Chapter 11
Drone Perspectives on Cetacean Mating and Sex

Eric Angel Ramos, Karin L. Hartman, Robin W. Baird, Jordan K. Lerma, Fabian Missael Rodríguez-González, and Dara N. Orbach

Abstract Mating and sociosexual behaviors of cetaceans are challenging to study in nature because most species spend only brief periods of time at the surface and most copulation and courtship occurs underwater. Recent advancements in technology have enabled a new perspective on these behaviors. Drones, or unoccupied aerial systems, have revolutionized studies of marine mammals by providing unparalleled aerial perspectives on the behaviors of whales, porpoises, and dolphins, including their use for investigating questions concerning the sexual behaviors and mating habits of species in near-surface waters. Drones offer numerous benefits over traditional boat- and land-based observational methods for studying mating in free-swimming cetaceans, including the ability to continuously film in high resolution for fine-scale tracking of activity and mating behaviors at and near the water's surface. This paper outlines various ways in which drone data can be used to understand mating in cetaceans, including novel drone-based video observations of six species of dolphins and whales. These examples illustrate specific sociosexual and mating behaviors and how drone-based data can be used to address questions

E. A. Ramos (✉)
The University of Vermont, Burlington, Vermont, USA

Fundación Internacional para la Naturaleza y la Sustentabilidad, Quintana Roo, Mexico

K. L. Hartman
Risso's Dolphin Research Center, Pico Island, Azores, Portugal

Nova Atlantis Foundation, Castricum, The Netherlands

R. W. Baird · J. K. Lerma
Cascadia Research Collective, Olympia, WA, USA

F. Missael Rodríguez-González
Departamento de Ciencias Marinas y Costeras, Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, Mexico

Laguna San Ignacio Ecosystem Science Program, Laguna San Ignacio, Baja California Sur, Mexico

D. N. Orbach
Texas A&M University-Corpus Christi, Corpus Christi, TX, USA

B. Würsig, D. N. Orbach (eds.), *Sex in Cetaceans*,
https://doi.org/10.1007/978-3-031-35651-3_11

about the diversity of sexual behaviors and mating strategies. The use of drones is improving opportunities to investigate the fitness advantages of mating tactics and their evolutionary drivers.

Keywords Aerial · Mating behavior · Mating tactics · Mysticete · Odontocete · Remote sensing · Sexual competition · Unoccupied aerial vehicles

11.1 Introduction

Studying the mating strategies and behaviors of free-swimming cetaceans is challenging due to the difficulty of observing and characterizing these behaviors in nature (Schaeff 2007; Lanyon and Burgess 2014). The mating tactics of cetaceans are diverse and vary between the sexes and in different ecological and social contexts (Dines et al. 2015; Orbach 2019). However, decades of research have provided a wealth of knowledge on sexual selection and mating strategies in cetaceans, including conceptive and non-conceptive sexual behaviors (Whitehead and Mann 2000; Furuichi et al. 2014; Orbach 2019; Ham et al. 2023, this book). Many studies rely on anatomical investigations or observations of captive animals (Glabicky et al. 2010; Hill et al. 2018, 2022; Manitzas Hil et al. 2023, this book; Orbach et al. 2023, this book).

Methods for studying cetacean mating behaviors often include boat-based underwater and surface observations (Herzing 1996; Bender et al. 2009; Orbach et al. 2015) and land-based platforms, such as bridges, for observing nearshore species (Keener et al. 2018; Webber et al. 2023, this book). Boat-based observations are the most prevalent method for studying mating and sociosexual behaviors of free-swimming cetaceans (Mann 1999). Long-term photo-identification and behavioral observations have been instrumental in uncovering the mating dynamics of cetaceans. Such studies have provided important insights into the complex social networks of species such as bottlenose dolphins (*Tursiops* spp.) and killer whales (*Orcinus orca*), revealing intricate associations influenced by relatedness and overlapping home ranges of kin (Connor et al. 1996; Randić et al. 2012; Connor et al. 2017; Miketa et al. 2018).

Recent advancements in technology have dramatically improved the ability to track the behaviors of marine mammals, both in shallow and pelagic habitats. Animal-borne tags and passive acoustic arrays enable the recording of fine- and broad-scale movements (Nowacek et al. 2016). In some cases, movements recorded with tags and acoustics can provide clues about mating behaviors, such as by measuring the distance between males and females at depth. However, these methods can be cost-prohibitive, and obtaining fine-scale observations of free-swimming cetacean behaviors remains challenging.

11.1.1 Aerial Perspectives

The use of unoccupied aerial vehicles (UAVs)/drones in marine mammal studies has significantly increased in recent years due to their versatility and multiple benefits. Drones consist of a multirotor or a fixed-wing aircraft equipped with cameras and other sensors, which are piloted remotely or autonomously. Drones have been used in a wide range of marine mammal research including photogrammetry to assess body size, health, and energetics (Christiansen et al. 2016; Torres et al. 2022), estimations of population or group size (Fettermann et al. 2022), tracking interactions with humans (Fiori et al. 2020; Pirotta et al. 2022), and observing the behaviors of cryptic species (Baird et al. 2022). Small (< 5 kg) multirotor drones flown over cetaceans may provide overhead views of behaviors inaccessible from boat-based observers or capture rare events, foraging patterns, socializations, and mother-calf interactions (Ramos et al. 2021). Drones can also facilitate the collection of blow samples for genetic, microbiome, and hormonal studies (Raudino et al. 2019; Centelleghe et al. 2020) and provide a means of photo-identifying taxa (Koski et al. 2015; Hartman et al. 2020; Landeo-Yauri et al. 2021). When combined with other methods of data collection, drones may provide valuable insights about the mating grounds of large whales (Cole et al. 2013) and the behavior of pelagic cetaceans (Smultea et al. 2018). Yet observations of mating are often brief and opportunistically gathered during surveys dedicated to estimating population distribution and abundance (Kingsley and Reeves 1998), often in remote and inaccessible regions (Angliss et al. 2018).

The widespread use of drone technology for behavioral studies in cetaceans requires careful consideration and adaptation to different contexts. A growing body of literature has been published on the disturbance impacts of drones on marine mammals, particularly on bottlenose dolphins and manatees (Ramos et al. 2018; Giles et al. 2021; Landeo-Yauri et al. 2021). The type of drone needed depends on the research question and target species. Numerous recent comprehensive reviews and synthesis of the benefits and pitfalls of drone use for marine megafauna studies provide insights of broad and specific applications (e.g., Nowacek et al. 2016; Raoult et al. 2020; King and Jensen 2022). We emphasize the value of drones compared to boat-based research when applied to studying sociosexual and mating behavior in cetaceans (Table 11.1).

11.2 Drones Applied to Assess the Sociosexual and Mating Behavior of Cetaceans

An increasing number of studies have reported sociosexual and mating behaviors of cetaceans using drones (e.g., Ramos et al. 2021; Hill et al. 2022; Lonati et al. 2022). The use of aerial drones for enabling direct overhead views of cetaceans and for gathering high-resolution videos of their interactions provides numerous benefits to

Table 11.1 Comparison of different aspects of boat- and drone-based methods for studying mating and sexual behavior in cetaceans

Characteristic	Boat	Aerial drone
Data sampling	Visual observations of animals at the surface and submerged near the surface (<1 m)	Surface and subsurface observations
Animal visibility	Visible primarily at the surface and possibly just beneath the surface	Visible for the duration of time within <1–3 m of the surface
Scale of observations	Within <200 m of the vessel or several km from shore	Fine-scale of meters to hundreds of meters across field-of-view
Follow type	Focal animal or focal group	Focal animal or focal group
Sampling strategy	Variety of sampling types (e.g., all event, ad libitum, scan, point) implemented by observer to account for need to track different numbers of individuals engaged in different activities	High-resolution recording enables resampling of videos to conduct multiple sampling types. For example, focal follows of all individuals paired with scan sampling every 30 sec to account for activity of the group
Duration of observation	At the surface for minutes to hours depending on the target species and other factors. Animals regularly go out-of-sight. Recording of the activity of multiple animals is often restricted by the number of observers	Each flight is limited in battery time (e.g., 20–45 min). Multiple flights can be flown back-to-back to overcome this
Behavioral activity	Observers tracking surface activity of subsets of animals and sampling sexual and mating behaviors	Detailed video record of all near-surface behavior in target animals. Videos can be scored for behaviors and associated factors (e.g., position, orientation, sex identification, quantification of mating behaviors)
Individual identification	Photo-identification using high-resolution cameras equipped with telephoto lenses to capture images of the dorsal fins, bodies, or flukes of individuals	Photo-identification feasible for species with sufficient scarring detectable
Tracking movements	Estimates between surfacings, measured by speed of surface movements	Tracked at fine-scale with onboard GPS sensor providing spatially and temporally fine-grained location and time data

Table adapted from King and Jensen (2022)

the study of cetacean mating behavior (Table 11.1). By enabling continuous observations of behavior at the surface and subsurface, it is possible to track individuals and groups and detect specific mating behaviors. High-resolution drone footage demonstrated that the sex-specific mating behaviors of dusky dolphins (*Lagenorhynchus obscurus*) varied with context (Orbach et al. 2020b); detailed analysis of footage enabled precise counts of mating behaviors, swimming speeds, bearing changes, and the percent of time dolphins spent at the surface (Orbach et al. 2020b). One male rough-toothed dolphin (*Steno bredanensis*) was video-recorded copulating with another dolphin on at least seven occasions within 7 minutes (Ramos et al. 2021). For some species like harbor porpoises (*Phocoena phocoena*), their tendency to avoid boats makes them particularly challenging to observe in nature; yet drone footage has captured mating attempts (Webber et al. 2023, this book).

