

Chapter 13

Sex and Sexual Strategies in Deep-Diving Risso's Dolphins



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Abstract Risso's dolphins (*Grampus griseus*) in the Azores maintain a sexually stratified community with males forming stable clusters, whereas females tend to associate in temporally stable units when calving and nursing. Large relative testes size indicates a mating system based on sperm competition. Small sexual size dimorphism and long interbirth intervals may facilitate male cooperation. We describe mating tactics observed in a resident population of Risso's dolphins based on data collected over 8 consecutive years. We distinguished groups by sex and age class and analyzed peaceful and aggressive behaviors using an ethogram. Males displayed a variety of mating tactics described in cetaceans, spanning display, contest, endurance, and scramble competition, in the assumed context of sperm competition. We observed rare behaviors including male care for neonates but also intense aggression toward newborn calves, leading to possible infanticide. Females' mating tactics included evasive behaviors and signal discrimination. We hypothesize that male mating tactics of Risso's dolphins are related to age class. For females, the polygynandrous mating system may serve to improve fertility, reduce sexual harassment, and reduce the risk of infanticide. Adult females seem to prefer older over younger male groups, suggesting that some level of female mate choice exists in this species.

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13.1 Introduction: Risso's Dolphin Life History and Social Structure

The Risso's dolphin (*Grampus griseus*) is a medium sized (3.6–4 m), deep-diving oceanic delphinid, feeding mainly on mesopelagic cephalopods (Hartman 2018). Both sexes have three to seven oval teeth present in the lower jaw, and their presence may have a specific social function in this species: they leave unpigmented linear scars on the skin, mostly during aggressive intraspecies interactions. This causes, especially in males, the distinctive light or white skin appearance, which may serve as an indicator of male quality (MacLeod 1998). The distinctive scarring marks are also visible on the dorsal fins and provide a unique opportunity for individual identification through standard photo-identification methods (Würsig and Jefferson 1990; Wells 2018). In Risso's dolphins, the changes in skin coloration over time can be used to classify an individual's life history stage, which can be linked to sex, social structure, and specific reproduction stages and strategies (Hartman et al. 2016). Besides having a more scarified skin, adult male Risso's dolphins have more bulbous heads, a more muscular body, and they tend to grow on average 10–15% larger than females. Thus, there is some degree of sexual size dimorphism in this species, impacting Risso's dolphin's social ecology and mating strategies.

Across populations, it appears that Risso's dolphins have medium-to-long interbirth intervals, based on a gestation period of 13–14 months (Amano and Miyazaki 2004; Bloch et al. 2012), followed by a period of up to 4 years of maternal care (Hartman 2018). During a successful nursing period, during which the female is presumably not in estrus, she is not available for reproduction for a period of up to 4–5 years. This contributes to a skewed operational sex ratio, which in combination with the sexual size dimorphism (Cox 2017) may lead to the formation of stable multi-male clusters (Möller 2012). This may be one of the drivers for the formation of stable groups of adult males, with clusters composed of 3–12 individuals of the same age class, reported from one single study site in the Azores (Hartman et al. 2008). In contrast to males, adult females of this population merge seasonally and form temporally stable units when calving and nursing. This particular social structure has been described as a “sexually stratified community” (Hartman et al. 2008, 2014).

Risso's dolphin males display a behavior of “synchronous breathing” in pairs or trios. Synchrony in free-ranging cetaceans is defined as two or more individuals who simultaneously break the surface to breathe, often in close proximity (less than 50 cm) of each other (Sakai et al. 2010). It has been reported for bottlenose dolphins (*Tursiops* spp.) and pilot whales (*Globicephala melas*) (Senigaglia and Whitehead

2012). Among Indo-Pacific bottlenose dolphins (*T. aduncus*), synchronous surfacing by allied males was linked to intense social behavior with female consorts (Connor et al. 2006; McCue et al. 2020). Male Risso's dolphins in the Azores bond with various or fixed "synchrony" partners, indicating a complex intragroup structure (Hartman et al. 2020). In addition, male Risso's dolphins have large testes in relation to body mass, which is a robust indicator of a mating system based on sperm competition (Connor et al. 2000). Stable and highly associated male groups may enhance their chances of having access to females in competition with other groups.

Little is known about social behavior and mating tactics in Risso's dolphins (Bearzi et al. 2011; Visser et al. 2011; Cipriano et al. 2022). There are aggressive inter-animal contacts (Kruse 1989) and potential hybridism between free-ranging Risso's dolphins and bottlenose dolphins (*Tursiops truncatus*) in UK waters (Hodgins et al. 2014). This chapter describes and interprets behavior in the context of mating tactic in one population of free-ranging Risso's dolphins studied off Pico Island, Azores, Atlantic Ocean, for which detailed long-term behavioral data are available.

13.2 Methods

13.2.1 Study Area

The volcanic islands of the Azores archipelago, central North-East Atlantic Ocean, are surrounded by deep waters. There is virtually no continental shelf, as steep submarine walls cause a rapid descent of the ocean floor within 5 km from the shore. This, in combination with the upwelling of nutrient-rich waters, results in high productivity and predictable food resources for marine megafauna (Morton et al. 1998). Over 25 species of cetaceans have been recorded in the Azores, and many species use these waters as breeding, nursing, and feeding grounds (Silva et al. 2014; Cascão et al. 2019). Because of the deep waters nearshore, several deep-diving species such as Risso's dolphins occur relatively close to the coast, creating unique opportunities for in-depth studies.

13.2.2 Data Collection

Data were collected off southeast Pico Island (central group, Azores), covering a survey area of approximately 540 km², 2004–2011. Field effort varied from year to year, with most sightings between May and September. Risso's dolphins were first detected from a land-based lookout at 45 m above sea level (38.4078 N, 28.1880 W—covering approximately 370 km²), at Santa Cruz das Ribeiras, using 20 × 80 binoculars (see Visser et al. (2011) for an overview of land-based methods). Research

vessels (rigid-hull inflatables 4.2–5.2 m long and a 6.7 m fiberglass motorboat) were then directed from land toward dolphin groups.

During surveys, we applied focal group follows (Altmann 1974; Mann 1999) and general individual photo-identification (Würsig and Jefferson 1990; Wells 2018). A group was defined at the start of each survey, applying the 15 m “chain rule” proposed by Smolker et al. (1992), considering social interaction and coordination of activities among individual group members (Whitehead 2003) at the start of each group observation. Two observers estimated group size at sea and refined this estimate after processing photo-identification data. Photographs were matched with the existing catalog, consisting of 1250 unique identifications (Hartman et al. 2008, 2015); new individuals were added to the database. For the present study, only the age class and sex classification per individual were used.

13.2.3 Sex and Age Class Determination

An individual was assumed female if observed on more than two separate days with the same calf. In other cases, sexing was based on photography of the genital area. For male individuals, additional characteristics were used, including long-term absence of calves in stable units, as well as skin coloration (Hartman et al. 2016). For 114 animals, the sex of individuals was later confirmed using molecular genotyping methods (Hartman, in review). For newly observed individuals, often younger animals, it was not always possible to define sex; hence, we classified these animals as “sex unknown.”

We assigned age classes per year based on scarification patterns as described in Table 13.1 (after Hartman et al. (2016); Fig. 13.1). Figure 13.2 shows three examples of long-term followed individuals of confirmed sex, displaying the changes and differences in scarification between males and females. In this species, these are important visual clues for the determination of sex and age classes.

For known individuals that we encountered every year, it was possible to assign intermediate age classes. As an example, a male halfway in age class M4 would be

Table 13.1 Skin stages based on scarification patterns, maturity stages, and age classes, after Hartman et al. (2016)

Skin stage	Scarification	Maturity stage		Age class	
		Males	Females	Males	Females
1	Unscratched	Nursing calf ^a		1 ^a	
2	Limited	Juvenile ^a		2 ^a	
3	Moderate	Subadult		M3	F3
4	Severe	Adult 1		M4	F4
5	Marbled	Adult 2		M5	F5
6	White	Adult 3	–	M6	–

^aThe sex of calves and juveniles is generally unknown, with the exception of a few individuals (*n* = 11; eight males and three females)



Fig. 13.1 Six categories for male and female age class determination based on skin coloration after Hartman et.al (2016): (a) calf (1), (b) juveniles (2), (c) subadult (M3/F3), (d) adult-phase 1 (M4/F4), (e) adult-phase 2 (M5/F5), and (f) adult-phase 3 (M6)

assigned a numerical age class value of 4.5. The numerical age class value assigned to unknown individuals was always “halfway” the age class (e.g., 3.5 for subadults, 4.5 for M4 males, etc.). Females in age class F4 were all assigned the numerical value 4.5, since for females the scarring pattern does not allow a more detailed age classification (Fig. 13.2). We calculated average age classes per group and per year using these numerical values.

