

Chapter 14

Sociosexual Behavior of Nocturnally Foraging Dusky and Spinner Dolphins



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Abstract Dusky and spinner dolphins are small-bodied odontocetes that show variation in socioecology across their range. New Zealand dusky dolphins and Hawaiian spinner dolphins of deep nearshore waters feed nocturnally upon prey species associated with the deep scattering layer, leaving the daytime free for rest and social interaction, often close to shore. In this chapter, we investigate relationships between foraging ecology, diel activity patterns, and sociosexual activities of dusky and spinner dolphins in breeding and nonbreeding contexts. We review similarities and differences between dusky and spinner dolphins related to mating strategies and tactics, socioecology, and evolution. We examine the effects of breeding season and variation in male testis mass and female receptivity on mating behavior. We further explore the influence of sociosexual behavior on female social grouping and calf rearing.

Keywords Dusky dolphin · Female choice · Hawai'i · Male-male competition · Mating behavior · New Zealand · Socioecology · Sociosexual · Spinner dolphin

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14.1 Introduction

Animal ecology profoundly influences social structure and reproduction (Clutton-Brock and Harvey 1977; Emlen and Oring 1977; Trivers 1985; Clutton-Brock 2016). Environmental factors affect animal social grouping patterns and behavior (Vehrencamp 1983; Kappeler and van Schaik 2002). Cetacean social structures have evolved in different ecological circumstances, resulting in intraspecific and intra-population variability in response to environmental challenges and opportunities (Bearzi and Stanford 2007). Odontocete mating systems, sexual behavior, and reproductive strategies are often a result of evolutionary history and environmental pressures (Norris and Schilt 1988; Whitehead and Mann 2000; Gowans et al. 2007; Orbach 2019). Spatiotemporal variation in prey availability and/or predation pressure can influence cetacean group size (Wells et al. 1999) as well as social unit size in fission-fusion societies (Dunbar 1992). Norris (1994) described dolphin socioecology in terms of dynamic social and behavioral responses to environmental changes. For dolphins, spatial and temporal predictability of resources and predation pressure are important drivers influencing group size, social structure, and mating interactions (Wells et al. 1999; Gowans et al. 2007; Acevedo-Gutiérrez 2009; Würsig et al. 2023, this book). Socioecological interactions of dolphins occur in three-dimensional space, perhaps with similarities to small primates that live in the three-dimensional rainforest canopy (Würsig and Pearson 2014). Much can be learned about delphinid sociality and evolutionary ecology by comparing behavior and mating systems among species living in similar or different habitats (Würsig and Pearson 2015). Herein, we compare and contrast the sociosexual behavior of spinner dolphins (*Stenella longirostris*) of Hawai'i and dusky dolphins (*Lagenorhynchus obscurus*) of New Zealand.

Despite living in different hemispheres and being connected by only distantly shared ancestry, Hawaiian spinner dolphins and New Zealand dusky dolphins have much in common. Both are small-bodied odontocetes ranging in length from 1.4 m to just over 2 m (Table 14.1), with spinner dolphins slightly larger than dusky dolphins. Dusky dolphins and Hawaiian spinner dolphins show little sexual size dimorphism, with maximum length at maturity varying <5% between the sexes for

Table 14.1 Reproductive life history parameters of spinner and dusky dolphins^a

Parameter	Hawaiian spinner dolphin	New Zealand dusky dolphin
Gestation length	10.7 months	11.4 months
Lactation duration	15–18 months	18 months
Calving season	Spring-fall	Spring-summer
Age at first reproduction	7 years	7–8 years
Size at birth	0.77 m	0.97–1.02 m
Size of adults	Female, 1.39–2.04 m Male, 1.60–2.08 m	Female, 1.60–1.78 m Male, 1.65–1.86 m

^aFrom: Norris and Dohl (1980), Leatherwood and Reeves (1983), Cipriano (1992), Würsig et al. (1997), Jefferson et al. (2015)