Drones have captured non-conceptive mating, which occurs in several species of cetaceans (Ham et al. 2023, this book). Non-conceptive male-male sexual interactions (swimming belly-to-belly with erect penises) were video-recorded between an adult male killer whale and a calf (Sanvito and Galimberti 2022); aerial imagery enabled identification of the animals from an established photo-identification catalog. Non-conceptive copulatory behavior has also been video-recorded by drone for North Atlantic right whales (*Eubalaena glacialis*; Lonati et al. 2022); the penis of an adult male was recorded entering a calf's genital slit (Lonati et al. 2022; Brown and Sironi 2023, this book). Distinguishing conceptive from non-conceptive mating is important to understand social bonding, dominance relationships, and social learning (Ham et al. 2023, this book).

The rapidly growing literature on applications of aerial drones to cetacean research supports their use for capturing unparalleled views of cetacean behavior in nature. However, the application of drones to explore sociosexual and mating behaviors is largely unexplored.

11.3 New Data Documented with Drones

To demonstrate the capabilities of drones to advance exploration of the mating behavior of cetaceans, we analyzed a selection of aerial footage from six different species of cetaceans (common bottlenose dolphins (*Tursiops truncatus*), rough-toothed dolphins, pygmy killer whales (*Feresa attenuata*), Risso's dolphins (*Grampus griseus*), dusky dolphins (*Lagenorhynchus obscurus*), and gray whales (*Eschrichtius robustus*)). We employed various models of small (< 5 kg) multirotor DJI drones, ensuring compliance with all local laws and regulations for drone operations in Belize, Mexico, New Zealand, the USA, and Portugal (Table 11.2). All videos were filmed in 4 K resolution during manually operated flights at a maximum duration of ~20 mins (Table 11.2).

Videos collected by drone were analyzed, and a subset that included repeated sociosexual or mating behaviors were reviewed in BORIS behavioral analysis software (Friard and Gamba 2016). To provide examples of different data acquired by drones, we reviewed video footage and conducted focal group follows using ad libitum sampling (Mann 1999). Sexual behaviors associated with different mating tactics of each sex were characterized according to behavioral ethograms (Table 11.3; Orbach 2016, 2019). Due to the limited duration of our follows and our overall dataset, we likely only captured a fraction of the sexual behaviors displayed by any of our study species.

Table 11.2 Information on the six species of cetacean filmed using small aerial DJI drones during focal group follows

Scientific name	Common name	Location	Body of water	Drone type	Flight altitudes (m)	Habitat type	Mean depth (m)	No. flights
Tursiops truncatus	Common bottlenose dolphin	Turneffe Atoll, Belize	Caribbean Sea	Phantom 4 Pro v2	20–35	Shallow lagoon	3	24
Lagenorhynchus obscurus	Dusky dolphin	Kaikoura, New Zealand	South Pacific Ocean	Phantom 4 Pro v2	10–20	Open sea	900	3
Eschrichtius robustus	Gray whale	San Ignacio Lagoon, Mexico	Eastern North Pacific Ocean	Inspire 2	20–40	Shallow lagoon	2–30	3
Steno bredanensis	Rough-toothed dolphin	Bay of Petatlan, Mexico	Eastern Tropical Pacific Ocean	Mavic Pro 2	20–40	Open sea	25	6
Feresa attenuata	Pygmy killer whale	Hawai'i, USA	Eastern Tropical Pacific Ocean	Mavic Pro 2	25–50	Open sea	1300	3
Grampus griseus	Risso's dolphin	Azores, Portugal	North Atlantic Ocean	Phantom 4/Mavic Pro 2 Zoom	15–40	Open sea	800	3

Table 11.3 Mating tactics and associated precopulatory behaviors in male and female cetaceans identifiable by drone observations

Sex	Mating tactic	Measurable from a drone	Example in our data
Male	Display competition	Measure body size and shape in sexually dimorphic species. Determine dominance relationships through group position (e.g., leaders)	Stereotypic copulation position in rough-toothed dolphins perpendicular to the female who swam ventrum-up
Male	Contest competition	Compare and quantify competitive behaviors and intrasexual competition in individual males during mating behavior	Male gray whales simultaneously jostled for position against the female during copulation attempts. Males interfered with the copulation attempts of rival males
Male	Endurance competition	Track individual male mating behaviors subsurface and over fine-spatial scales. Identify roles in consortships and occurrences of cooperative mating tactics (i.e., herding)	Two adult male bottlenose dolphins herded a sexually immature female to prevent her from leaving the area and copulating with other males
Male	Scramble competition	Measure individual male speed during mating chases and compare between successful and rejected copulations between rival males	Female dusky dolphins led multiple males on energetically costly chases involving deep dives, leaps, and abrupt changes in swim speeds and directions.
Female	Signal discrimination	Measure characteristics of male chases (e.g., maneuverability, speed)	Female gray whale behavior in response to multiple different males
Female	Evasive behaviors	Sex identification and fine-scale behavior of individuals including the detection and frequency of behavioral events	Female dusky dolphins avoided males with reorientation leaps, accelerated swim speed, and reorientation ventrum-up to prevent genital access
Female	Polyestry and multiple matings	Identify male roles in infanticide associated with social networks and measure synchrony and inter-animal distances	Multiple matings in bottlenose dolphins and Risso's dolphins of known age and sex to track reproductive status in relation to individual mating partners

Table is modified from Orbach (2016, 2019)

11.3.1 Sex Identification

Observations of the genitals of cetaceans, which are a necessity to verify the sex of an individual in the absence of genetic analyses, were often possible during post hoc video review of sociosexual interactions and mating behaviors (Fig. 11.1). All cetaceans analyzed rotated numerous times during sexual interactions, exposing their ventra at the surface (Fig. 11.1). Males were identified in videos of all six species based on observation of their everted penises (Fig. 11.1). It was

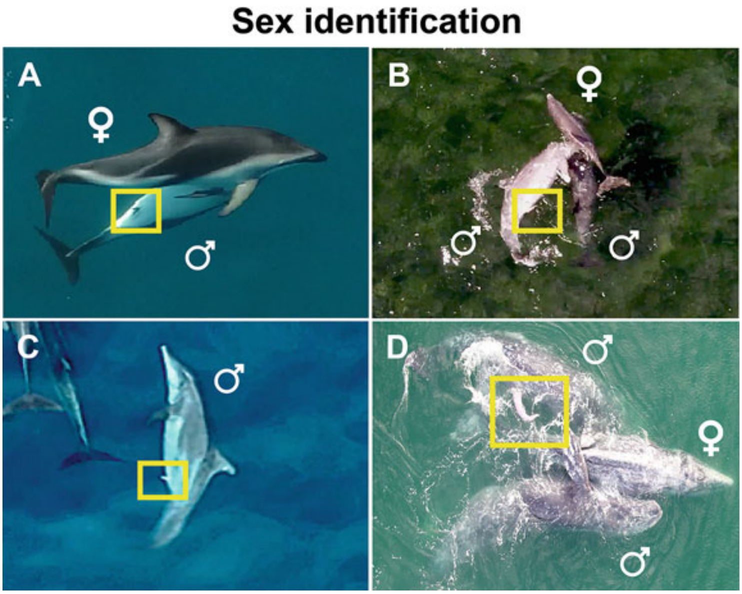

Fig. 11.1 Examples of sex identification of cetaceans from aerial drone observations. The extruded penis of males provides the most reliable indicator of sex in a wild cetacean from aerial drone observations. (**a**) Dusky dolphins (*Lagenorhynchus obscurus*), (**b**) common bottlenose dolphins (*Tursiops truncatus*), (**c**) rough-toothed dolphins (*Steno bredanensis*), (**d**) gray whales (*Eschrichtius robustus*). ♀ = female; ♂ = male

comparatively easy to observe the large penises of large odontocetes and baleen whales (Fig. 11.1d).