13.2.4 Underwater Video Recordings

We used a handheld underwater camera (GoPro 4 and 6) attached to a 1.5 m pole, when the engine was still or at low speed, to record underwater behavior on video.



Fig. 13.2 Life history patterns illustrated by three resident individuals, displaying the changes and differences in the scarification process between males and females, captured over a period of 11–18 years. Left column: the resident female M32a, first observed in 2004 as a subadult of unknown sex, approximately 7–8 years old. In 2009, at the age of 12–13 years, her first (female) calf was born, followed in 2014 by a male calf. Her third calf (unknown sex) was born in 2019, suggesting an interbirth interval of approximately 5 years. Overall, her scarring pattern increased little over time. Center column: M32a_c1, a female who left her mother’s side in 2014 at the age of 5. She was seen with her first newborn calf in 2021, when she was 12 years old. In 2022, M32a_c1 was sighted without her calf. Her scarring patterns increased little over time, with large areas of unscarred skin. Right column: M1d_c1, a male born in 2003. At the age of 9 (2012), his skin was already severely scarred

13.2.5 Synchrony

We recorded the occurrence of “synchronous behavior” when two or more individuals swam next (<50 cm) to each other and simultaneously broke the surface for breathing (Sakai et al. 2010; Hartman et al. 2020).

13.2.6 Selection of Groups and Behavioral Data Scoring

Data for this analysis were selected from observations including previously identified male or female clusters (Hartman et al. 2008). We included groups with more than 75% individuals of known sex and more than 75% individuals of known age class. Unknown sex often concerned juveniles and calves, whereas unknown age class concerned infrequently sighted individuals. We considered the following group types: all-female (100% of individuals of known sex were females), all-male (100% males), and mixed-sex groups (containing males and females). Within the mixed-sex groups, we made a further distinction based on the average age class of the males: M3 (the average age class of the males with known age class was subadult), M4

Table 13.2 Overview of group descriptions, according to composition and restrictions of sex and male age class, with indications of individuals' appearance

Composition	Group description	Restrictions	Appearance
All-female	100% females	Females, including their calves	Limited scarification
Mixed male/female	Subadult males	Average age class of males M3	Limited/moderate scarification
	Adult male stage 1	Average age class of males M4	Severe overlapping scarification
	Adult male stage 2/3 ^a	Average age class of males M5/M6 ^a	Marbled/white, overlapping scarification
All-male	100% males	Males, all age classes	Limited scarification to white

^aGroups with average age class M6 were combined with M5, since the number of groups with average age class M6 ($n = 13$) was insufficient to make any statistically significant analysis. References to M5 in this study therefore include individuals from age class M6

(average age class adult-phase 1), and M5 combined (average age class adult stages 2 and 3; Table 13.2).

13.2.7 Ethogram Definitions

We scored specific behavioral states for the selected all-female, all-male, and mixed-sex groups, using an ethogram. “Main” and “secondary” behaviors were determined for the first 20 minutes of each observation, of four behavior types: resting, traveling, socializing, and foraging (Altmann 1974; Shane 1990; Visser et al. 2011; Hartman 2018). “Main behavior” was defined as the behavior observed most frequently during the first 20 minutes of an observation and “secondary behavior” as the second most frequently observed behavior. We focused on socializing behavior. Displays (e.g., aggression) were noted. Observations were classified as “aggressive” in case any aggressive interaction (see below) was recorded over the timespan of the observation or as “peaceful” in all other cases.

For situations in which females associated with males, we considered the following types of groups:

1. Confirmed female(s) swimming synchronized with a male “partner” (paired consortship)
2. Confirmed female(s) swimming freely close to or surrounded by males, <15 m distance (loose consortship)
3. Confirmed female(s) swimming freely with no interaction with males, >15m distance (no consortship)
4. Males present in, or following, a nursery with females and calves (no consortship)

Females meeting the descriptions 1 and 2 were marked as “targets.”

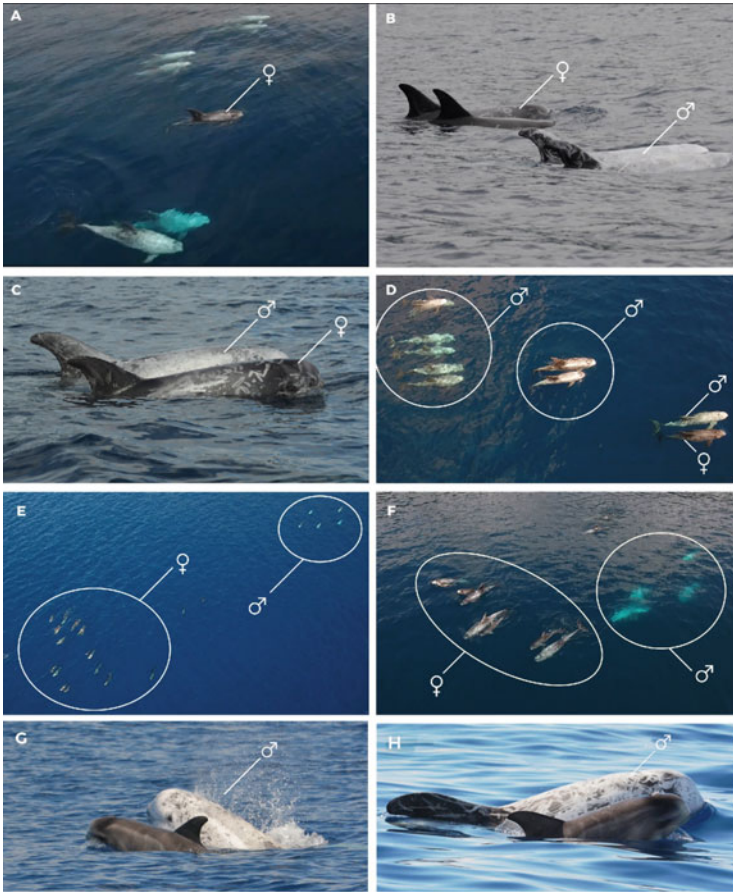


Fig. 13.3 Examples of peaceful male-female association types and exceptional male-neonate behavior: (a) a female swimming free (non-escorted) in the center of a male cluster (loose consortship), (b) two females swimming synchronously within a male cluster (loose consortship), (c) a young female and an adult male swimming synchronously (sync consortship), (d) a female and male swimming synchronously in a frontal position in the group (sync consortship), (e) a male cluster following a nursery at a distance >15 m (no consortship), (f) males mixed in a nursery (no consortship), (g–h) an M4 male accompanying a newborn after the mother left her calf when diving, during a mixed-sex group foraging event

Examples of “peaceful” associations are given in Fig. 13.3.

Aggressive behavior was defined as individuals engaging in physical contact and performing combinations of the following displays: handstands, flipper slaps, tail slaps, tail strikes, breaches, frequent opening of mouths, biting, ramming heads (head butting) into one another, and/or chasing one or more individuals. For displays of aggressive behavior, a distinction was made between male-only events and female-directed aggression by males. Aggression directed at females with nursing calves was recorded as a distinct behavior. A specific type of aggressive behavior,