Fig. 14.1 A female dusky dolphin (left) engages in a high headfirst reentry leap, followed closely by a male dolphin (right) with penis extended. Dusky dolphins have minimal sexual dimorphism, with the male often leaping second during a chase. (Photo by: B. Würsig)

both species (dusky dolphins 4%, spinner dolphins 2%; Table 14.1). These two dolphin species live in large, fission-fusion societies and demonstrate considerable behavioral flexibility (Lammers 2019; Pearson 2019). They share similar life history traits with respect to reproduction, including age at first reproduction, gestation length, size of newborns relative to adults, and age at weaning (Table 14.1). Both species are also known for their aerial behaviors such as acrobatic head-over-tail leaps in dusky dolphins (Würsig et al. 1994, 1997) and spins along the body axis in spinner dolphins (Norris and Dohl 1980). Backslaps, tail slaps, and nose-out behaviors are also exhibited in small and large groups of dusky and spinner dolphins (Norris and Dohl 1980; Würsig and Würsig 1980; Norris et al. 1994; Markowitz 2004). Headfirst reentry leaps by dusky dolphins are commonly associated with feeding and mating behavior (Markowitz et al. 2004, 2010; Fig. 14.1). Similar arched leaps occur in spinner dolphins (Norris et al. 1994) but are not as commonly described in the context of mating interactions (Norris and Dohl 1980).

Spinner dolphins along the coast of the Big Island of Hawai'i and dusky dolphins along the coast of Kaikoura, New Zealand, are similar in their foraging ecology and diel activity patterns. Both species feed nocturnally upon prey associated with the deep scattering layer in deep nearshore waters, leaving the daytime free for resting, social interactions, and very rare feeding close to shore (Würsig et al. 1994, 1997;

Markowitz 2004). Diurnal use of nearshore habitats by these two populations is particularly conducive to the study of sociosexual interactions, which are readily observed during the daytime, especially during the breeding season. We review research from the past 40 years on the sociosexual behavior of spinner and dusky dolphins, highlighting commonalities and differences within and between the species.

14.2 Mating Systems: Anatomical, Behavioral, and Social Context

Much can be inferred about the mating systems of cetaceans, particularly the degree and form of male-male competition, based on relative testis mass and sexual size dimorphism (Dines et al. 2015). Among spinner dolphins, divergent sexual selection based on differences in mating systems may be an evolutionary force driving population subdivision (e.g., between ecotypes in the Eastern Tropical Pacific; Andrews et al. 2021). Anatomical comparisons based on sexual size dimorphism and testis mass suggest variability in mating systems among different populations of spinner dolphins (Perrin and Mesnick 2003). For example, spinner dolphins of the Eastern Tropical Pacific (presently listed as *Stenella longirostris orientalis* and *S. l. centroamericana*) exhibit sexual dimorphism. Small relative testis mass and sperm content are associated with forward-canted dorsal fins and an enlarged postanal hump, indicating polygynous mating with aggressive male-male behavioral competition (Perrin and Mesnick 2003). In contrast, the Gray's spinner dolphins (*S. l. longirostris*), the most common worldwide form, are characterized by relatively large testis mass (>700 g) and a lack of marked sexual dimorphism. The latter characteristics are indicative of sperm competition and a polygynandrous mating system (multi-mate for both sexes) with less aggressive male-male behavioral competition than those of the Eastern forms. Gray's spinner dolphins include the Hawaiian and whitebelly spinner dolphin. The whitebelly spinner dolphin is an intermediate form between those with less sexual dimorphism and is presently not recognized as a subspecies (Perrin and Mesnick 2003; Lammers 2019). Observations of multiple partners mating in small groups of just a few individuals and in large groups of dozens of individuals appear to support polygynandry in these latter spinner dolphin forms (Norris and Dohl 1980; Norris 1994).

Although dusky dolphins show some variation in body size among populations, they do not display the evident sexual size dimorphism characterizing some spinner dolphin populations. Adult male dusky dolphins have somewhat different dorsal fin morphology than adult females. Male dorsal fins appear larger, thicker, and more curved than female dorsal fins (Van Waerebeek and Würsig 2009). Male dusky dolphins have exceptionally large testes for their body size. The maximum reported testis mass (5120 g) and high ratio of testis-to-body mass (0.085) in sexually mature males are one of the highest of any mammal. The large testis-to-body mass ratio



Fig. 14.2 Dusky dolphins copulating belly-to-belly at the surface, with the male underneath and the female on top. The characteristic “U-shaped” position is held by the female at the surface during copulation (Photos by W.J. Markowitz)

indicates an important role for sperm competition (Cipriano 1992; Van Waerebeek and Read 1994). Although lower than the maximum testis mass of dusky dolphins, the maximum testes mass of Gray’s (whitebelly) spinner dolphin (1354 g) also indicates a role for sperm competition (Perrin and Mesnick 2003).