Differences in mating behaviors within and across species resulted in varying degrees of visibility of the act of intromission (penile penetration). For instance, intromission was rarely visible in dusky dolphins as females swam ventrum-down and belly-to-belly with a male, thereby obscuring views of copulation from the overhead view of the drone (Fig. 11.1a). In contrast, intromission was sometimes visible for common bottlenose dolphins as males had a perpendicular orientation to a female while thrusting their pelvises toward her genitals (Fig. 11.1b). Males of all species we analyzed approached females with their penises extruded during copulation attempts, sometimes successfully achieving intromission (Fig. 11.2). Successful intromission was not observed in gray whales although it should be overt as mating occurs primarily at the surface and the penis is sizeable and highly visible (Fig. 11.1d). The gray whale penis may be sufficiently large to detect ejaculation from aerial drone footage. Caution may be warranted in determining sex based on behaviors alone during mating interactions since homosexuality is common among cetaceans (Ham et al. 2023, this book; Würsig et al. 2023, this book).

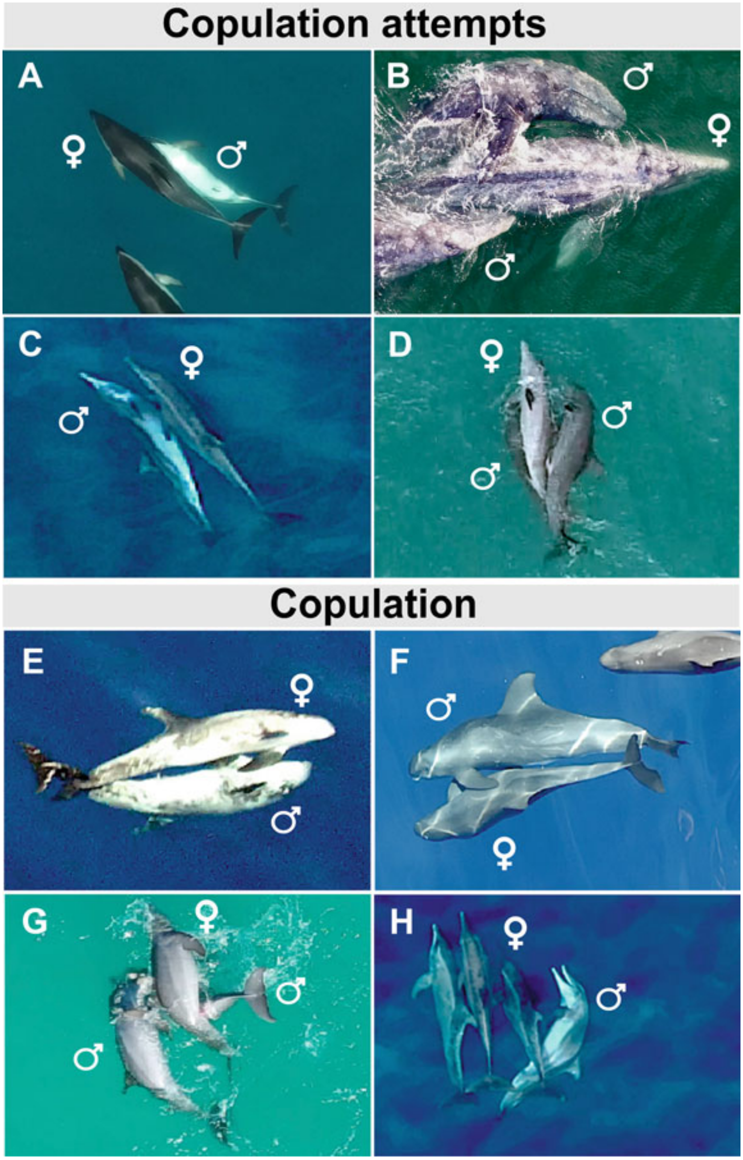

Fig. 11.2 Copulation attempts and copulations involving intromission in six species of cetaceans. Copulation attempts varied across species in orientation, intensity of approach, and receptivity of females. (**a**) Dusky dolphins (*Lagenorhynchus obscurus*), (**b**) gray whales (*Eschrichtius robustus*), (**c**) rough-toothed dolphins (*Steno bredanensis*), (**d**) common bottlenose dolphins (*Tursiops truncatus*), (**e**) Risso's dolphins (*Grampus griseus*), (**f**) pygmy killer whales (*Feresa attenuata*), (**g**) common bottlenose dolphins, (**h**) rough-toothed dolphins. ♀ = female; ♂ = male

11.3.2 Individual Identification

The ability to identify particular individuals during mating encounters can yield insights into sexual selection pressures. For example, certain males may have a particular attribute that is desirable to a female or increases copulation opportunities. Drones offer the potential for photo-identification or tracking of cetaceans that have scarring or unique body markings and features that are discernible from an aerial perspective (Hartman et al. 2020; Ramos et al. 2021). Rough-toothed dolphins, Risso's dolphins, pygmy killer whales, and gray whales had individually identifiable features visible in drone footage that provided the ability to distinguish individuals in mating interactions. For example, we could distinguish which male gray whales pursued females and count the frequency at which a male interrupted a rival's copulation attempt (Fig. 11.3). ImageJ (Abràmoff et al. 2004) was used to alter the color scheme of images to make scars appear prominent, and the measure particle tool was used to extract prominent features (Fig. 11.3c).

We caution that the overhead angle of drones can reduce visualization of certain body features typically used for photo-identification (e.g., perpendicular photographs of dorsal fins, undersides of flukes). However, body scarring can often be used to match individuals to identification photos taken from a boat simultaneous to drone operations. When flown at a steep angle to one side of a group, it may be possible to photograph the dorsal fins of cetaceans with sufficient quality images to match boat-based photo-identification images (e.g., dwarf sperm whales, *Kogia sima*, Baird et al. 2022). While drones are unlikely to serve as an alternative to boat-based photography during behavioral follows, they serve as a complementary tool.

11.3.3 Female Cetacean Mating Tactics

Cetacean mating tactics are diverse and vary between the sexes, ecological conditions, and social contexts (Orbach 2019). The mating strategies and tactics used by female cetaceans to control paternity are not well understood nor known for most species (Boness et al. 2002). Given the energetic costs associated with producing large gametes and investing in parental care (Trivers 1972), females likely play an active role in the selection of mating partners to improve the fitness of their offspring (Orbach 2019). However, male intrasexual competition and sexual coercion can obscure female preferences, leading to the historic belief that females have more passive roles in paternity control than males (Clutton-Brock and McAuliffe 2009). Thus, research has largely focused on understanding the temporal and energetic investments females make in rearing viable offspring (Whitehead and Mann 2000). However, female cetaceans may use several mating tactics to control paternity.

Of the five female mating tactics characterized for cetaceans (i.e., signal discrimination, mate choice copying, evasive behaviors, polyestry/multiple matings,

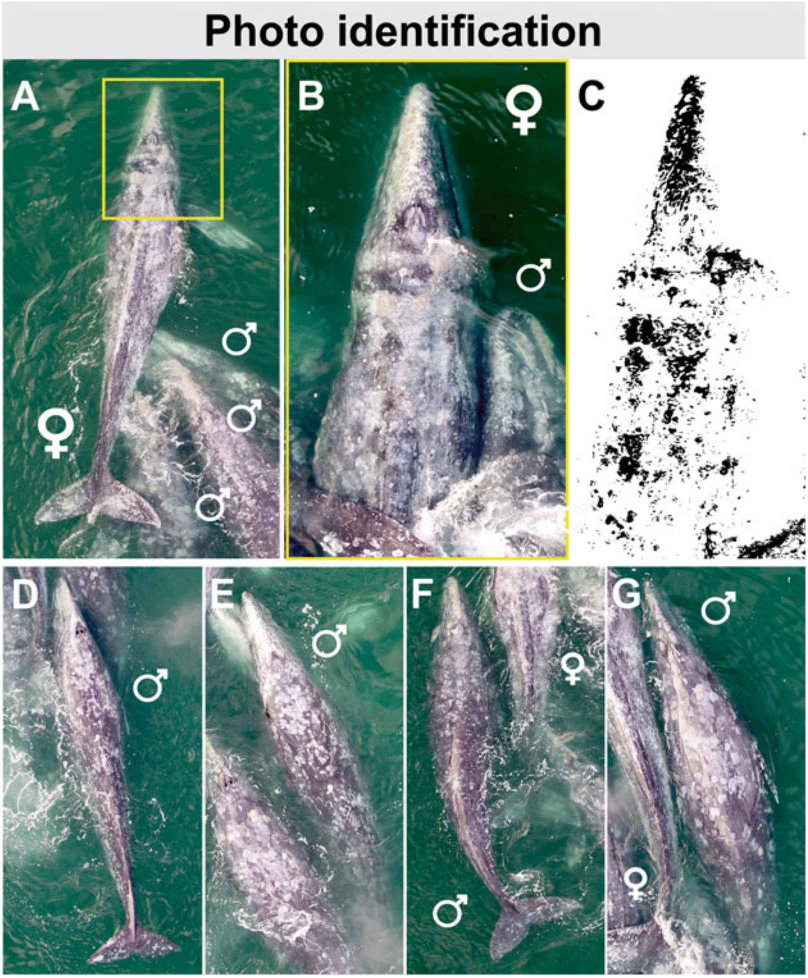

Fig. 11.3 An example of photo-identification of individual female and male gray whales (*Eschrichtius robustus*) during mating behavior in a group of adults observed in San Ignacio Lagoon, Mexico. Whales are covered in markings that enable reidentification of individuals throughout drone-based focal follows and in future sightings. (**a**) A female gray whale as multiple males nuzzle her genitals with their rostrums. (**b**) The head and anterior body of the same female zoomed in (yellow box in A). (**c**) Features extracted from B using the analyze particle feature in ImageJ (Abràmoff et al. 2004) to illustrate some features for use in photo-identification. (**d–g**) Different male gray whales observed in a mating chase in pursuit of a single female. ♀ = female; ♂ = male

modified genitalia; Orbach 2019), we focus on examples of evasive behaviors, signal discrimination, and polyestry/multiple matings because of the possibilities to detect evidence of these tactics using aerial videos collected by small multirotor drones (Table 11.3).