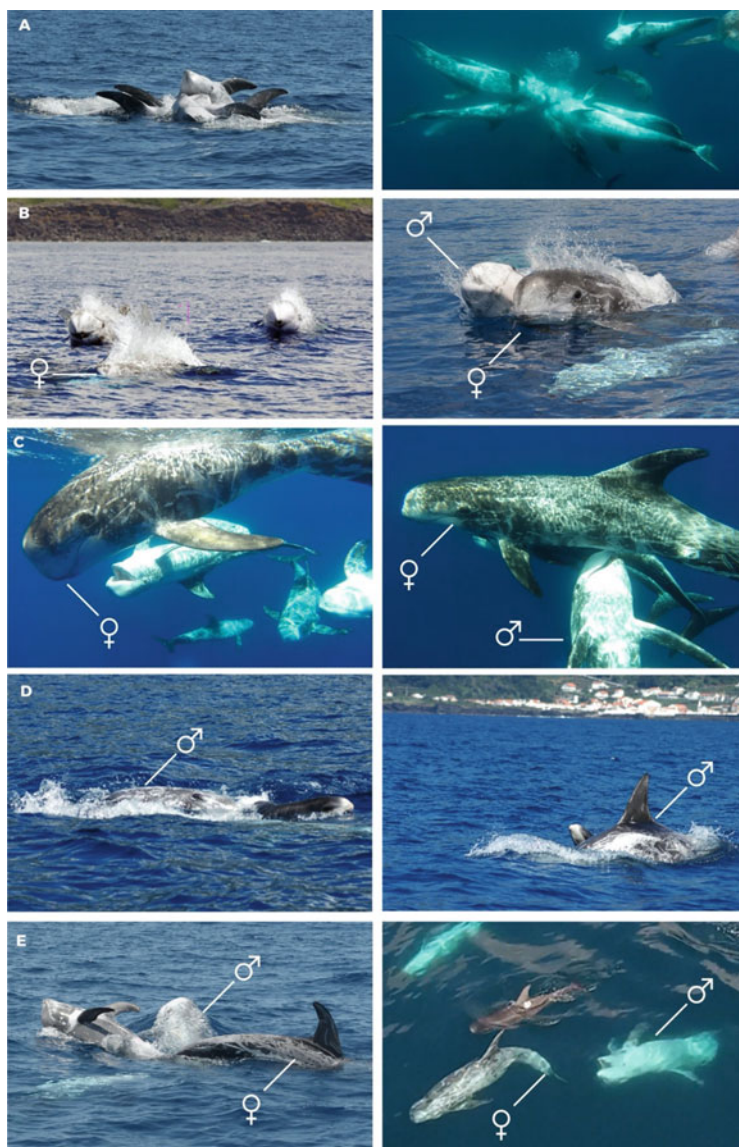


Fig. 13.4 Examples of aggressive behavior: (a) male individuals headbutting in “star formation” at the surface and underwater, (b) males chasing a female during a bull chase, (c) a female being exposed to aggressive behavior such as biting, (d) a male chasing a newborn calf, (e) males harassing females with older calves

noted as “bull (male) chasing,” was defined as male individuals chasing a female at high speed for prolonged periods of time, often including the displays described above and mating events. Examples of aggressive behavior are given in Fig. 13.4. Females who were the object of male aggression were also marked as “targets.”

13.2.8 Mating

Mating in aquatic mammals is difficult to observe in the wild. However, based on underwater video footage of copulations with clear intromission, we recognized mating events from the surface by the characteristic belly-to-belly movement and brief “logging” (resting at the surface) by the male after copulation (unpublished data KL Hartman). “Multi-male mating” was recorded when several males mated frequently one after the other with the same female, during one continuous observation (Fig. 13.5).

13.2.9 Data Analysis

For statistical significance (further referred to as “significant”), we applied a p -value < 0.05 . We calculated average group sizes, numbers of males and females, number of males per female and per target, and number of females in consortships across different male age classes (M3, M4, and M5). For behavioral data, we calculated the percentage of observations during which the behavior was observed, per male

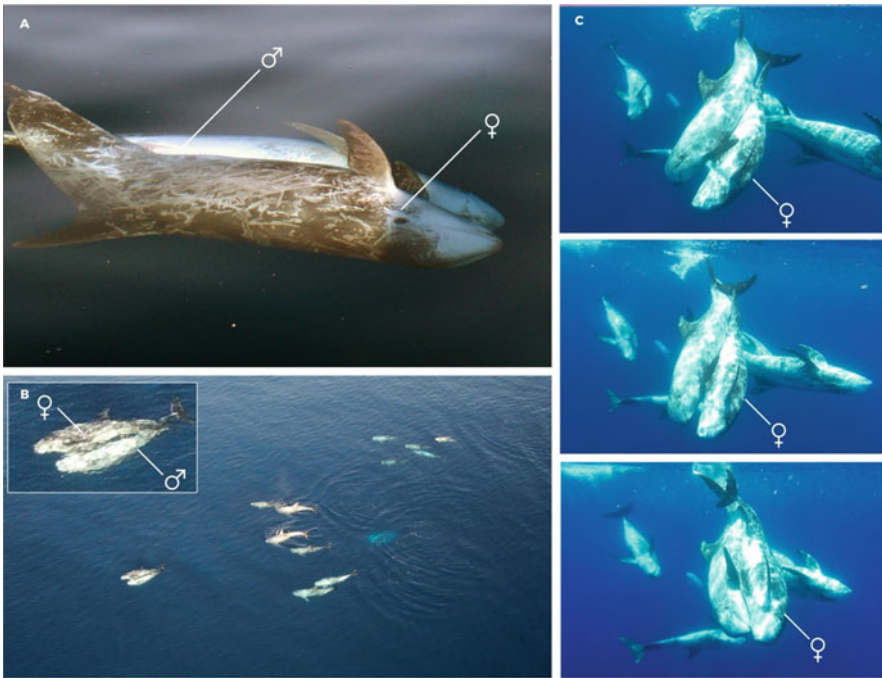


Fig. 13.5 Examples of mating events. (a) Mating observed from the surface, (b) captured by a drone (outside the duration of this study), and (c) captured with an underwater camera

age class. All model calculations were performed using R statistical software (R core team 2022), with two main statistical tests used depending on data to be compared. Behavioral data expressed as percentages were compared using a Bayesian proportions test by means of the *bayes.prop.test* function of the *BayesianFirstAid* package (Bååth 2014). Ninety-five percent confidence intervals (95% CI; presented in square brackets) were given for the estimated differences between groups. Second, for comparisons of count averages (e.g., numbers of males or females per male age class group), sample distribution was described and assessed for count data using the *descdist* function from the *fitdistrplus* package (Delignette-Muller and Dutang 2015) and also visually assessed by means of a histogram and the *fitdist* function. The best fitting distribution (either Poisson or negative binomial) was used to fit a linear model (GLM) by group, and the *Anova* function in the *car* package (Fox and Weisberg 2019) was used to evaluate the deviance of the model residuals. Finally, a post hoc analysis was conducted with the *emmeans* package (Lenth 2023) to estimate marginal means from the linear model and obtain 95% CI of the count averages.

13.3 Results

13.3.1 Survey Effort and Data Collection

For this study, we used data collected between 2004 and 2011 during 925 sea-based surveys in 591 days. We conducted 2367 hours of focal follows of Risso's dolphins, of which 309 hours (first 20 minutes for each selected group) were used for further analysis. We identified 1246 groups, of which 925 met the criteria described in Sect. 13.2.6 (at least 75% individuals of known sex and age class present per group) and were selected for further analysis, comprising 11,789 individuals (including resightings). The average percentage of individuals of unknown sex was 4%; the average percentage of individuals of unknown age class was also 4%. Mean group size was 13.1 dolphins (range, 4–45; SD, 10.1; mode, 9; median, 10.0). The average similarity tests and Bayesian proportion tests of the differences between age classes are presented in Supplementary Material Table 13.1.

13.3.2 Group Types

13.3.2.1 All-Female Groups Including Calves

We observed 91 groups exclusively consisting of females and calves. Average group size was 9.81 individuals, including 5.4 females (55%), 2.6 calves (26%), 1.7 juveniles of unknown sex (18%), and 0.13 subadults of unknown sex (1%).

Table 13.3 Composition and specific behavior of all-female groups. Percentages are calculated against the number of observations

# Observations	91	
# Individuals	893	
Average group size	9.81	
Composition	#	%
Average # subadult females (F3)	0.57	6%
Average # reproducing females (F4-F5)	4.80	49%
Average # juveniles	1.73	18%
Average # calves	2.58	26%
Average # subadults unknown gender	0.13	1%
Socializing	20	22%

Table 13.4 Composition and specific behaviors of all-male groups, per age class. Percentages are calculated against the number of observations

Group type	M3		M4		M5	
# Observations	95		184		76	
# Individuals	672		1521		608	
Average group size [95% CI]	7.07 [6.07, 8.25]		8.27 [7.42, 9.20]		8.0 [6.76, 9.47]	
Behaviors	#	%	#	%	#	%
Socializing	35	37%	36	20%	11	14%
Male-male aggression	1	1%	4	2%	0	0%

Socializing behavior was recorded during 20 observations (22%); no aggression was observed in all-female groups (Table 13.3).