Behavioral field observations of spinner and dusky dolphins indicate that although aggressive interactions occur between males in a mating context, they are relatively rare when compared to other delphinid species; for example, common bottlenose dolphins (*T. truncatus*) routinely engage in physically aggressive contest competition (Johnson and Norris 1994; Markowitz et al. 2010; Markowitz 2012; Orbach 2019). This does not mean, however, that these smaller-bodied, low aggression spinner and dusky dolphins are non-discriminate breeders. Field observations indicate polygynandrous mating systems for Hawaiian spinner and New Zealand dusky dolphins. Mating tactics include postcopulatory sperm competition and precopulatory male-male competition, such as scramble competition (Johnson and Norris 1994; McOmber 1999; Markowitz et al. 2010; Orbach et al. 2015a; Lammers 2019). For example, male dusky dolphins rarely interfere overtly or aggressively with other males copulating with females; however, the copulation rate per male decreases as group size increases, indicating that males are in competition (Orbach et al. 2015b, c).

As with most delphinids and other social mammals, social and sexual behavior occurs in episodes or bouts in spinner and dusky dolphins. Caressing of the pectoral fin, flukes, and full body contact in the mating posture often occur in mixed-sex interactions involving the entire subgroup (Johnson and Norris 1994; Markowitz et al. 2010). Dolphins within these groups are active with frequent ventral flashes toward partners of both sexes, possibly signaling an invitation to join (Norris 1994; Markowitz 2012). Male and female spinner and dusky dolphins can mate with multiple partners within a few minutes (Johnson and Norris 1994; Würsig 1999; Orbach et al. 2015a). Spinner and dusky dolphins mate ventrum-to-ventrum. Male dusky dolphins typically approach and mate ventrum-up from beneath the female (Markowitz et al. 2010; Fig. 14.2). Spinner dolphins show more variation, with

females at times approaching males from below, leading to copulation (Norris and Dohl 1980).

Sexual interactions can be social as well as reproductive and include same sex pairings (Norris and Dohl 1980; Markowitz et al. 2010; Ham et al. 2023, this book). Dusky dolphins sometimes engage in sociosexual interactions with common dolphins (*Delphinus delphis*; Markowitz et al. 2010) in mixed-species assemblages (Cords and Würsig 2014). Apparent hybrids of the two species have been observed in New Zealand (Markowitz 2004) and Peru (Reyes 1996).

14.3 Influence of Habitat Structure on the Social Context of Sexual Interactions

Deep waters not far from shore provide abundant food resources for Hawaiian spinner and New Zealand dusky dolphins, and both species capitalize on this prey availability while also minimizing predation risk. In the evening, dolphins in both populations move offshore into waters ranging in depth from 200 m to >2000 m to feed on prey that become more accessible with the nightly vertical migration of the deep scattering layer (Benoit-Bird and Au 2004, 2009; Benoit-Bird et al. 2004, 2009; Au and Benoit-Bird 2008). During the day, they move inshore to rest, play, and socialize in relatively shallow habitats of <50 m depth that likely provide protection from predators (Norris and Dohl 1980; Markowitz 2004; Thorne et al. 2012). However, they may encounter more frequent anthropogenic disturbances in these areas (Courbis and Timmel 2009; Lundquist et al. 2013; Heenehan et al. 2017; Tyne et al. 2017, 2018). Daytime observations have revealed many similarities in social and sexual behaviors of spinner dolphins in Hawai'i and dusky dolphins in New Zealand waters. These behaviors, including mating, likely help strengthen social bonds in these night-foraging societies with many complex associations (Norris 1994; Würsig and Pearson 2014).