11.3.3.1 Evasive Behaviors

To ensure the reproductive success of their progeny, females assess the quality of potential mates before selecting preferred mates and rejecting undesirable mates. Behavioral studies using drones could identify and quantify female responses to copulation attempts and levels of proceptivity, receptivity, or resistance to males. Thus, drone footage can provide a valuable tool to improve understanding of the complex and nuanced ways in which females express their mate choice. Our data demonstrate that female cetaceans display many short-duration, easily detectable evasive behaviors during mating chases that can be examined in aerial drone video across different species and environmental conditions.

Females may prevent copulations by changing their body position to make their genitalia inaccessible to suitors. Female dusky dolphins repeatedly make deep dives and swim inverted at the surface so that their genital opening is inaccessible to pursuing males (Orbach et al. 2015). Similarly, we observed from drone footage that female bottlenose dolphins frequently rolled while stationary to turn their ventra away from approaching males (Fig. 11.4c). We observed a single female repeatedly roll to her left and right to avoid copulation attempts from three pursuing males (Figs. 11.2d, 11.4c). In contrast, female rough-toothed dolphins sometimes evaded approaching males by rapidly swimming forward.

In most species for which we observed evasive female displays, females also exhibited receptive behaviors to mating attempts. In a group of 12 pygmy killer whales, a single female was not observed actively maneuvering or turning her ventrum to block male access to her genitals (Fig. 11.2f). Similarly, a female rough-toothed dolphin did not resist copulations by multiple males and maintained her swimming speed.

11.3.3.2 Signal Discrimination

Female selection of desired mates involves choices of heritable characteristics that can include access to ample resources, morphological traits, behavioral displays, and overall competitive abilities (Darwin 1871). Signal discrimination of secondary sexual characteristics is a common tactic used by females to choose high quality mates. For example, female dusky dolphins swim ventrum-down, which may regulate copulations by restricting the breathing rate of competing ventrum-up males attempting to copulate (Markowitz et al. 2010; Orbach et al. 2015). These behaviors seem to drive extended mating chases during which females may assess the fitness of potential mates based on their agility and behavior.

Our analysis revealed that several cetacean species display behaviors consistent with female signal discrimination in mating contexts. Dusky dolphins and gray whales engaged in long mating chases, with multiple males pursuing a female that was swimming ventrum-down (Fig. 11.2a, b). During copulation attempts, male dusky dolphins briefly approached females and maintained a ventrum-up posture to

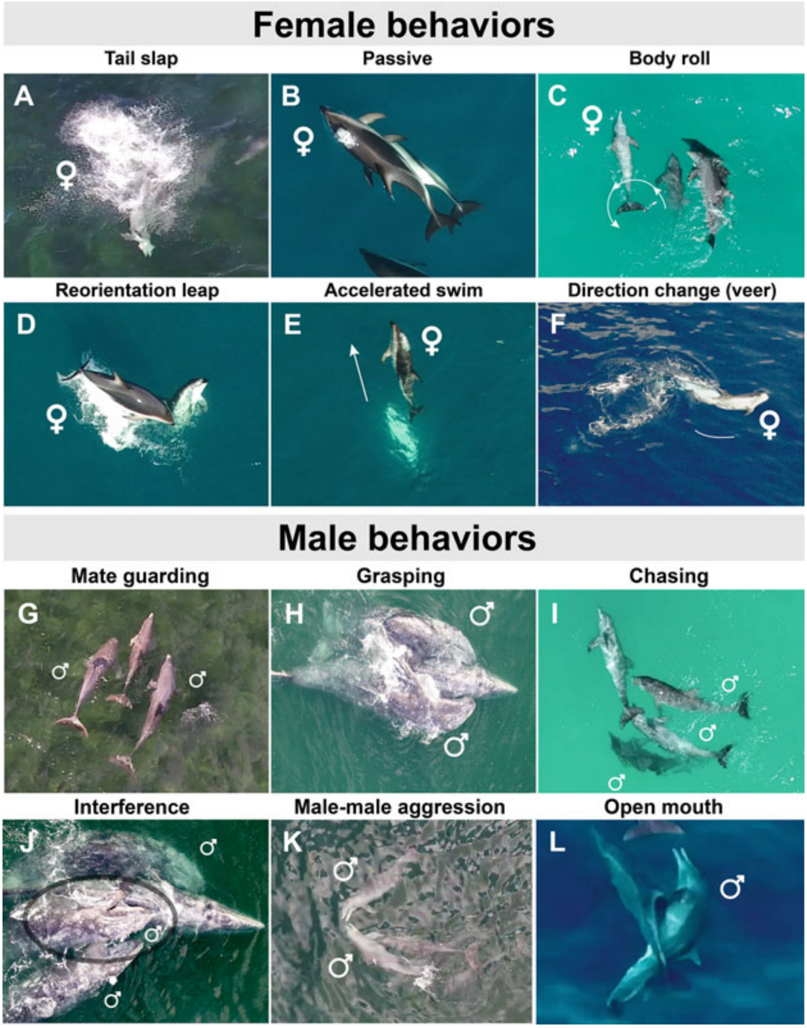

Fig. 11.4 Examples of different mating behaviors of female and male cetaceans identified in aerial drone observations. (**a**) Common bottlenose dolphins (*Tursiops truncatus*), (**b**) dusky dolphins (*Lagenorhynchus obscurus*), (**c**) common bottlenose dolphins, (**d–e**) dusky dolphins, (**f**) Risso's dolphins (*Grampus griseus*), (**g**) common bottlenose dolphins, (**h**) gray whales (*Eschrichtius robustus*), (**i**) common bottlenose dolphins, (**j**) gray whales, (**k**) common bottlenose dolphins, (**l**) rough-toothed dolphins (*Steno bredanensis*). ♀ = female; ♂ = male

align themselves with a female and match her swim speed (Figs. 11.1a, 11.2a). Male dusky dolphins also leaped multiple times while in pursuit of females, which may function as a behavioral display; mating attempts may provide females with opportunities to assess potential suitors' characteristics such as swim speed and body size (Markowitz et al. 2010). Male gray whales also actively competed to be proximate to the female and copulate, pushing away other males and grasping the female with their flippers (Figs. 11.1a, 11.2b); a female gray whale may evaluate a male's ability to remain proximate to her. In rough-toothed dolphins, food sharing may have played a role in maintaining females nearby during copulation attempts (Ramos et al. 2021).

Alternatively, photogrammetric measurements of the size of individual males may help reveal mate choice driven by body characteristics of different possible mates (e.g., the choice of a large male). We did not consistently collect data on animal size, but future studies using drones equipped with a GPS/LiDAR sensor payload (e.g., Dawson et al. 2017) would enable precise measurements of male and female sizes to associate with behavioral data on individual success at copulation.

11.3.3.3 Polyestry and Multiple Matings

In some species and populations in which male cetaceans coerce females to mate, females may exert control over paternity through polyestrous cycling and multiple mating (Connor et al. 1996). Polyestry is hypothesized to obscure calf paternity, reduce sexual harassment, and prevent infanticide by conspecifics (Hrdy 1979; Connor et al. 1996; McEntee et al. 2023, this book). Repeated estrous cycles, coupled with limited periods of ovulation and mating with multiple males, may aid a female in siring the offspring of a desired mate while obscuring the paternity of her calf. Infanticide (intentional killing of non-descendent young) may induce lactating females to begin estrous cycling and thereby increase the potential for a male to sire an offspring (Hrdy 1979). Multiple species of dolphins commit infanticide (McEntee et al. 2023, this book).

