of spatio-temporal association patterns of dusky dolphins (*Lagenorhynchus obscurus*) off Kaikoura, New Zealand. *Aquatic Mammals*, *44*, 608–619.

Orbach, D. N., Rosenthal, G. G., & Würsig, B. (2015b). Copulation rate declines with mating group size in dusky dolphins (*Lagenorhynchus obscurus*). *Canadian Journal of Zoology*, *93*, 503–507.

Pearson, H. C., Jones, P. W., Srinivasan, M., Lundquist, D., Pearson, C. J., Stockin, K. A., & Machovsky-Capuska, G. E. (2017). Testing and deployment of C-VISS (cetacean-borne video camera and integrated sensor system) on wild dolphins. *Marine Biology*, *164*, 42.

R Core Team (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ramos, E. A., Maloney, B., Magnasco, M. O., & Reiss, D. (2018). Bottlenose dolphins and Antillean manatees respond to small multi-rotor unmanned aerial systems. *Frontiers in Marine Science*, *5*, 316.

Schaeff, C. M. (2007). Courtship and mating behavior. In D. L. Miller (Ed.), *Reproductive biology and phylogeny of cetacean* (pp. 349–370). Boca Raton, FL: CRC Press.

Smultea, M. A., Fertl, D., Bacon, C. E., Moore, M. R., James, V. R., & Würsig, B. (2017). Cetacean mother-calf behavior observed from a small aircraft off southern California. *Animal Behavior and Cognition*, *4*, 1–23.

Stern, S. J., Keener, W., Szczepaniak, I. D., & Webber, M. A. (2017). Return of harbor porpoises (*Phocoena phocoena*) to San Francisco Bay. *Aquatic Mammals*, *43*, 691–702.

Torres, L. G., Nieukirk, S. L., Lemos, L., & Chandler, T. E. (2018). Drone up! Quantifying whale behavior from a new perspective improves observational capacity. *Frontiers in Marine Science*, *5*, 319.

Van Waerebeek, K., & Read, A. J. (1994). Reproduction of dusky dolphins, *Lagenorhynchus obscurus*, from coastal Peru. *Journal of Mammalogy*, *75*, 1054–1062.

Weir, J. S., Deutsch, S., & Pearson, H. C. (2010). Dusky dolphin calf rearing. In B. Würsig & M. Würsig (Eds.), *The dusky dolphin: Master acrobat off different shores* (pp. 177–193). Amsterdam, The Netherlands: Elsevier/Academic Press.

Weir, J. S., Duprey, N. M. T., & Würsig, B. (2008). Dusky dolphin (*Lagenorhynchus obscurus*) subgroup distribution: Are shallow waters a refuge for nursery groups? *Canadian Journal of Zoology*, *86*, 1225–1234.

Weir, J. S., Fiori, L., Orbach, D. N., Piwetz, P., Protheroe, C., & Würsig, B. (2018). Dusky dolphin (*Lagenorhynchus obscurus*) mother-calf pairs: An aerial perspective. *Aquatic Mammals*, *44*, 603–607.

Würsig, B., & Jefferson, T. A. (1990). Methods of photo-identification for small cetaceans. *Report of the International Whaling Commission, Special Issue 12*, 43–52.

Würsig, B., Cipriano, F., Slooten, E., Constantine, R., Barr, K., & Yin, S. (1997). Dusky dolphins (*Lagenorhynchus obscurus*) off New Zealand: Status of present knowledge. *Report of the International Whaling Commission*, *47*, 715–722.

Würsig, B., Duprey, N., & Weir, J. (2007). Dusky dolphins (*Lagenorhynchus obscurus*) in New Zealand waters: Present knowledge and research goals. In *DOC Research and Development Series 270*. Wellington, New Zealand: Department of Conservation.

How to cite this article: Orbach DN, Eaton J, Fiori L, et al. Mating patterns of dusky dolphins (*Lagenorhynchus obscurus*) explored using an unmanned aerial vehicle. *Mar Mam Sci*. 2020;1–14. https://doi.org/10.1111/mms.12695