Whether in remote atolls or where islands and atolls are within a few kilometers of each other, spinner dolphins associated with shorelines prefer to rest during daylight in shallow habitats adjacent to deep water (within 1.5–2.5 km) where nocturnal foraging occurs (Norris and Dohl 1980; Norris 1994). Hawaiian spinner dolphins exhibit site fidelity to island coastlines where they rest during the day; however, they frequently reassociate in small groups and in different bays from one day to the next, resulting in shifting fission-fusion associations within and among days (Lammers 2019). Active leaping, surface behaviors, and sociosexual behaviors are most common in the early morning while dolphins begin to move toward the coast from offshore feeding grounds. The transition to full rest once dolphins enter shallow bays can take as long as 2 hours, with groups predominantly resting at around midday (Johnson and Norris 1994). Social and other active behaviors then decrease as tight-knit groups rest close to shore with little sociosexual activity (Norris 1994). Spinner dolphins spend at least 30% of their time in caressing bouts

in the morning and afternoon, but do not engage in caressing or sexual behavior while resting during midday in shallow sandy areas of the bay (Johnson and Norris 1994). Coming out of rest in the afternoon, spinner dolphins become more active, “zig and zag,” and begin to associate sexually, with mating occurring in groups of one dozen or more individuals (Johnson and Norris 1994; Würsig et al. 1994). Spinner dolphin sociosexual behavior increases as they become active in preparation for moving offshore for nighttime foraging, with most sociosexual activity occurring in deep water or bay entrances in the afternoon or evening (Norris and Dohl 1980; Norris 1994).

Spinner dolphins in the main Hawaiian Islands show strong site fidelity, a fission-fusion society, and genetic differentiation among some islands (Andrews et al. 2010). In more remote atolls, such as Midway Atoll and other locations in the Northwestern Hawai'i Archipelago (100+ km apart), spinner dolphins do not show the same daily fluid fission-fusion social structure (Karczmarski et al. 2005). Site fidelity for spinner dolphins in remote atolls is very high, and competition for atolls can be intense. This difference in social structure and habitat use is likely related to habitat structure. Remote atolls likely do not provide opportunities for large scale day-to-day fission-fusion associations since there is only one resting place available (Karczmarski et al. 2005; Gowans et al. 2007).

Like Hawaiian spinner dolphins, dusky dolphins live in a fission-fusion society (Markowitz 2004; Pearson 2009; Orbach et al. 2018). In contrast to spinner dolphins, New Zealand dusky dolphins move large distances seasonally (Markowitz et al. 2004). Despite differences in seasonal residency and habitat use, New Zealand dusky dolphins show no sign of population subdivision (Harlin et al. 2003). In the deep waters of the Kaikoura Canyon, dusky dolphins feed at night on prey associated with the deep scattering layer (Würsig et al. 1997; Dahood and Benoit-Bird 2010). Although dusky dolphins are present in the Kaikoura Canyon year-round, photo-identification records indicate individual dolphins remain in the area seasonally, with different assemblages of individuals in summer and winter seasons. Winter movements take some dolphins to other shallow water habitats in the Marlborough Sounds where they feed diurnally in coordinated groups on schooling fishes (Markowitz et al. 2004), similar to daytime foraging by dusky dolphins in shallow waters off Argentina (Würsig 1975, 1989; Würsig and Würsig 1980; Degradi et al. 2019). The shallow bays of the Marlborough Sounds provide a winter habitat for primarily male dusky dolphins, with some nonbreeding sociosexual behavior observed between bouts of daytime feeding (Markowitz et al. 2010).

14.4 Breeding Seasonality, Circadian Rhythm, and Reproductive Physiology

Among marine mammals, female delphinids generally have relatively long seasons of receptivity, averaging 4 months (Boness et al. 2002; Boness 2009). Spinner and dusky dolphins are seasonal breeders with female receptivity, male testis mass and

testosterone levels, and conception peaking in the summer-autumn season (Cipriano 1992; Van Waerebeek and Read 1994; Perrin and Mesnick 2003; Perrin 2009; Markowitz et al. 2010; Table 14.1). Like other dolphins (e.g., bottlenose dolphins, Schroeder 1990), female spinner and dusky dolphins are seasonally polyestrous (Cipriano 1992; Van Waerebeek and Read 1994; Wells and Norris 1994). Seasonal polyestry may be an adaptive strategy to guarantee conception (McEntee et al. 2023, this book). Seasonal breeding is timed such that calves are born, following just under 1 year of gestation, at a time when sea surface temperatures rise in spring and summer, reducing thermal demands on small neonates (Weir et al. 2010).