Polyestry is a physiological mechanism and cannot be identified directly from drone observations. However, tracking individuals with drones paired with information on the estrous cycling of specific females could facilitate investigation of cetacean reproduction and heredity. Detailed behavioral observations of cetaceans during mating chases and infanticide attempts could be used to identify evidence of males driving specific non-receptive females into estrus (Table 11.3). Target populations require extensive photo-ID and life history information where observations of female choice of mates could be associated with behavioral data and genetic information on dolphins (Connor 2000).

Multiple matings were readily detectable from aerial drone observations with all species we observed, sometimes involving possible signaling of receptivity to copulation with one or multiple males at a time. In contrast to the ventrum-up orientation of female gray whales typically observed during evasive mating chases (Swartz 2018), the female we observed maintained a ventrum-down position during a mating chase, possibly indicating receptivity to the mating attempts by numerous competing males (Figs. 11.1d, 11.3). Male Risso's and rough-toothed dolphins individually approached females resulting in multiple mating attempts (Fig. 11.5). In Risso's dolphins and dusky dolphins, copulation attempts occur in quick succession with multiple males (Hartman et al. 2023, this book; Markowitz et al. 2023, this

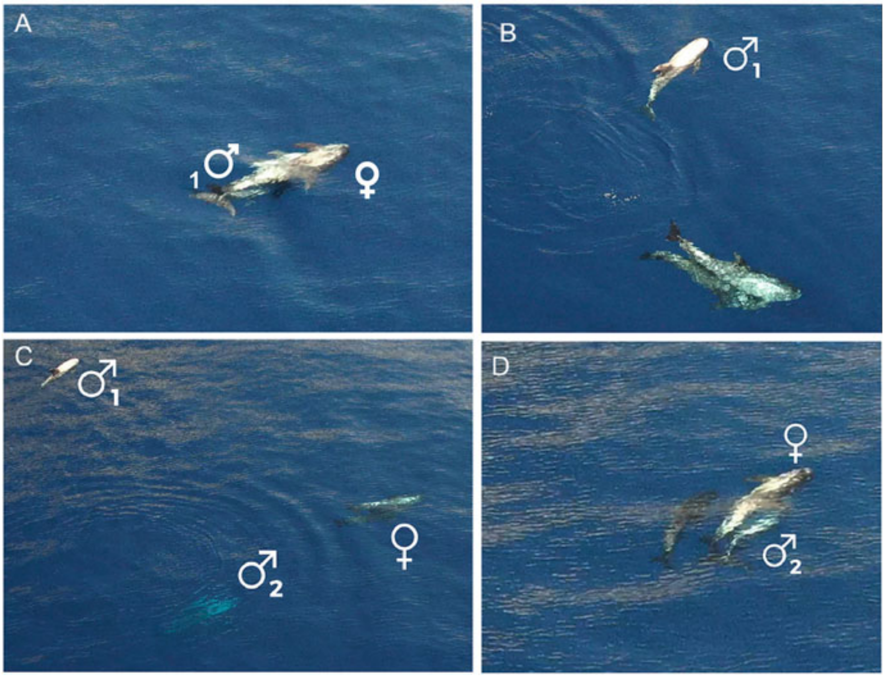

Fig. 11.5 One example from mutual mating in Risso's dolphins (*Grampus griseus*) captured by a drone in 2022 (Mavic Pro 2). (**a**) Copulation between Male 1 and female. (**b**) Male 1 leaves the female and her calf. (**c**) The distance increases between Male 1 and the female with her calf as Male 2 approaches. (**d**) Male 2 in mating position beneath the female with the calf nearby. ♀ = female; ♂ = male

book). Data on the estrous cycling of these species could be associated with drone-based mating observations to disentangle the dynamics of mating.

11.3.4 Male Cetacean Mating Tactics

Male cetaceans primarily use five competitive mating tactics: display, scramble, contest, endurance, and sperm competition. These tactics can be observed visually and are more amenable to drone-based studies compared to the covert tactics used by females (Table 11.3).

11.3.4.1 Display Competition

In display competition, males engage in courtship displays that use morphological or behavioral signals to attract the attention of females. These displays can reflect dominance, genetic quality, readiness to breed, and access to resources. For example, male humpback whales (*Megaptera novaeangliae*) have elaborate songs, and Amazon river dolphins (*Inia geoffrensis*) carry sticks (Martin et al. 2008; Allen et al. 2018). The improved vantage point provided by drones enables capturing rarely seen displays and allows for detailed tracking of male and female interactions, which is not possible from a boat perspective (Fig. 11.4).

Although we did not observe cetacean males displaying overt behaviors that were interpretable as evidence of display competition, males frequently pursued females with their penises extruded prior to attempting copulation. An everted penis may increase the chances of intromission when near a female and could also serve as a signal to females of readiness to mate (Keener et al. 2018). In gray whales, an extruded penis would likely be visible to females during mating chases and may partially explain why males maintained their erections while swimming in pursuit of females instead of only immediately prior to attempting intromission (Fig. 11.1d).

11.3.4.2 Contest Competition

Contest competition involves one or more males attempting to prevent other males from approaching reproductive females through aggression, sometimes escalating into violent intrasexual interactions (Tyack and Whitehead 1982; Orbach 2019). For some species, detailed and repeated observations of contest competition are available from boat-based studies (e.g., humpback whale competitive groups), as they typically occur near the surface and in clear water (Clapham et al. 1992). Common and Indo-Pacific bottlenose dolphins in many populations display aggression and violent behavior during male-male competition and sexual coercion, typically resulting in dolphins biting each other and leaving extensive tooth rake markings across bodies (Connor et al. 2006). Similar aggressive male-male interactions are reported in Risso's dolphins, including headbutting (Hartman et al. 2023, this book).

Intense competition among males was seen in multiple species we examined based on drone footage. Several male common bottlenose dolphins and Risso's dolphins engaged in aggressive exchanges with each other in the presence of a single female being pursued. Two male bottlenose dolphins in a group of eight engaged in repeated head-on charges, during which both males had their mouths open and attempted to hit each other with their flukes while passing each other (Fig. 11.4k). Multiple competing male gray whales repeatedly interfered with the copulation attempts of other males by using their rostrums to wedge between rivals and the female and pushing the competing male out of the way while occupying its previous position (Fig. 11.4j).

11.3.4.3 Endurance Competition

In endurance competition, multiple males attempt to outlast their competitors for durations long enough to cause major energetic and temporal costs. Male

Indo-Pacific bottlenose dolphins in Shark Bay, Australia, work with alliance members to sequester and isolate the female for up to several months and aggressively copulate with her (Connor et al. 1992). Allied males coordinate to "herd" a female and restrain her movements by producing loud and threatening "pop" sounds (Smolker and Connor 1996) and aggressively charging, biting, and colliding with her. Alliance formation among bottlenose dolphins is reviewed in this book (Brightwell and Gibson 2023, this book) as is endurance competition in Risso's dolphins (Hartman et al. 2023, this book).

We observed common bottlenose dolphins engaged in sociosexual behaviors in small (group size = 3) to large groups (group size = 16); some included male cooperative mate guarding and herding of females and intense aggressive fights between multiple males competing for access to the female (Fig. 11.6). Mating behaviors frequently involved high-energy chases of females and frequent surface displays (Fig. 11.6).

11.3.4.4 Scramble Competition

Scramble competition manifests as males rapidly finding and mating with as many reproductively ready females as possible over a short time. Males fight for the closest position to the reproductively ready female to mate with her, providing her opportunities to exert selection over mates during extended chases (Clapham et al. 1992). During scramble competition, male cetaceans typically engage in energetic chases or surface displays in pursuit of females, changing their swimming speed and direction frequently and incurring energetic costs for both sexes (Orbach et al. 2014). For example, groups of four sexually mature male dusky dolphins typically chased a single female for 10 minutes (Orbach et al. 2015).

In our data, evidence of scramble competition was most salient in mating interactions of dusky dolphins. Dusky dolphin males engage in high-speed chases and rapid copulation attempts with a target female, often including surface-active behaviors and leaps. Male gray whales display numerous behaviors associated with scramble competition. Most baleen whales, including humpback whales and North Atlantic right whales, migrate to breeding grounds annually (Clapham et al. 1992; Kraus and Hatch 2001). Similarly, gray whales are commonly observed in surface-active groups engaging in vigorous sexual activity during their breeding season. Drone footage captured many surface-active groups including multiple gray males simultaneously pursuing a single female (Fig. 11.4h, j). It is unclear from our observations alone if multiple males pursue multiple females over short times in the other four species of cetacean we observed, as most observations involved a single female pursued by multiple males. In Risso's dolphins, scramble competition filmed with a drone showed that not all males participating during a chase were able to mate or obtain access to a female.