13.3.2.2 All-Male Groups

We observed 355 groups consisting exclusively of males, of which 95 were subadult (M3) groups, 184 were of stage 1 adult male (M4) groups, and 76 were mature adult male (M5) groups. The average number of males per age class varied from 7.1 (M3) to 8.3 (M4) and 8.0 (M5). No significant differences occurred among age classes. Socializing behavior decreased with age, from 37% of observations in M3 groups, to 20% in M4 groups, and 14% in M5 groups. Estimated group differences among M3 versus both M4 and M5 were significant, whereas the estimated group differences between M4 and M5 were not. Male-male aggression was higher in M4 groups (2% of observations), compared to M3 groups (1%), and M5 groups, where aggression was not observed, but the estimated group differences were not significant among groups (Table 13.4; Supplementary Material Table 13.1).

Table 13.5 Composition, key data, and behaviors of mixed-sex groups, per average male age class

5a Group type	M3		M4		M5	
# Observations	135		225		113	
# Individuals	2031		4352		1578	
Average group size	15.04		19.34		13.96	
5b Composition	#	[95% CI]	#	[95% CI]	#	[95% CI]
Average # males	8.89	[7.72, 10.24]	10.46	[9.40, 11.64]	6.13	[5.20, 7.23]
Average # females	3.23	[2.73, 3.82]	3.87	[3.42, 4.38]	4.50	[3.80, 5.34]
Average # males per female	4.50	[3.67, 5.43]	4.61	[3.97, 5.39]	2.51	[1.99, 3.20]
Average # females in consortship	1.75	[1.04, 2.95]	1.58	[1.22, 2.04]	2.35	[1.73, 3.18]
Average # males per target	7.69	[6.11, 9.58]	8.25	[7.39, 9.16]	4.10	[3.32, 5.05]
Average age class females	F3		F4		F4	
5c Consortships	#	%	#	%	#	%
Consortships	15	11%	62	28%	31	27%
Peaceful	13	10%	43	19%	29	26%
Aggressive	0	0%	17	8%	0	0%
# Targets	25		100		71	
Average # targets	1.92		1.67		2.45	
Average # males per target	4.62		6.27		2.50	
Targets paired with male *	7	28%	51	51%	6	8%
Targets non-paired *	18	72%	49	49%	65	92%
Nursery present	8	6%	61	27%	32	28%
5d Behaviors	#	%	#	%	#	%
Peaceful behavior	126	93%	208	92%	110	97%
Females free, no consortship	113	84%	165	73%	81	72%
Peaceful consortship	13	10%	43	19%	29	26%
Female-directed aggression	9	7%	17	8%	3	3%
Of which bull chase	9	7%	12	5%	3	3%
Socializing	67	50%	104	46%	23	20%
Male-male aggression	4	3%	16	7%	3	3%
*Percentage calculated against # targets						

A target was defined as a consorted female. Unless indicated otherwise, percentages are calculated against the number of observations. Definitions are described under 2.7

13.3.2.3 Mixed-Sex Groups

We observed 473 groups of both males and females. We split these groups according to average male age class, resulting in 135 M3 groups, 225 M4 groups, and 113 M5 groups (Table 13.5a). The average number of male individuals was significantly higher in mixed-sex groups compared to all-male groups, for M3 groups (8.9 vs. 6.4)

and for M4 groups (10.5 vs. 7.9). For M5 groups, however, the average number was lower, though not significantly, in mixed groups (6.1 vs. 7.8). The average number of males per female was significantly similar for M3 and M4 groups (4.50 and 4.61, respectively) but significantly lower (2.51) for M5 groups (Table 13.5b; Supplementary Material Table 13.2).

13.3.3 *Peaceful Associations and Consortships*

Significantly similar numbers were found for the average number of females in mixed-sex groups for M3 (3.2) and M4 (3.9) and for M4 vs. M5 (4.5), whereas M3 vs. M5 group averages were significantly different. The average number of “targets” (females in consortships) was much lower: 1.8 in M3 groups, 1.6 in M4 groups, and 2.4 in M5 groups (see Fig. 13.4); but the differences between age classes were not significant (Table 13.5b-c; Supplementary Material Table 13.1).

A total of 108 observations were classified as “consortships,” involving 196 females. The majority (79%) of consortships were peaceful. The highest percentage of targets paired with a male (sync consortships) was observed in M4 groups (51%), followed by 28% in M3 and 8% in M5 groups. Estimated differences were significant among all age class groups. Non-paired targets (loose consortships) were predominantly observed in M5 groups (92%) but also frequently in M3 (72%) and in 49% of all observations of consortships in M4 groups. The number of males per target ranged from 7.7 in M3 groups to 8.3 in M4 groups (difference not significant) and 4.1 in M5 groups (significantly different from both M3 and M4; Table 13.5c; Supplementary Material Table 13.1). The average age class of males varied according to the composition of mixed-sex groups; when >50% of individuals were male, the average age class of the males was M4, whereas for groups composed of ≥50% females, the average age class of males was M5. M3 groups were present in or following nurseries in 6% of observations, versus 27% and 28%, respectively, for M4 and M5 groups. The estimated group differences between M3 and both M4 and M5 groups showed significantly lower proportions in M3, but no significant differences were found between M4 and M5 groups (Table 13.5c; Supplementary Material Table 13.1).

13.3.4 *Socializing and Aggression*

Male-male aggression was infrequently observed but higher in mixed-sex groups than in all-male groups. We recorded male-male aggression in 1% of observations in all-male M3 groups and in 3% of observations in mixed-sex M3 groups. For M4 males, the percentages were 2% for all-male groups and 7% for mixed-sex groups and for M5 males, 0% and 3%, respectively (Fig. 13.5a). Only the difference for M4 groups was significant. Similarly, socializing was seen more frequently in mixed-sex

groups than in all-male groups. For M3 groups, the percentages were 50% and 37%, respectively, compared to 46% and 20% for M4 groups and 20% and 14% for M5 groups. Significant estimated differences between mixed-sex and all-male groups were found in M3 and M4 groups, but for M5 groups, the estimated difference was not significant (Table 13.5d; Supplementary Material Table 13.2).

13.3.5 Female-Directed Aggression

Within the mixed-sex groups, we recorded 444 observations of peaceful behavior (no aggression observed; 94% of the observations). Clear aggression by males directed at females was observed on 29 occasions, notably in the M3 (7% of observations) and M4 groups (8%), compared with 3% in M5 groups (Fig. 13.5c +e). The estimated differences between M3, M4, and M5 groups were however not significant. Among the aggressive interactions, we recorded 24 bull chases (Fig. 13.5b). M3 groups were observed chasing a female in 7% of the observations, followed by M4 groups (5%). The lowest percentage was found in M5 groups (3%), but here again, the estimated differences between M3, M4, and M5 groups were not significant (Table 13.5d; Supplementary Material Table 13.1).

Figure 13.6 shows the durations of observed bull chases in relation to group size. Durations of bull chases varied from 8 minutes to 1 hour 11 minutes, with an average of 23 minutes. Male group sizes involved in bull chases varied from 5 to 38 male individuals (mean 13.4, SD 6.5). During all of these events, only one female was chased. The average travel speed ranged between 18 and 32 km/h (boat speed travelling alongside the group taken as a proxy).

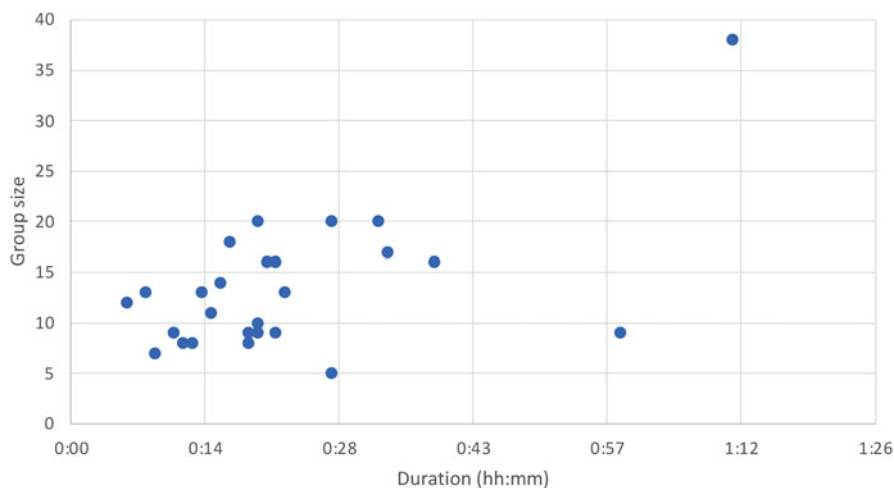


Fig. 13.6 Distribution of the durations of observed bull chases in relation to group size

13.3.6 *Mating Events*

Male Risso's dolphin chases often led to intense mating sessions, during which the targeted female could be violently pushed and squeezed between males (Fig. 13.4b and c). Mating was also observed in more peaceful settings, usually taking place when a female was consorted by one single male group (in which the female was swimming in synchrony with one male (size, 3–12; Hartman et al. 2008), and no competing male pods were involved or nearby (Fig. 13.5a and b). Copulation was observed during 38% of the bull chases (Fig. 13.5c).