While sociosexual activity occurs year-round in spinner and dusky dolphins, it is most pronounced during the breeding season, coinciding with peak testosterone levels in males and receptivity in females (Johnson and Norris 1994; Markowitz et al. 2010). In a breeding context apparently tied to seasonal changes in hormone profiles, increased sexual activity coincides with spinner and dusky dolphins gathering in small, tight-knit, highly active mating groups (Johnson and Norris 1994; Markowitz et al. 2010; Markowitz 2012). A captive study of Hawaiian spinner dolphin behavioral endocrinology found that genital-to-genital contact occurred only between male and female spinner dolphins when male testosterone levels were high; mutual ventral presentations were correlated with both male testosterone levels and female estradiol levels (Wells and Norris 1994). Male New Zealand dusky dolphins show large seasonal variation in testis mass, peaking at >3 kg in the spring and remaining high in summer through autumn (Cipriano 1992). Sociosexual activity is relatively uncommon during the winter in both the deep-water habitat off Kaikoura where dolphins feed primarily at night and in the shallow habitat of the Marlborough Sounds where they feed during the day (Markowitz et al. 2010; Markowitz 2012). Thus, seasonal changes in female receptivity, male testis mass, and sex hormones are correlated with sociosexual activity for both species (Wells and Norris 1994; Markowitz et al. 2010).

Mating, which occurs in nonbreeding and breeding contexts, can be playful and relaxed as well as competitive. Frequent intromission among spinner dolphins is most observed during the breeding season (Wells and Norris 1994), similar to dusky dolphins (Markowitz et al. 2010). However, sociosexual behavior among spinner dolphins occurs throughout the year and is described as a “marked” feature of this species’ society outside of the breeding season (Norris 1994). For dusky dolphins, sexual behaviors, even in competitive mating groups during the breeding season, occur alongside play behaviors (e.g., playing with kelp; Markowitz 2012). Outside the breeding season, sociosexual interactions among dusky dolphins are less frequent and often take on a “lazy” quality that appears to be part of the fluid suite of interactive behaviors that include other forms of touching and play (Markowitz et al. 2010). These sexual interactions likely serve to strengthen social bonds, as seen in many primate species and other mammals (Würsig and Pearson 2015; da Silva and Spinelli 2023, this book).

Sexual activity of Hawaiian spinner dolphins and New Zealand dusky dolphins is not uniformly distributed throughout the day. Rather, it follows predictable circadian rhythms of rest and social interaction. Both populations rest predominantly during

midday with high activity levels early in the morning following offshore feeding and late in the day prior to returning offshore to nocturnally feed (Würsig et al. 1994; Markowitz 2004). Sociosexual behavior of Hawaiian spinner dolphins often occurs in the morning before resting in nearshore waters (Würsig et al. 1994). Spinner dolphins off the Brazilian coast also engage in reproductive activity most often during the morning (Silva and Da Silva 2009). Similarly, dusky dolphins off Kaikoura, New Zealand, exhibit high levels of sociosexual activity in the morning followed by predominant midday rest but exhibit even higher sociosexual activity levels late in the day prior to moving offshore to feed at night (Markowitz et al. 2010). While sociosexual activity occurs at all times of day among dusky dolphins, it is least frequent around the midday rest period (Markowitz 2004).

In contrast, dusky dolphins in Golfo San José, Argentina, and Admiralty Bay, New Zealand, feed during the day in shallow bays where low predation pressure appears to have released them from assembling in large groups (Würsig and Pearson 2014). Daytime social and sexual interactions of dusky dolphins in these habitats occur within a diel activity schedule that includes diurnal foraging and feeding (Vaughn et al. 2010). In these habitats, most social and sexual interaction occurs following a successful feeding bout (Würsig and Würsig 1980; Würsig and Pearson 2014).