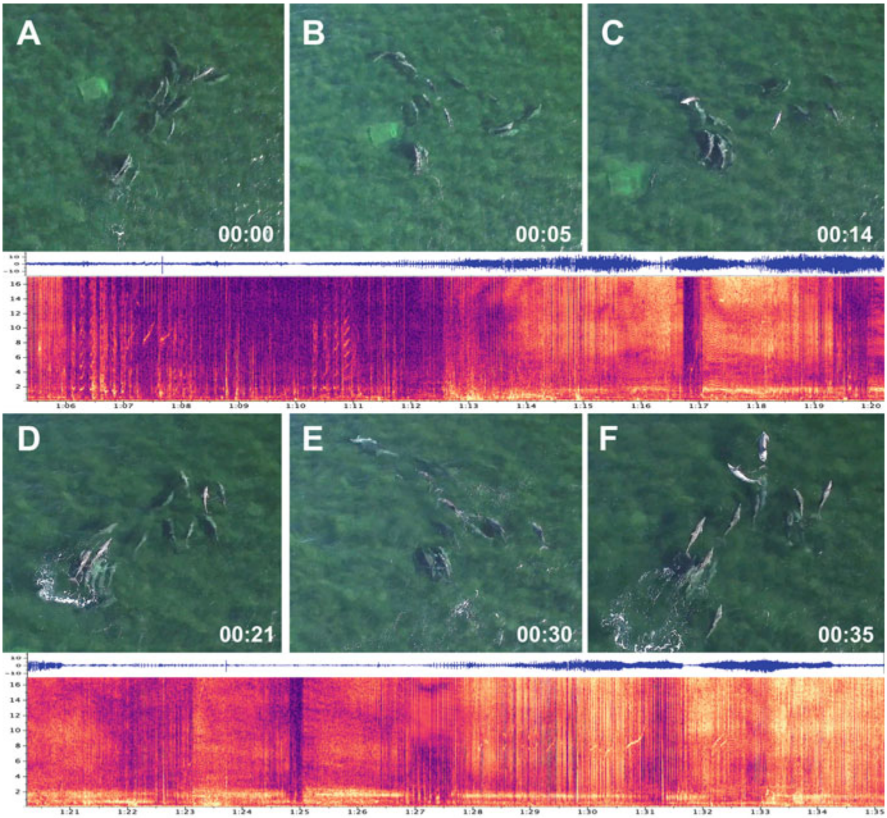

Fig. 11.6 Aerial drone observations of common bottlenose dolphins (*Tursiops truncatus*) engaged in sociosexual behavior during concurrent boat-based acoustic recordings of their sounds. (**a–f**) The interactions involved active chases, surface displays, numerous copulation attempts, and aggressive intrasexual interactions among 16 dolphins. The timestamps are in mm: ss. The waveform and spectrograms below the panels depict the sounds recorded during this 35 second clip, primarily consisting of the vocalizations of dolphins (bright orange). Sounds were graphed using Raven 1.6.3 (K. Lisa Yang Center for Conservation Bioacoustics 2023)

11.4 New Mating Behaviors Documented via Drone

Drones hold immense potential to capture new mating behaviors among cetaceans. Continuous observations of cetacean mating interactions revealed a variety of behaviors that were previously undetected from a boat or any other platform of observation. For example, a rough-toothed dolphin that copulated repeatedly with a female displayed an open mouth behavior, moving its jaw up and down with its mouth agape while aligned perpendicularly with the female (Fig. 11.4l); the open mouth behavior occurred eight times within 12 minutes of video footage during a single focal follow, indicating it may be commonly associated with mating in this species or population. Open mouth displays may signal threats to the female, as open mouth behaviors have typically been reported during agonistic interactions between conspecifics and heterospecifics in multiple species of cetaceans (Herzing 1996). The use of open mouth behaviors during copulation attempts could signal to the female potential negative consequences of resisting copulation attempts or signal to other nearby males to stay away.

We documented a variety of mating behaviors involving close physical contact between animals at the surface and subsurface. For example, male gray whales regularly used their pectoral flippers to grasp the female across her peduncle, appearing to slow her movement and prevent evasion (Fig. 11.4h). Similar behaviors were observed in multiple bottlenose dolphin males sandwiching a female between them (Figs. 11.1b, 11.4g) and during individual male approaches in pygmy killer whales (Fig. 11.2f). Grasping behavior may function to constrain female evasion, prevent copulations from rival males by limiting access to the female, be part of a male display to the female or other male, or aid in intromission by enabling the male to direct its penis more effectively toward the female's genital slit (Fig. 11.1d). Male cetaceans may orient their bodies in specific positions to align their genitalia with females as physical alignment of genitalia at specific angles is essential for high likelihood of fertilization success (Orbach et al. 2020a).

In gray whales, common bottlenose dolphins, and pygmy killer whales, we observed males repeatedly nuzzling their rostra against the genital region of females and engaging in close physical contact with females; these sociosexual behaviors may play an important role in mating and were detected because of the overhead view from the drone coupled with high-resolution video recording. Clitoral stimulation is likely pleasurable to common bottlenose dolphins (Brennan et al. 2022). Dolphins of other species and populations engage in genital stimulation, sometimes coupled with a buzzing with the melon against the genital area of a conspecific (Herzing 1996). Dolphin echolocation sounds have high energy, which could provide extensive vibration and stimulation of the genitals.

11.5 Understanding Sound Production and Mating Behavior

The sounds produced by cetaceans can play an important role in mating and reproduction, sometimes functioning in sexual displays and competition (Clapham et al. 1992). During cooperative mate herding, pairs of male Indo-Pacific bottlenose dolphins consort females through aggression and produce "pop" vocalizations that threaten her to stay close (Smolker and Connor 1996; Vollmer et al. 2015). Associating specific sounds with behavior and attributing calls to specific individuals are often limited to classifying behaviors of individuals or a group during brief surfacings and comparing these with recorded sounds (Tyack 2000). Drones provide a valuable observational tool to identify behaviors associated with acoustic production in cetaceans and enhance our ability to contextualize the use of different sounds. Drones used to observe dolphin behavior during acoustic playback experiments have enhanced understandings of social associations of male Indo-Pacific bottlenose dolphins (King and Jensen 2022). Concurrent flights of multiple drones, some equipped with passive acoustic recorders (Frouin-Mouy et al. 2020), are a promising area of future research to associate acoustic sounds with mating specific behaviors.

We demonstrate an example of acoustic recordings of the vocalizations of a group of 16 common bottlenose dolphins with concurrent aerial observations in the lagoons of Turneffe Atoll, Belize, on August 1, 2016. An SQ26-08 (Cetacean Research Technology) hydrophone was suspended 1 m under the water's surface from the boat, recording to a Tascam DR-05 digital recorder with a 96 kHz sample rate in 16-bit to WAV format files. Spectrograms of acoustics recordings were reviewed by EAR in Raven 1.6.3 (K. Lisa Yang Center for Conservation Bioacoustics 2023) to identify and classify dolphin vocalizations as tonal whistles, burst-pulse calls, or echolocation clicks (Tyack 2000).

The bottlenose dolphins engaged in vigorous mating and sociosexual behavior throughout multiple flights (Fig. 11.6). Numerous dolphins pursued a single individual within the group (possibly a female), swimming fast to stay close to each other as the group collectively turned in the same direction (Fig. 11.6a). Half of the group appeared to pursue the single dolphin, while the other half oriented toward the possible mating chase (Fig. 11.6c). The fleeing dolphin leaped several times (Fig. 11.6d) and accelerated to swim ahead of its pursuers close behind (Fig. 11.6e).

We plotted the waveform and spectrogram of a 35 second clip of sounds recorded in the time series of aerial imagery of the dolphin group (Fig. 11.6). Multiple dolphins produced longs bouts of low- and high-frequency burst-pulse signals, repeated bouts of echolocation clicks, and numerous frequency-modulated narrow-band whistles (Fig. 11.6). Several low-frequency sounds have been associated with allied male bottlenose dolphin aggression toward females during consortships, such as "pops" (Smolker and Connor 1996; King et al. 2019; Casoli et al. 2022), and with attempted infanticides perpetrated by males (Perrtree et al. 2016).

The above observations illustrate the power of aerial drone video to identify the surface and subsurface activity of cetacean mating groups associated with their sound production. For instance, most of the bottlenose dolphins recorded were completely underwater during our observations and largely out-of-sight to surface observers (Fig. 11.6). Paired subsurface observations and underwater recordings of animal sounds provide a previously unattainable capacity to identify the behavioral context of sound production.

11.6 Conclusions

The improvement of our understanding of the diversity of mating strategies, tactics, and behaviors that evolved across whales, dolphins, and porpoises encourages the development of novel methods to quantify animal behavior in nature. We demonstrate how drone-based imaging can be applied to the study of sociosexual and mating behavior of free-ranging cetaceans, providing increased observational power in capturing behavior and enabling detailed animal tracking. The inclusion of aerial drones as a data collection tool allows for unparalleled views of animals, their behavior, and collection of robust video and imagery for multiple uses. The use of drones for observing the behavior of cetaceans paired with traditional methods of field data collection and laboratory analyses has the potential to help contextualize the activities of rarely observed species and optimize limited surface times with difficult to study species. Advancements in drone and imaging technologies continue to rapidly improve the flight time and resolution of imagery while decreasing in costs; growing commercial popularity makes drone purchases and use more available to the global community of scientists.