13.3.7 *Rare Observations*

13.3.7.1 *Males Associating Peacefully with Neonates*

On four different occasions, we observed four different (confirmed) males (3x M4, 1x M3) associating with four different neonate calves for short periods of time. This behavior only occurred during mixed-sex foraging events. Calves were observed in “calf-position” next to the male, on three occasions within 10 seconds and on one occasion within 16 seconds after the mother had disappeared from the surface to forage. During the interaction, the male was swimming at low speed (less than 2.5 km per hour). The calf was retrieved by the mother after 8–12 minutes, with the male calmly swimming in the vicinity of the group (Fig. 13.3g–h).

13.3.7.2 *In-Nursery and Calf-Directed Aggression by Males*

We only occasionally ($n = 4$) witnessed males harassing females and calves in nurseries. These events lasted for less than a minute, with females avoiding interactions by performing shallow dives, surfacing after some minutes at 150–300 m from the males.

However, on two occasions, we observed males displaying highly aggressive behavior toward neonates (Fig. 13.4d–e). Confirmed resident males were seen chasing a single neonate at high speed, during which attempts to bite, slap, or jump on top of the neonate were recorded. Some of these displays clearly made it difficult for the neonate to breathe. During 1 occasion (group size, 32 animals), a mother was chased by 6–8 males of the same social male unit, separating the female from her calf and preventing the mother from protecting her offspring. Two older male pods were following but not interfering and seemed occupied with other females. Other nursing females and some subadult units were staying close to the aggressors, without interfering. The male aggression may have led to its death, although we did not observe an actual kill during this occasion. Nevertheless, the neonate was not resighted the following days, and the mother was seen without this

calf on several occasions after the event (and for the rest of the particular season), so we assumed it had died. On another occasion, males chased a female with a neonate without separating them. We observed highly aggressive and coordinated behavior with around five to six males trying to bite, headbutt, and beat both the mother and the calf. Chasing lasted for at least two sessions of 30 minutes during this observation. This group was a nonresident pod including 45–50 individuals, organized in subunits of similar age classes. The mother and calf were not resighted in the following days or years.

13.4 Discussion

13.4.1 *Mating Tactics*

The social ecology and mating system of Risso's dolphins studied off Pico Island appear to be diverse and complex, considering the range of patterns observed in this dataset. Table 13.6 lists the observed behaviors in this study, distinguishing peaceful and aggressive behaviors in relation to male and female mating tactics observed in mixed-sex groups.

13.4.2 *Contest Competition*

Although intense male-male aggression was observed on multiple occasions, these only represented a small percentage of all observations: male-male aggression was only recorded in 3% ($n = 28$) of all observations ($n = 834$) of all-male and mixed-sex groups combined. Individuals may avoid intense aggressive events, given the risk of injury and the high energetic costs. In contrast, females never exhibited or initiated aggressive behaviors against other females or during social events involving male individuals. During aggressive events among males, "headbutting" was regularly observed. The fact that within the M4 age class male-male aggression occurred significantly more frequently in mixed-sex groups than in all-male groups suggests that the presence of females increased the competitive pressure. These fights may be related to competition between dominant and competing male pods and individuals (Clutton Brock 2016). Similar contest behavior has been reported in male northern bottlenose whales (*Hyperoodon ampullatus*; Gowans and Rendell 1999).

Subadult (M3) male groups socialized more than males in older age classes, although the difference was only significant with M5 groups. This might be explained by the fluid association patterns of subadults, illustrated by weak to moderate associations between pairs (Hartman et al. 2008). We hypothesize that during the stage when male groups are formed, it may be useful for subadult males to assess relationships with their peers in social events that include fighting. In subsequent life stages, this "testing" of relationships may continue to be a useful tool for

Table 13.6 Ethogram with definitions of peaceful and aggressive behavior states in Risso's dolphins off Pico Island, classified according to mating tactics (after Orbach 2019)

Group composition	Definition	Behavior type	Male mating tactic	Female mating tactic
Peaceful behaviors				
All-male/all-female	Calm, paired or non-paired, often resting/travelling, few interactions	Calm		
Mixed	General socializing events with frequent semi-peaceful to moderately aggressive interactions	Socializing		
Mixed	Confirmed female(s) swimming synchronized with a male "partner," no aggressive interactions	Consortship (sync)	Endurance competition	Mate choice
Mixed	Confirmed female(s) swimming synchronized with a female "partner," no aggressive interactions	Consortship (loose)	Endurance competition	Mate choice
Mixed	Confirmed female(s) swimming freely close to or surrounded by males, <15 m distance	Consortship (loose)	Endurance competition	Mate choice
Mixed	Confirmed female(s) swimming freely with no interaction with males, >15 m distance	No consortship	Endurance competition	Mate choice
Mixed	Males present in, or following, a nursery with females and calves	No consortship	Endurance competition	Mate choice
Mixed	Several males (repeatedly) attempting to mate with the female, who may cooperate or evade	Mating	Sperm competition	Mate choice/evasive behavior
Mixed	Male individuals taking care of a neonate during mixed foraging events	Neonate care	Endurance competition	Mate choice
Aggressive behaviors				
All-male	General aggressive displays	Aggression	Contest competition	-
All male	Individuals turn backward at the surface and headbutt/bite one another in star formation	Headbutting/biting	Contest competition	-
All male	Individuals strike tails at one another at the surface	Tail striking	Contest competition	-
Mixed	Males chasing (a) female(s) at high speed (25–32 km/h) for prolonged periods getting access to/isolating/or stealing females from other males	Bull chase	Scramble competition	Signal discrimination
Mixed	Aggressive displays toward female observed (e.g., biting, pushing, tail striking, enclosing, and squeezing)	Female-directed aggression	Scramble competition	Evasive behavior

(continued)

Table 13.6 (continued)

Group composition	Definition	Behavior type	Male mating tactic	Female mating tactic
Mixed	Males chasing females and calves for short periods, often females with larger calves	Male harassment of nursery	Scramble competition	Signal discrimination/evasive behavior
Mixed	Actual mating	Mating	Sperm competition	Signal discrimination/evasive behavior
Mixed	Males chasing neonates highly aggressively, frequent body contact	Potential infanticide	Contest competition	Signal discrimination/evasive behavior

individuals in assessing the costs and benefits of belonging to a specific cluster, but it seems to reduce with age, as is illustrated by the significant difference in socializing between M4 and M5 groups. Male Risso's dolphins from all age classes engaged in intense fights, displaying aggression toward each other through tail striking, biting, and/or headbutting. Fresh and bloody scars were often visible after these events.

13.4.3 Endurance Competition, Display Competition, and Female Mate Choice

The two types of consortships (synchronized and loose formation) in this study are interpreted as manifestations of endurance competition. This, together with synchronized mixed-sex couples during consortships, has not been described before in this species. During consortships, not all females in mixed-sex groups were consorted; the average number of consorted females was much lower than the average number of females present, across all male age classes. This may be related to the paucity of fertile females as a result of the male-biased operational sex ratio, but it could also reflect the number of males required to control a female. Average number of males per female in consortships varied strongly with male age class, suggesting that factors related to age play a stronger role than the operational sex ratio. The highest number of sync consortships (52%) was observed in M4 male groups, comprising both subadult and adult females. This group type also shows the highest average number of males. The significantly higher level of male-male aggression compared to all-male M4 groups is an indicator of intense competition for access to females. Females may thus be more motivated to escape male aggression, which may require closer control of the females and a higher number of cooperating males to prevent females from escaping or defend against "theft" of these females by competing male

groups. Similar patterns of male aggression toward females during consortships occur in Indo-Pacific bottlenose dolphins (Connor et al. 1992, 1996), where they are also indicated by numerous tooth marks on both sexes (Scott et al. 2005).