14.5 Competition, Collaboration, and Choice

Male spinner and dusky dolphins have high testis-to-body mass ratios and high brain-to-body mass ratios (Kelley et al. 2014; Ridgway et al. 2016). Their large gonads and brains play a role in sociosexual interactions. The mating system of spinner dolphins is serial polygynandry, with multiple males mating with a single female in quick succession and those males then mating with other females as well, but not necessarily in the same male groupings as before (Johnson and Norris 1994). While mating behavior of Hawaiian spinner dolphins often occurs in pairs and trios, during the estrus season, it also occurs in larger, bunched, interweaving groups of a dozen or more dolphins termed “wuzzles” (Johnson and Norris 1994; Würsig 1999). Similarly, mating in dusky dolphins is sometimes observed in pairs or trios but more commonly occurs in tight groups that engage in particularly frenzied activity during the breeding season. The average dusky dolphin mating group size is five dolphins comprised of four male dolphins chasing a lone female (Markowitz et al. 2010; Orbach et al. 2015a). Neither spinner nor dusky dolphin males engage in the overtly aggressive male-male physical competition or mate guarding observed in bottlenose dolphins (Wells and Norris 1994; Connor et al. 2000; Markowitz 2004; Brightwell and Gibson 2023, this book). Unlike bottlenose dolphins, male spinner and dusky dolphins appear unable, either singly or cooperatively, to monopolize females (Wells and Norris 1994; Markowitz et al. 2010). Male dusky dolphins appear to engage in “mating of the quickest” (Markowitz et al. 2010), a form of scramble competition in which not all participants succeed in copulating with the female (Orbach et al. 2014).



Fig. 14.3 Dolphin social contact in the context of mating is shown. One dolphin is performing a “rollover” in an attempt to break up a mating pair. A fourth dolphin is approaching from behind the group (Photo by W.J. Markowitz)

While overtly aggressive physical interactions among dusky dolphin males are rare, males jostling for position at times collide midair or engage in a “rolling over” behavior in which one male separates a copulating female and male at the surface (Markowitz 2012; Fig. 14.3). Similar competitive mating behavior occurs in spinner dolphins (Norris and Dohl 1980).

Close social associations frequently occur within male spinner dolphin groups off Hawai’i and male dusky dolphin groups in New Zealand; this suggests the possibility of collaboration among male dolphins during competitive sexual encounters (Östman 1994; Markowitz et al. 2004; Pearson et al. 2019). While male Hawaiian spinner dolphins maintain close associations and often swim side-by-side, sociosexual behavior, including touching, rubbing, and nuzzling of the genital area, occurs most often among males and females (Östman 1994). In New Zealand, a group of closely associated male dusky dolphins that chased females together off Kaikoura in the summer breeding season also engaged in coordinated diurnal fish feeding in Admiralty Bay during the winter nonbreeding season; this suggests that these males most likely use “team mates to get mates” (Markowitz et al. 2010). Although male-male competition generally decreases copulation rate per male (Orbach et al. 2015b, c), observations of apparent mate sharing in small mating groups with the first male copulating longest suggest that male dusky dolphins may allow rivals opportunities to mate but that the sharing may not be equal (Markowitz 2012). Such mate sharing among alliance partners is common among primate societies and has also been observed in male alliances of bottlenose dolphins engaged in more aggressive competition and mate guarding (Connor et al. 1992).

As is common in large-brained mammals where females invest most heavily in offspring and provide most parental care (Trivers 1985), female choice plays a major role in the mating system of many social odontocetes (Orbach 2019). Among cetaceans, where some aspects of matrilineal cultures often occur (e.g., Betty et al. 2023, this book), females play a key role in shaping social structure, behavioral biology, and sexual interactions (Whitehead and Mann 2000). Female mate choice, hormonal state, libido, and prowess appear to be key components in sexual interactions (Würsig et al. 2023, this book). There is strong sexual selection for those traits that make males successful in their attempts to copulate with females and females successful in copulating with the highest-quality males. Females appear to actively engage in mate selection, including exhibiting extensive evasive behaviors (Orbach et al. 2015a). Females appear to pay attention to the mating behaviors of males and adjust their responses accordingly, providing strong evidence of discrimination in mates (Orbach et al. 2015a). Female vaginal morphology of spinner and dusky dolphins also supports an active female role in controlling paternity. Female cetaceans possess vaginal folds that create a labyrinth for the penis and sperm inside their reproductive tracts (Orbach et al. 2019, 2020a). Research with captive spinner dolphins showed that females initiated sociosexual beak-to-genital interactions with males when their estradiol levels were highest (Wells and Norris 1994). Underwater observations of Hawaiian spinner dolphins in nature found that social contact behaviors were more common in female-male pairs than in male-male pairs, with the females most often initiating these behaviors including social rubbing, “hitchhiking” (assisted locomotion), and genital rubbing (Östman 1994).