Acknowledgments The authors thank the New Zealand dusky dolphin research team consisting of Lorenzo Fiori, Bernd Würsig, Melany Würsig, Jody Weir, and Sarah Piwetz. We thank the teams that assisted in field work in Belize and Mexico. Thanks to Diana Reiss and Marcelo O. Magnasco for supporting research and data collection at Turneffe Atoll. We thank Katherina Audley and the Whales of Guerrero for their efforts in gathering rough-toothed dolphin data examples. We thank the team at Cascadia Research Collective and everyone who participated in research with pygmy killer whales in Hawaiian waters. We thank the Nova Atlantis team, in particular drone pilots Pieter van der Harst and Martijn van Schie. All data were gathered under permits from respective governments. In Belize, research was permitted by the Forest and Fisheries Departments and the Civil Aviation Authority. In Mexico, research was permitted by the Mexican government, SEMARNAT, and CONANP. In New Zealand, research was permitted by the Department of Conservation and Kaikoura Runanga. In the Azores, research was permitted by the Regional Secretariat of the Sea, Science and Technology. In Hawai'i, research was permitted by the Office of Protected Resources, National Marine Fisheries Service. We thank Bernd Würsig and Lorenzo Fiori for helpful edits.

References

Abràmoff MD, Magalhães PJ, Ram SJ (2004) Image processing with image. J Biophotonics Int 11(7):36–42

Allen JA, Garland EC, Dunlop RA, Noad MJ (2018) Cultural revolutions reduce complexity in the songs of humpback whales. Proc R Soc Lond B 285(1891):20182088

Angliss RP, Ferguson MC, Hall P, Helker V, Kennedy A, Sformo T (2018) Comparing manned to unmanned aerial surveys for cetacean monitoring in the Arctic: methods and operational results. J Unman Veh Sys 6(3):109–127

Baird RW, Mahaffy SD, Lerma JK (2022) Site fidelity, spatial use, and behavior of dwarf sperm whales in Hawaiian waters: using small-boat surveys, photo-identification, and unmanned aerial systems to study a difficult-to-study species. Mar Mamm Sci 38(1):326–348

Bender CE, Herzing DL, Bjorklund DF (2009) Evidence of teaching in Atlantic spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their calves. Anim Cogn 12(1):43–53

Boness DJ, Clapham PJ, Mesnick SL (2002) Life history and reproductive strategies. In: Hoelzel AR (ed) Marine mammal biology: an evolutionary approach. Blackwell Science, Oxford, pp 278–324

Brennan PL, Cowart JR, Orbach DN (2022) Evidence of a functional clitoris in dolphins. Curr Biol 32(1):R24–R26

Brightwell K, Gibson Q (2023) Inter- and intra-population variation in bottlenose dolphin mating strategies. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

Brown MW, Sironi M (2023) Right whale sexual strategies and behavior. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

Casoli M, Johnson M, McHugh KA, Wells RS, Tyack PL (2022) Parameterizing animal sounds and motion with animal-attached tags to study acoustic communication. Behav Ecol Sociobiol 76(4):1–21

Centelleghe C, Carraro L, Gonzalvo J, Rosso M, Esposti E, Gili C, Bonato M, Pedrotti D, Cardazzo B, Povinelli M, Mazzariol S (2020) The use of unmanned aerial vehicles (UAVs) to sample the blow microbiome of small cetaceans. PLoS One 15(7):e0235537

Christiansen F, Dujon AM, Sprogis KR, Arnould JP, Bejder L (2016) Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales. Ecosphere 7(10):e01468

Clapham PJ, Palsbøll PJ, Mattila DK, Vasquez O (1992) Composition and dynamics of humpback whale competitive groups in the West Indies. Behaviour 122:182–194

Clutton-Brock T, McAuliffe BK (2009) Female mate choice in mammals. Q Rev Biol 84(1):3–27

Cole TV, Hamilton P, Henry AG, Duley P, Pace RM III, White BN, Frasier T (2013) Evidence of a North Atlantic right whale *Eubalaena glacialis* mating ground. Endang Spec Res 21(1):55–64

Connor RC (2000) Group living in whales and dolphins. In: Whitehead H, Mann J, Tyack PL, Connor RC (eds) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, IL, pp 199–218

Connor RC, Smolker RA, Richards AF (1992) Two levels of alliance formation among male bottlenose dolphins (Tursiops sp.). Proc Natl Acad Sci 89(3):987–990

Connor RC, Richards AF, Smolker RA, Mann J (1996) Patterns of female attractiveness in Indian Ocean bottlenose dolphins. Behaviour 133(1–2):37–69

Connor R, Mann J, Watson-Capps J (2006) A sex-specific affiliative contact behavior in Indian Ocean bottlenose dolphins, *Tursiops* sp. Ethology 112(7):631–638

Connor RC, Cioffi WR, Randić S, Allen SJ, Watson-Capps J, Krützen M (2017) Male alliance behaviour and mating access varies with habitat in a dolphin social network. Sci Rep 7(1):1–9

Darwin C (1871) The descent of man and selection in relation to sex, 2nd edn. J. Murray, London

Dawson SM, Bowman MH, Leunissen E, Sirguey P (2017) Inexpensive aerial photogrammetry for studies of whales and large marine animals. Front Mar Sci 4:366

Dines JP, Mesnick SL, Ralls K, May-Collado L, Agnarsson I, Dean MD (2015) A trade-off between precopulatory and postcopulatory trait investment in male cetaceans. Evolution 69(6): 1560–1572

Fettermann T, Fiori L, Gillman L, Stockin KA, Bollard B (2022) Drone surveys are more accurate than boat-based surveys of bottlenose dolphins (*Tursiops truncatus*). Drones 6(4):82

Fiori L, Martinez E, Orams MB, Bollard B (2020) Using unmanned aerial vehicles (UAVs) to assess humpback whale behavioral responses to swim-with interactions in Vava'u, Kingdom of Tonga. J Sust Tour 28(11):1743–1761

Friard O, Gamba M (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Meth Ecol Evol 7(11):1325–1330

Frouin-Mouy H, Tenorio-Hallé L, Thode A, Swartz S, Urbán J (2020) Using two drones to simultaneously monitor visual and acoustic behaviour of gray whales (*Eschrichtius robustus*) in Baja California. Mexico J Exp Mar Biol Ecol 525:151321

Furuichi T, Connor R, Hashimoto C (2014) Non-conceptive sexual interactions in monkeys, apes, and dolphins. In: Yamagiwa J, Karczmarski L (eds) Primates and cetaceans. Springer, Tokyo, pp 385–408

Giles AB, Butcher PA, Colefax AP, Pagendam DE, Mayjor M, Kelaher BP (2021) Responses of bottlenose dolphins (*Tursiops* spp) to small drones. Aqua Cons Mar Freshw Ecosyst 31(3):677–684

Glabicky N, DuBrava A, Noonan M (2010) Social–sexual behavior seasonality in captive beluga whales (*Delphinapterus leucas*). Polar Biol 33(8):1145–1147

Ham JR, Lilley MK, Manitzas Hill HM (2023) In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

Hartman K, Van der Harst P, Vilela R (2020) Continuous focal group follows operated by a drone enable analysis of the relation between sociality and position in a group of male Risso's dolphins (*Grampus griseus*). Front Mar Sci 7:283

Hartman KL, van der Harst PA, Vilela R (2023) Sex and sexual strategies in deep diving Risso's dolphins. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

Herzing DL (1996) Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis,* and bottlenose dolphins, *Tursiops truncatus*. Aqua Mamm 22:61–80

Hill HM, de Oliveira Silva-Gruber DG, Noonan M (2018) Sex-specific social affiliation in captive beluga whales (*Delphinapterus leucas*). Aqua Mamm 44(3):250–255

Hill HM, Ham JR, Lilley MK (2022) Observations of mating practice by non-non-sexually mature male belugas (*Delphinapterus leucas*). Aqua Mamm 48(6):541–546

Hrdy SB (1979) Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethol Sociobio 1(1):13–40

K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology. (2023). Raven Pro: Interactive Sound Analysis Software (Version 1.6.4) [Computer software]. Ithaca, NY: The Cornell Lab of Ornithology. Available from https://ravensoundsoftware.com/

Keener W, Webber MA, Szczepaniak ID, Markowitz TM, Orbach DN (2018) The sex life of harbor porpoises: male lateralized and aerial behavior. Aqua Mamm 44(6):620–632