In the M3 groups, males and females tended to be subadults. Average number of males was lower than in M4 groups, and even though M3 groups engage significantly more in socializing than the older age classes, they show the lowest (though not significantly lower) percentage of male-male aggression. M3 groups spend more time and energy on socializing. This may explain why the percentage of sync consortships is significantly lower than in M4 groups that appear to be more focused on gaining access to, and guarding, females.

In contrast, M5 groups had the highest percentage of loose consortships and the lowest number of males per consorted female, suggesting a more relaxed group behavior compared to the sync consortships. The lowest number of males per female was observed in these mature male groups. This can be an indication of female (mate) choice, allowing older males to gain access to females in smaller numbers. Earlier theoretical models predicted that female individuals prefer to mate with older males, who would pass on so-called good genes to their offspring through viability selection (Trivers 1972; Kokko and Lindström 1996; Kokko 1998). In contrast, other models predicted the evolution of female preference for young males, since fertility reduces with male age (Beck and Promislow 2007), while yet other studies highlight the importance of other factors than age (Scauzillo and Ferkin 2019; Aich et al. 2020). Our findings suggest that, apart from the possible selection of higher genotypic quality, there could be other reasons why female Risso's dolphins may favor older over younger males. For one, mature males are overall more peaceful, reflected by the lowest percentage in time spent on socializing and on female-directed aggression compared to the younger age classes. Given the risk of injury (also for offspring), and the energetic costs involved, females may prefer to be around nonaggressive older males rather than frisky subadults and M4 males. Besides, the skin coloration of Risso's dolphin males has been suggested to serve as an indicator of male quality (MacLeod, 1998), and a whiter color may also assist to deter conspecific competitors. It is also possible that potential fathers may be present among these M5 groups, who by guarding a group may defend their possible offspring through display competition. Similar patterns of male protection have been suggested in Indo-Pacific bottlenose dolphins (Lusseau 2007). Finally, M5 groups maintain stable associations (Hartman et al. 2008), an indication for successful cooperation among individuals. Overall, the maintenance of social relationships in groups with male mammal individuals is complex given the intragroup rivalry for reproduction (De Waal and Tyack 2009; Clutton Brock 2016). Hence, mature M5 male groups may not only provide a safer environment but also display desirable qualities for viable offspring and therefore be attractive to females.

A remarkable finding in this study is the regular presence of multiple (consorted) females in mixed-sex units of Risso's dolphins. In Indo-Pacific bottlenose dolphins over a 30-year study, only one case was reported of a male trio herding two females simultaneously (Connor and Krützen 2015). The group sizes in Risso's dolphins are greater, with 4.10 (M5 groups) to 8.25 (M4 groups) males per target, compared with

the two or three males in the first order alliances in Indo-Pacific bottlenose dolphins, but the presence of multiple Risso's dolphin females in male groups may also be related to female choice, especially in the older ones. An alternative explanation would be the occurrence of synchronous interbirth cycles, in combination with the temporally stable associations between non-nursing and nursing females (Hartman et al. 2008, 2014; Mann 2019).

13.4.4 Scramble Competition, Signal Discrimination, and Evasive Behavior

Male Risso's dolphin chases, an example of scramble competition, were only occasionally observed (in 4.6% of observations of mixed-sex groups), which is probably due to the high energetic costs for a species that has to save energy for deep foraging dives. It is unknown whether this mating tactic is initiated by males or females. It is plausible that these events were initiated by males (potentially following the escape of a female), since they were generally characterized by aggression toward the female by the male participants. During chases, not all male individuals were "in the frontline," and only a subset of male individuals involved in a chase were close to the female during mating events, indicating that not all males could mate with the female. We observed clear signals of stress and exhaustion in the female target, as well as attempts to avoid mating (evasive behavior). Nevertheless, the phenomenon might also be an instance of the female signaling a discrimination mating tactic, allowing the fittest males to mate (Orbach, 2019), as illustrated by the longest chase observed in this study, involving 38 males. During such long contests, the targeted female stands a good chance to mate and become fertilized by the fittest individual (Markowitz et al. 2010).

During or at the end of such chases, intense multi-male mating sessions often took place once the female was exhausted. In 1 observation in 2017, more than 80 mating events were recorded with an underwater camera involving 10 males and 1 female during 1h 15 min (K.L. Hartman, personal observation). Most of the male group members displayed aggressive behavior toward the female, including biting, tail striking, headbutting, and mating. Between mating sessions, the female tried to escape from the group but during 2 hours of observation did not succeed (Supplementary Material Video).

13.4.5 Mating

Mating occurred among male individuals from competing clusters or from the same cluster, usually in response to a mating event between another male and a female during a consortship. However, these intragroup mating events were often peaceful. Males consecutively mated with the same female one after the other. Figure 1a–b in

Supplementary Materials shows two occasions of intragroup multiple mating events captured.

13.4.6 *Male Care of Calves*

Our dataset comprised four observations of peaceful interactions between single males and neonates. Like most mammals, long-term parental care in cetaceans is generally provided by females (Whitehead and Mann 2000; Mann 2019). However, a limited number of observations concerning males taking care of calves have been recorded in killer whales (*Orcinus orca*; Bigg et al. 1990), involving care for related calves within a family pod. In bottlenose dolphins, males may escort females with calves to prevent infanticide of their (possible) offspring by outsiders (Lusseau 2007; Brightwell and Gibson 2023, this book; McEntee et al. 2023, this book), whereas in Atlantic spotted dolphins (*Stenella frontalis*), males may be involved with young to teach “desired behavior” (Weinpress and Herzing 2015). Furthermore, in long-finned pilot whales (*Globicephala Melas*), sporadic male care has been suggested to be a by-product of their matrilineal social structure and by another strategy described as “social prestige” (Zahavi 1975, 1995), where males show their mating potential to females through calf care (Augusto et al. 2017).

Risso’s dolphins seem to have a polygynandrous mating system, where male care of calves is unlikely to be inspired by paternity, and the observations of several individual males guarding neonates in this study are viewed as extraordinary. This behavior was only observed during mixed-sex foraging behavior, when female Risso’s dolphins regularly left their offspring in the care of allied females (and, occasionally, males). One explanation might be that males and females of the same age class had spent the first years of their lives together in a nursery, which may have created a basis for female-male trust in a later stage of their lives. Other explanations include the possibility that the male and female are (half-) siblings or that the male displays a “social” behavior, hoping to improve his chances of mating in the future (Zahavi 1975, 1995; Augusto et al. 2017), a form of endurance competition.

13.4.7 *Calf-Directed Aggression*

Based on the sexual selection hypothesis, male mammals commit infanticide to enhance their fitness, since after having killed a calf the female stops lactating and may become fertile again, which enhances mating opportunities, and in addition infanticide removes unrelated males from the gene pool (Hrdy 1979). In cetaceans, conspecific infanticide is relatively rare, but it has been described in various dolphin species: common bottlenose dolphins (Patterson et al. 1998; Dunn et al. 2002; Kaplan et al. 2009; Robinson 2014; Perrtree et al. 2016; Díaz López et al. 2018), Indo-Pacific humpback dolphins (*Sousa chinensis*; Zheng et al. 2016), Guiana

dolphins (*Sotalia guianensis*; Nery and Simão 2009), and killer whales (Towers et al. 2018; McEntee et al. 2023, this book).

Overall, calf-directed aggression by male Risso's dolphins has rarely been observed, with only two documented occasions over an extended research period that may have led to infanticide. On both occasions, several males attacked the female and calf, giving the impression of an organized action to eliminate the calf. It is impossible for male Risso's dolphins to be sure of their paternity, but it is plausible that males know whether they have mated with a female or not. Thus, it is possible that calf-directed aggression is initiated by males who have not had the opportunity to mate with the mother. For this reason, female Risso's dolphins may reduce the risk of infanticide by mating with as many males as possible, as has been suggested for Indo-Pacific bottlenose dolphins (Connor et al. 1996).

13.5 Conclusions and Future Directions

Previous studies reported the existence of genetically distinct populations of Risso's dolphins (Gaspari et al. 2007; Chen et al. 2018), highlighting that social ecology may vary between (sub-) populations. This study presents data coming from one field site. Therefore, it is highly recommended to compare present results with data from other populations. For example, the chases observed in the Mediterranean Sea (Cipriano et al. 2022) may be an indication of similar scramble competition tactics in another population. However, at present, there are not sufficient data available from other study sites.

Risso's dolphins observed off Pico Island display a range of mating strategies, influenced by big testes, 4- to 5-year interbirth intervals, and small sexual size dimorphism, which cause a male-biased operational sex ratio. Their pelagic habitat may require a robust number of "allies" to gain and maintain access to females, and this may have contributed to the formation of stable male groups of the same age class and presumably of similar strength. In females, a diet based on deep-sea cephalopods and avoidance of male aggression may have promoted the formation of temporally stable female clusters in the same reproductive stage, a system in which they gain protection for neonates and young calves through babysitting when foraging (Hartman et al. 2014; Hartman 2018).

Mating tactics (and success) seem related to age class, reproductive stage, and possibly the strength of association between individuals. Mating tactics in this study correspond to those of different cetacean species (Orbach 2019; Würsig et al. 2023, this book), ranging from two types of peaceful consortships to aggressive male chases. Mating behavior regularly involved multiple mating sessions where the same female mates with different males. These events could be either aggressive (typically when multiple groups were involved and there was intergroup competition) or peaceful (generally when one social unit was involved and there was only intragroup competition). Rare behaviors included male care for neonates and, in contrast, intense aggression from males toward newborn calves, leading to possible

infanticide. The apparent preference of females for mature over younger male groups, combined with the peaceful character of these interactions, suggests some level of female mate choice.

Present findings invite further research. Long-term association data analyzed at individuals' level may clarify the evolution of male group structures and their drivers. For females, preference for certain males or male clusters may clarify the degree of mating choice. Future studies should include investigation of synchronous mixed-sex couples during consortships, as it seems a striking behavior. Furthermore, studies focusing on the degree of kinship may reveal if kinship is a driver for stable male units and forms a basis for potential matrilineal group formation.

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References

- Aich U, Bonnet T, Fox RJ, Jennions MD (2020) An experimental test to separate the effects of male age and mating history on female mate choice. *Behav Ecol* 31:1353–1360. <https://doi.org/10.1093/beheco/araa092>
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–266. <https://doi.org/10.1163/156853974X00534>
- Amano M, Miyazaki N (2004) Composition of a school of Risso's dolphins, *Grampus griseus*. *Mar Mamm Sci* 20:152–160. <https://doi.org/10.1111/j.1748-7692.2004.tb01146.x>
- Augusto JF, Frasier TR, Whitehead H (2017) Characterizing alloparental care in the pilot whale (*Globicephala melas*) population that summers off Cape Breton, Nova Scotia, Canada. *Mar Mamm Sci* 33:440–456. <https://doi.org/10.1111/mms.12377>
- Bååth R (2014) Bayesian First Aid: a package that implements Bayesian alternatives to the classical *.test functions in R. In: *Proceedings of UseR*
- Bearzi G, Reeves RR, Remonato E, Pierantonio N, Airoidi S (2011) Risso's dolphin *Grampus griseus* in the Mediterranean Sea. *Mamm Biol* 76:385–400. <https://doi.org/10.1016/j.mambio.2010.06.003>
- Beck CW, Promislow DEL (2007) Evolution of female preference for younger males. *PLoS one* 2: e939. <https://doi.org/10.1371/journal.pone.0000939>
- Bigg MA, Olesiuk PF, Ellis GM, Ford JK, Balcomb KC (1990) Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Rep Int Whal Commn* 12:383–405
- Bloch D, Desportes G, Harvey P, Lockyer C, Mikkelsen B (2012) Life history of Risso's dolphin (*Grampus griseus*) (G. Cuvier, 1812) in the Faroe Islands. *Aqua Mamm* 38:250–266. <https://doi.org/10.1578/AM.38.3.2012.250>
- 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

- Cascao I, Domokos R, Lammers MO, Santos RS, Silva MA (2019) Seamount effects on the diel vertical migration and spatial structure of micronekton. *Prog Oceanogr* 175:1–13. <https://doi.org/10.1016/j.pocean.2019.03.008>
- Chen I, Nishida S, Chou LS, Tajima Y, Yang WC, Isobe T, Yamada TK, Hartman K, Hoelzel AR (2018) Concordance between genetic diversity and marine biogeography in a highly mobile marine mammal, the Risso's dolphin. *J Biogeogr* 45:2092–2103. <https://doi.org/10.1111/jbi.13360>
- Cipriano G, Carlucci R, Bellomo S, Santacesaria FC, Fanizza C, Ricci P, Maglietta R (2022) Behavioral pattern of Risso's dolphin (*Grampus griseus*) in the Gulf of Taranto (Northern Ionian Sea, Central-Eastern Mediterranean Sea). *J Mar Sci Eng* 10:175. <https://doi.org/10.3390/jmse10020175>
- Clutton Brock T (2016) Relationships between males in multi-male groups. In: Clutton-Brock TH (ed) *Mammal societies*. John Wiley & Sons, Chichester, pp 466–492
- Connor RC, Krützen M (2015) Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. *Anim Behav* 103:223–235. <https://doi.org/10.1016/j.anbehav.2015.02.019>
- Connor RC, Smolker RA, Richards AF (1992) Two levels of alliance formation among male bottlenose dolphins (*Tursiops sp.*). *Proc Nat Acad Sci USA* 89:987–990. <https://doi.org/10.1073/pnas.89.3.987>
- Connor RC, Richards AF, Smolker RA, Mann J (1996) Patterns of female attractiveness in Indian ocean bottlenose dolphins. *Behaviour* 133:37–69
- Connor RC, Read AJ, Wrangham R (2000) Male reproductive strategies and social bonds. In: Mann JC, Connor RC, Tyack PL, Whitehead H (eds) *Cetacean societies: field studies of dolphins and whales*. The University of Chicago Press, Chicago, IL, pp 91–126
- Connor RC, Smolker R, Bejder L (2006) Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Anim Behav* 72:1371–1378. <https://doi.org/10.1016/j.anbehav.2006.03.014>
- Cox R (2017) Sexual size dimorphism. In: Shackelford TK, Weekes-Shackelford VA (eds) *Encyclopedia of evolutionary psychological science*. Springer International Publishing, Cham, pp 1–6
- De Waal F, Tyack PL (eds) (2009) *Animal social complexity: intelligence, culture, and individualized societies*. Harvard University Press, Harvard, MA
- Delignette-Muller ML, Dutang C (2015) fitdistrplus: an R Package for Fitting Distributions. *J Stat Softw* 64:1–34. <https://doi.org/10.18637/jss.v064.i04>
- Díaz López B, López A, Methion S, Covelo P (2018) Infanticide attacks and associated epimeletic behaviour in free-ranging common bottlenose dolphins (*Tursiops truncatus*). *J Mar Biol Assoc UK* 98:1159–1167. <https://doi.org/10.1017/S0025315417001266>
- Dunn DG, Barco SG, Pabst DA, McLellan WA (2002) Evidence for infanticide in bottlenose dolphins of the western north atlantic. *J Wildl Dis* 38:505–510. <https://doi.org/10.7589/0090-3558-38.3.505>
- Fox J, Weisberg S (2019) *An R companion to applied regression*, 3rd edn. Sage Publications, Thousand Oaks, CA
- Gaspari S, Airoidi S, Hoelzel AR (2007) Risso's dolphins (*Grampus griseus*) in UK waters are differentiated from a population in the Mediterranean Sea and genetically less diverse. *Cons Gene* 8:727–732. <https://doi.org/10.1007/s10592-006-9205-y>
- Gowans S, Rendell L (1999) Head-butting in northern bottlenose whales (*Hyperoodon ampullatus*): a possible function for big heads? *Mar Mamm Sci* 15:1342–1350
- Hartman KL (2018) Risso's dolphin: *Grampus griseus*. In: Würsig B, Thewissen JGM, Kovacs KM (eds) *Encyclopedia of marine mammals*, 3rd edn. Academic Press, London, pp 824–827
- Hartman K, Visser F, Hendriks A (2008) Social structure of Risso's dolphins (*Grampus griseus*) at the Azores: a stratified community based on highly associated social units. *Can J Zool* 86:294–306. <https://doi.org/10.1139/Z07-138>

- Hartman KL, Fernandez M, Azevedo JMN (2014) Spatial segregation of calving and nursing Risso's dolphins (*Grampus griseus*) in the Azores, and its conservation implications. *Mar Biol* 161:1419–1428. <https://doi.org/10.1007/s00227-014-2430-x>
- Hartman KL, Fernandez M, Wittich A, Azevedo JMN (2015) Sex differences in residency patterns of Risso's dolphins (*Grampus griseus*) in the Azores: causes and management implications. *Mar Mamm Sci* 31:1153–1167. <https://doi.org/10.1111/mms.12209>
- Hartman KL, Wittich A, Cai JJ, Van Der Meulen FH, Azevedo JM (2016) Estimating the age of Risso's dolphins (*Grampus griseus*) based on skin appearance. *J Mamm* 97:490–502. <https://doi.org/10.1093/jmammal/gyv193>
- 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. <https://doi.org/10.3389/fmars.2020.00283>
- Hodgins NK, Dolman SJ, Weir CR (2014) Potential hybridism between free-ranging Risso's dolphins (*Grampus griseus*) and bottlenose dolphins (*Tursiops truncatus*) off north-east Lewis (Hebrides, UK). *Mar Biodiv Rec* 7:e97. <https://doi.org/10.1017/S175526721400089X>
- Hrdy SB (1979) Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethol Sociobiol* 1:13–40. [https://doi.org/10.1016/0162-3095\(79\)90004-9](https://doi.org/10.1016/0162-3095(79)90004-9)
- Kaplan JD, Lentell BJ, Lange W (2009) Possible evidence for infanticide among bottlenose dolphins (*Tursiops truncatus*) off St. Augustine, Florida. *Mar Mamm Sci* 25:970–975. <https://doi.org/10.1111/j.1748-7692.2009.00323.x>
- Kokko H (1998) Good genes, old age and life-history trade-offs. *Evol Ecol* 12:739–750. <https://doi.org/10.1023/A:1006541701002>
- Kokko H, Lindström J (1996) Evolution of female preference for old mates. *Proc Royal Soc Lond B* 263:1533–1538. <https://doi.org/10.1098/rspb.1996.0224>
- Kruse SL (1989) Aspects of the biology, ecology and behavior of Risso's dolphins (*Grampus griseus*) off the California coast. MS thesis, University of California
- Lenth R (2023) emmeans: estimated marginal means, aka least-squares means. R package version 1 (8):7. <https://CRAN.R-project.org/package=emmeans>
- Lusseau D (2007) Why are male social relationships complex in the doubtful sound bottlenose dolphin population? *PLoS one* 2:e348. <https://doi.org/10.1371/journal.pone.0000348>
- MacLeod CD (1998) Intraspecific scarring in odontocete cetaceans: an indicator of male 'quality' in aggressive social interactions? *J Zool* 244:71–77. <https://doi.org/10.1111/j.1469-7998.1998.tb00008.x>
- Mann J (1999) Behavioral sampling methods for cetaceans: a review and critique. *Mar Mamm Sci* 15:102–122. <https://doi.org/10.1111/j.1748-7692.1999.tb00784.x>
- Mann J (2019) Maternal care and offspring development in odontocetes. In: Würsig B (ed) *Ethology and behavioral ecology of odontocetes*. Springer Nature, Cham, pp 95–116
- Markowitz TM, Markowitz WJ, Morton LM (2010) Mating habits of New Zealand dusky dolphins. In: Würsig B, Würsig M (eds) *The dusky dolphin: master acrobat off different shores*. Elsevier, Amsterdam, pp 151–176
- McCue LM, Cioffi WR, Heithaus MR, Barrè L, Connor RC (2020) Synchrony, leadership, and association in male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Ethology* 1–10. <https://doi.org/10.1111/eth.13025>
- 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
- Möller LM (2012) Sociogenetic structure, kin associations and bonding in delphinids. *Mol Ecol* 21: 745–764. <https://doi.org/10.1111/j.1365-294X.2011.05405.x>
- Morton B, Britton JC, de Frias Martins AM (1998) Coastal ecology of the Açores. Sociedade Afonso Chaves, Ponta Delgada, Azores
- Nery MF, Simão SM (2009) Sexual coercion and aggression towards a newborn calf of marine tucuxi dolphins (*Sotalia guianensis*). *Mar Mamm Sci* 25:450–454. <https://doi.org/10.1111/j.1748-7692.2008.00275.x>

- Orbach DN (2019b) Sexual strategies- male and female mating tactics. In: Würsig B (ed) *Ethology and behavioral ecology of odontocetes*. Springer Nature, Cham, pp 75–93
- Patterson IA, Reid RJ, Wilson B, Grellier K, Ross HM, Thompson PM (1998) Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? *Proc R Soc Lond B* 265:1167–1170. <https://doi.org/10.1098/rspb.1998.0414>
- Perret 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* 32:376–385. <https://doi.org/10.1111/mms.12248>
- R core team (2022) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. <https://www.R-project.org>
- Robinson KP (2014) Agonistic intraspecific behavior in free-ranging bottlenose dolphins: calf-directed aggression and infanticidal tendencies by adult males. *Mar Mamm Sci* 30:381–388. <https://doi.org/10.1111/mms.12023>
- Sakai M, Morisaka T, Kogi K, Hishii T, Kohshima S (2010) Fine-scale analysis of synchronous breathing in wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Behav Proc* 83:48–53. <https://doi.org/10.1016/j.beproc.2009.10.001>
- Scauzillo RC, Ferkin MH (2019) Factors that affect non-independent mate choice. *Biol J Linn Soc* 128:499–514. <https://doi.org/10.1093/biolinnean/blz112>
- Scott EM, Mann J, Watson-Capps JJ, Sargeant BL, Connor RC (2005) Aggression in bottlenose dolphins: evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour* 142:21–44. <https://doi.org/10.1163/1568539053627712>
- Senigaglia V, Whitehead H (2012) Synchronous breathing by pilot whales. *Mar Mamm Sci* 28: 213–219. <https://doi.org/10.1111/j.1748-7692.2011.00465.x>
- Shane SH (1990) Behavior and ecology of the bottlenose dolphin at Sanibel Island Florida. In: Leatherwood S, Reeves RR (eds) *The bottlenose dolphin*. Academic Press, New York, NY
- Silva MA, Prieto R, Cascão I, Seabra MI, Machete M, Baumgartner MF, Santos RS (2014) Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. *Mar Biol Res* 10:123–137. <https://doi.org/10.1080/17451000.2013.793814>
- Smolker RA, Richards AF, Connor RC, Pepper JW (1992) Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour* 123:38–69. <https://doi.org/10.1163/156853992X00101>
- Towers JR, Hallé MJ, Symonds HK, Sutton GJ, Morton AB, Spong P, Borrowman JP, Ford JK (2018) Infanticide in a mammal-eating killer whale population. *Sci Rep* 8:4366. <https://doi.org/10.1038/s41598-018-22714-x>
- Trivers R (1972) Parental investment and sexual selection. In: *Sexual selection and the descent of man*. Aldine, Chicago, IL, p 378
- Visser F, Hartman KL, Rood EJ, Hendriks AJ, Zult DB, Wolff WJ, Huisman J, Pierce GJ (2011) Risso's dolphins alter daily resting pattern in response to whale watching at the Azores. *Mar Mamm Sci* 27:366–381. <https://doi.org/10.1111/j.1748-7692.2010.00398.x>
- Weinpress MR, Herzing DL (2015) Maternal and alloparental discipline in atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas. *Anim Behav Cogn* 2:348–364. <https://doi.org/10.12966/abc.11.04.2015>
- Wells RS (2018) Identification methods. In: Würsig B, Thewissen JGM, Kovacs KM (eds) *Encyclopedia of marine mammals*, 3rd edn. Academic Press, London, pp 503–509
- Whitehead H (2003) *Sperm whales: social evolution in the ocean*. University of Chicago Press, Chicago, IL
- Whitehead H, Mann J (2000) Female reproductive strategies of cetaceans: life histories and calf care. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) *Cetacean societies: field studies of dolphins and whales*. University of Chicago Press, Chicago, IL, pp 219–246
- Würsig B, Jefferson TA (1990) Methods of photo-identification for small cetaceans. *Rep Int Whal Commn Special issue* 12:43–52

- Würsig B, Rich J, Orbach DN (2023) Sex and behavior. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham
- Zahavi A (1975) Mate selection—a selection for a handicap. *J Theor Biol* 53:205–214. [https://doi.org/10.1016/0022-5193\(75\)90111-3](https://doi.org/10.1016/0022-5193(75)90111-3)
- Zahavi A (1995) Altruism as a handicap: the limitations of kin selection and reciprocity. *J Avian Biol* 26:1–3. <https://doi.org/10.2307/3677205>
- Zheng R, Karczmarski L, Lin W, Chan SC, Chang WL, Wu Y (2016) Infanticide in the Indo-Pacific humpback dolphin (*Sousa chinensis*). *J Ethol* 34:299–307. <https://doi.org/10.1007/s10164-016-0475-7>

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