In some cases, female choice may occur indirectly in the form of females encouraging male-male competition (Boness et al. 2002), often by making it difficult for males to access a female who is ventrum-up at the surface, as in right whales (*Eubalaena* spp., Brown and Sironi 2023, this book), bowhead whales (*Balaena mysticetus*, Koski et al. 2023, this book), and gray whales (*Eschrichtius robustus*, Swartz et al. 2023, this book). In addition to initiating sociosexual interactions, female odontocetes often engage in a variety of elusive behaviors, probably to ensure that they mate with the highest-quality prospective mates (Orbach 2019). This appears to be the case for dusky dolphins off Kaikoura during the breeding season (Markowitz et al. 2010; Markowitz 2012), where mating chases in small groups occur in fits and starts with the female engaged in evasive behaviors at the front of the group (Orbach et al. 2015a). Females may prolong mating chases to improve the likelihood that only the most adept male chasers successfully copulate. This notion is supported by copulation rate decreases with reorientation rate in mating groups during the breeding season (Markowitz 2012). With frequent changes in direction, the swimming speeds of dolphins engaged in mating chases vary considerably more than in groups traveling in a linear direction or resting, reaching top speeds exceeding 20 km/h (Markowitz et al. 2010). In such mating groups, female dusky dolphins extend chases by frequently changing direction and head-up braking maneuvers (Markowitz et al. 2010), as well as deep dives and inverted swimming (Orbach et al. 2015a). Reentry leaps are common among mating groups of dusky dolphins, occurring more often than in other social groups, and often associated with high-speed

surface chasing (Markowitz 2004, 2012). Typically, the female in the group leaps first and is often followed immediately by one or more of her male suitors (Fig. 14.1). High rates of reentry leaping are correlated with reduced copulation rates, suggesting that females may use reentry leaps to break away from chasing males near the surface and extend mating chases in three-dimensional space down through the water column (Markowitz et al. 2010). Drone footage of subsurface activities has revealed that chasing continues during dives, with male dolphins following the female throughout the dive sequence (Orbach et al. 2020b). In form, and perhaps also in function, female dusky dolphins are leaders in sociosexual interactions.

14.6 Sociosexual Development and Learning

Spinner and dusky dolphins have opportunities to learn about sociosexual interactions long before they reach sexual maturity at about 7 years of age (Norris and Dohl 1980; Cipriano 1992; Table 14.1). In spinner dolphins, sociosexual behavior commonly occurs in mixed age class resting groups (Johnson and Norris 1994). Dusky dolphin calves may witness their mothers and/or other adult companions engage in sociosexual behavior (Markowitz et al. 2010). One function of dusky dolphin nursery groups may be the reduction of harassment by males during the breeding season (Weir et al. 2008). Calves and their mothers also frequently join large groups, where more relaxed sociosexual interactions are common (Markowitz 2012). As they mature into juveniles, reproductive behavioral patterns are practiced in social interactions among spinner dolphins (Norris 1994) and may also occur in playful subgroups of dusky dolphins (Markowitz 2004).

14.7 Summary and Future Directions

Hawaiian spinner dolphins and New Zealand dusky dolphins live in large societies in which associations change frequently despite evidence of preferred companions (Markowitz 2004; Andrews et al. 2010; Pearson et al. 2016; Orbach et al. 2018). Sexual interactions occur in busy, ever-changing social environments within these two populations, both of which forage nocturnally (Johnson and Norris 1994; Markowitz et al. 2010). Off Kaikoura, New Zealand, large groups of dusky dolphins, typically numbering in the hundreds, facilitate diverse social interactions that require social rules and communication relative to organizing group movements (Markowitz 2004). Small subgroups, including mating groups, split off from the large groups and rejoin them throughout the day. This results in a busy network of social interactions that can change seasonally, daily, and from one moment to the next (Markowitz 2012). Although spinner dolphins in the main Hawaiian Islands show strong general site fidelity (Andrews et al. 2010; Lammers 2019), different groups come and go

from individual bays with much social mixing (Würsig and Pearson 2015). In their shallow (< 50 m), sandy, daytime resting habitat along the shores of the main Hawaiian Islands, spinner dolphin group sizes do not reach the numbers observed in dusky dolphins inhabiting deep nearshore waters of the Kaikoura Canyon during daytime. However, group size and membership can change throughout the day, and sociosexual behavior is observed in both small groups and large “wuzzles” (Johnson and Norris 1994).

Dusky and spinner dolphins appear to have two different modes of exhibiting sexual behavior: an active competitive form involving multiple partners and a more relaxed, “lazy” form. Both these forms of sociosexual behavior can include intromission, although their function appears to be quite different. In a breeding context, high activity levels among dusky dolphins show a role for sexual selection in male-male competition and female choice (Markowitz et al. 2010). Copulations in small groups of spinner dolphins tend to involve two successful males mating with one female; these interactions are not particularly active with minimal chasing and no leaping. Females are not isolated from the large group for long and mating occurs quite briefly (Johnson and Norris 1994). Sexual behavior also occurs in large interactive groups of spinner dolphins with high activity levels (Johnson and Norris 1994; Würsig 1999). In a nonbreeding context, sex also plays an important role, strengthening social bonds within fission-fusion societies of nocturnally foraging dolphins that depend on one another for survival (Norris and Schilt 1988; Markowitz 2012).

In this chapter, we reviewed research conducted over the past 40 years on the sexual behavior of night-foraging spinner and dusky dolphins and how mating fits into their circadian and seasonal rhythms, rich social lives, and fission-fusion societies. These studies were facilitated by a combination of ingenuity and technological advances that improved the ability to better understand the mysterious and complex social and sexual lives of dolphins. In Hawai’i, spinner dolphin groups were monitored in Kealahou Bay from research vessels and by theodolite tracking from shore stations (Würsig et al. 1994). Some vessel-based work included observations of spinner dolphin social behaviors from underwater viewing platforms, yielding a better and extended view of subsurface behavior including sociosexual interactions (Norris and Wells 1994; Östman 1994). Captive research has provided invaluable insights into the role of hormone levels in sociosexual behavior of male and female spinner dolphins (Wells and Norris 1994). In New Zealand, early work relying on stopwatches, datasheets, and photo-identification using film photography gave way to digital video, digital audio, and high-resolution digital SLR photography (Markowitz et al. 2003; Markowitz 2012). Within dusky dolphin mating groups, high-resolution video and photography provided improved quality information on individual identity and roles in sexual encounters and also the sex of the participants using anogenital digital records (AGDRs, Markowitz et al. 2010). Recently aerial drones were used to provide both a broader view of group interactions from above and a view of behavior underwater as seen from above (Orbach et al. 2020b; Ramos et al. 2023, this book).

New research approaches have given us previously unavailable glimpses into the social and sexual lives of spinner and dusky dolphins, but much remains to be discovered. Important questions to be explored include: how do spinner dolphin “wuzzles” and dusky dolphin mating groups influence reproductive success and fitness for females and males? What is the relationship between nocturnal foraging success and diurnal sexual activity? How do sociosexual interactions influence other socioecological interactions and vice versa? What can similarities and differences in the sex lives of spinner dolphins, dusky dolphins, and other cetaceans teach us about the roles of sex in shaping complex cetacean societies? We expect much will be learned in the future regarding these and other questions as new methodological approaches are incorporated into research efforts. For example, further photo-identification and behavioral research, facilitated by ever-improving technology (Markowitz et al. 2003; Orbach et al. 2020b), will provide new insights into social partnerships in sexual and other interactions for both populations. Future work using drones might include hormonal sampling from exhaled air (Abele 2021) to provide real-time field data on the hormonal states of dolphins engaged in sociosexual interactions. The use of noninvasive tags for dive records, underwater video capture, and documentation of other parameters also shows great promise for future advances in our understanding of dolphin sociosexual interactions (Pearson et al. 2017, 2019).

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