King SL, Jensen FH (2022) Rise of the machines: integrating technology with playback experiments to study cetacean social cognition in the wild. Meth Ecol Evol. https://doi.org/10.1111/2041-210X.13935

King SL, Allen SJ, Krützen M, Connor RC (2019) Vocal behaviour of allied male dolphins during cooperative mate guarding. Anim Cogn 22(6):991–1000

Kingsley MCS, Reeves RR (1998) Aerial surveys of cetaceans in the Gulf of St. Lawrence in 1995 and 1996. Can J Zool 76(8):1529–1550

Koski WR, Gamage G, Davis AR, Mathews T, LeBlanc B, Ferguson SH (2015) Evaluation of UAS for photographic re-identification of bowhead whales, *Balaena mysticetus*. J Unman Veh Sys 3(1):22–29

Kraus SD, Hatch JJ (2001) Mating strategies in the North Atlantic right whale (*Eubalaena glacialis*). J Cetacean Res Manag 2:237–244

Landeo-Yauri SS, Castelblanco-Martínez DN, Hénaut Y, Arreola MR, Ramos EA (2021) Behavioural and physiological responses of captive Antillean manatees to small aerial drones. Wild Res 49(1):24–33

Lanyon JM, Burgess EA (2014) Methods to examine reproductive biology in free-ranging, fully-marine mammals. In: Holt W, Brown J, Comizzoli P (eds) Reproductive sciences in animal conservation. Advances in experimental medicine and biology, vol 753. Springer, New York, NY, pp 241–274

Lonati GL, Hynes NJ, Howe KR, Durette-Morin D, Brown MW, Davies KTA (2022) Observations of adult–calf nonreproductive copulatory behavior in North Atlantic right whales (*Eubalaena glacialis*). Aqua Mamm 48(6):639–645

Manitzas Hil HM, Dudzinski KM, Lilley MK, Ham JR (2023) In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

Mann J (1999) Behavioral sampling methods for cetaceans: a review and critique. Mar Mamm Sci 15(1):102–122

Markowitz TM, Markowitz WJ, Morton LM (2010) Mating habits of New Zealand dusky dolphins. In: Würsig B, Würsig M (eds) The dusky dolphin. Academic Press, pp 151–176

Markowitz T, Markowitz W, Würsig B, Orbach DN (2023) Socio-sexual behavior of nocturnally foraging dusky and spinner dolphins. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

Martin AR, Da Silva VM, Rothery P (2008) Object carrying as socio-sexual display in an aquatic mammal. Biol Lett 4(3):243–245

McEntee M, MacQueeney M, Alvarado D, Mann J (2023) Infanticide and sexual conflict in cetaceans. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

Miketa ML, Patterson EM, Krzyszczyk E, Foroughirad V, Mann J (2018) Calf age and sex affect maternal diving behaviour in Shark Bay bottlenose dolphins. Anim Behav 137:107–117

Nowacek DP, Christiansen F, Bejder L, Goldbogen JA, Friedlaender AS (2016) Studying cetacean behaviour: new technological approaches and conservation applications. Anim Behav 120:235–244

Orbach DN (2016) Mating strategies of female cetaceans. PhD thesis, Texas A & M University at Galveston. https://hdl.handle.net/1969.1/156924

Orbach DN (2019) Sexual strategies: male and female mating tactics. In: Würsig B (ed) Ethology and behavioral ecology of odontocetes. Springer Nature, Cham, pp 75–93

Orbach DN, Packard JM, Würsig B (2014) Mating group size in dusky dolphins (*Lagenorhynchus obscurus*): costs and benefits of scramble competition. Ethology 120(8):804–815

Orbach DN, Packard JM, Kirchner T, Würsig B (2015) Evasive behaviours of female dusky dolphins (*Lagenorhynchus obscurus*) during exploitative scramble competition. Behaviour 152(14):1953–1977

Orbach DN, Brennan PL, Hedrick BP, Keener W, Webber MA, Mesnick SL (2020a) Asymmetric and spiraled genitalia coevolve with unique lateralized mating behavior. Sci Rep 10(1):1–8

Orbach DN, Eaton J, Fiori L, Piwetz S, Weir JS, Würsig M, Würsig B (2020b) Mating patterns of dusky dolphins (*Lagenorhynchus obscurus*) explored using an unmanned aerial vehicle. Mar Mamm Sci 36(4):1097–1110

Orbach DN, Gorter U, Mesnick SL (2023) Sexual anatomy of female cetaceans: art and science contribute insights into functionality. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

Perrtree RM, Sayigh LS, Williford A, Bocconcelli A, Curran MC, Cox TM (2016) First observed wild birth and acoustic record of a possible infanticide attempt on a common bottlenose dolphin (*Tursiops truncatus*). Mar Mamm Sci 2(1):376–385

Pirotta V, Hocking DP, Iggleden J, Harcourt R (2022) Drone observations of marine life and human–wildlife interactions off Sydney, Australia. Drones 6(3):75

Ramos EA, Maloney B, Magnasco MO, Reiss D (2018) Bottlenose dolphins and Antillean manatees respond to small multi-rotor unmanned aerial systems. Front Mar Sci 5:316

Ramos EA, Kiszka JJ, Pouey-Santalou V, Ramirez Barragan R, Garcia Chavez AJ, Audley K (2021) Food sharing in rough-toothed dolphins off southwestern Mexico. Mar Mamm Sci 37(1):352–360

Randić S, Connor RC, Sherwin WB (2012) A novel mammalian social structure in Indo-Pacific bottlenose dolphins (*Tursiops* sp.): complex male alliances in an open social network. Proc R Soc Lond B 279(1740):3083–3090

Raoult V, Colefax AP, Allan BM, Cagnazzi D, Castelblanco-Martínez N, Lerodiaconou D, Johnston DW, Landeo-Yauri S, Lyons M, Pirotta V, Schofield G (2020) Operational protocols for the use of drones in marine animal research. Drones 4(64):1–35

Raudino HC, Tyne JA, Smith A, Ottewell K, McArthur S, Kopps AM, Chabanne D, Harcourt RG, Pirotta V, Waples K (2019) Challenges of collecting blow from small cetaceans. Ecosphere 10(10):e02901

Sanvito S, Galimberti F (2022) Male–male sexual interactions between an adult and a calf killer whale (*Orcinus orca*) of the Falkland Islands. Aqua Mamm 48(6):759–763

Schaeff CM (2007) Courtship and mating behavior. In: Miller DL (ed) Reproductive biology and phylogeny of cetacea: whales, dolphins, and porpoises. Science Publishers, Enfield, NH, pp 349–370

Smolker RA, Connor RC (1996) 'Pop' goes the dolphin: a vocalization male bottlenose dolphins produce during consortships. Behaviour 133(9–10):643–662

Smultea MA, Lomac-MacNair K, Nations CS, McDonald T, Würsig B (2018) Behavior of Risso's dolphins (*Grampus griseus*) in the Southern California bight: an aerial perspective. Aqua Mamm 44(6):653–667

Swartz SL (2018) Gray whale: *Eschrichtius robustus*. In: Würsig B, Thewissen JGM, Kovacs K (eds) Encyclopedia of marine mammals, 3rd edn. Academic Press, London, pp 423–428

Torres LG, Bird CN, Rodríguez-González F, Christiansen F, Bejder L, Lemos L, Urban J, Swartz S, Willoughby A, Hewitt J, Bierlich KC (2022) Range-wide comparison of gray whale body condition reveals contrasting sub-population health characteristics and vulnerability to environmental change. Front Mar Sci 511

Trivers RL (1972) Parental investment and sexual selection. In: Campbell BG (ed) Sexual selection and the descent of man 1871–1971. Aldine, Chicago, IL, pp 136–179

Tyack PL (2000) Cetacean communication. In: Whitehead H, Mann J, Tyack PL, Connor RC (eds) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, IL, pp 270–208

Tyack P, Whitehead H (1982) Male competition in large groups of wintering humpback whales. Behaviour 83(1–2, 132):–154

Vollmer NL, Hayek LA, Heithaus MR, Connor RC (2015) Further evidence of a context-specific agonistic signal in bottlenose dolphins: the influence of consortships and group size on the pop vocalization. Behaviour 152(14):1979–2000

Webber MA, Keener W, Wahlberg M, Elliser CR, MacIver K, Torres Ortiz S, Jakobsen F, Hamel H, Rieger A, Siebert U, Dunn H, Anderson D, Hall AM, Birdsall C, Pielmeier K, Paiu RM, Boege Tobin DD, Orbach DN (2023) Sexual behavior and anatomy in porpoises. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

Whitehead H, Mann J (2000) Female reproductive strategies of cetaceans. In: Whitehead H, Mann J, Tyack PL, Connor RC (eds) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, IL, pp 219–246

Würsig B, Rich J, Orbach DN (2023) Sex and behavior. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham