

Measuring the Mating Behaviors of Free-Ranging Dusky Dolphins (*Lagenorhynchus obscurus*)

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Dolphins, whales, and porpoises generally have a polygamous (multi-partner) mating system [1]. Males use a variety of mating tactics to acquire paternity such as contest (e.g. fighting) and sperm competition [1]. Male mating strategies are conditional and depend on the distribution and monopolization potential of receptive females [2]. Among dolphin species, male mating tactics have been predicted based on sexual size dimorphism and relative testes mass in lieu of direct observations of mating events [1]. Mating behaviors are poorly described for most cetacean species and are generally limited to anecdotal reports with inadequate quantitative data [e.g. 3] or studies of captive animals with restricted inter-sexual interactions [e.g. 4]. It is logistically challenging to assess cetacean mating behaviors in nature as the animals are far off-shore and submerged underwater more often than they are visible to observers at the surface.

The dusky dolphin (*Lagenorhynchus obscurus*) population off Kaikoura, New Zealand (42° S, 173° E) provides a unique opportunity to assess cetacean mating behaviors and evaluate this population's mating system and tactics. There are ~ 2,000 individuals present at any given time, which form highly fission-fusion groups with continuous group size changes [5]. Foraging and mating behaviors are temporally and spatially separated [5-7]. Copulation events occur frequently near-shore during the breeding season in water visibility conditions that are good for above-water videography (>10 meters) [5, 8-10]. The mating system of dusky dolphins has been described as promiscuous with random breeding and polygandrous (multiple males mate with multiple females) with non-random breeding [reviewed in 10]. We describe techniques to measure mating behaviors that will determine if free-ranging dusky dolphins demonstrate mate choice.

Dusky dolphin mating groups were followed from a 6 m research vessel during the peak breeding season from October through January in 2011-2012 and 2013-2014. Mating groups were defined as small isolated pods (< 50 individuals) with a constant group size in which either attempted copulations or an individual with an erect penis was observed [10]. Individuals in a group remained within 10 m of each other for an extended period of time [11]. Dusky dolphins in mating groups off Kaikoura typically perform simultaneous aerial leaps involving 1-3 individuals [10]. Mating groups were detected by three onboard researchers who scanned the horizon for leaping dolphins while travelling parallel to shore [9]. Follows were conducted in good boating conditions (Beaufort <3) where the dolphins could be tracked at ~ 5 m distance from the vessel. Follows ended when mating behaviors stopped, the group size changed, or the animals exhibited evasive behaviors towards the research vessel (e.g. resurfacing >50 m distance). Mating groups rarely evaded the research vessel. We adhered to the operating regulations set by the Marine Mammals Protection Act 1978, Marine Mammal Protection Regulation 1992, and local dolphin conservation guidelines [12]. No permit was required for this study.

Approximately 1,200 minutes of dusky dolphin mating video footage and 960 copulation events were video-recorded while travelling parallel to 91 mating groups. Continuous videos were recorded using a Sony Handycam HDR-XR550V recorder mounted to a chest-pod to reduce vibrations. Detailed *ad libitum* narrations included the group size, composition (adult, sub-adult, or calf), observed behaviors, initiation and termination of behaviors, and the sex of the dolphin performing the behavior. We calculated the number, duration, and frequency of copulation

events and sex-specific mating behaviors. Males and females were distinguished based on observations of ano-genital slits and erect penises or ventrum orientation during attempted copulations [8-10]. Dusky dolphins copulate in ventrum-to-ventrum position with the female ventrum-down [5, 8-10]. We defined the duration of copulation bouts as the time between commencement and termination of ventrum-to-ventrum swimming. All approaches by the inverted male which resulted in ventral contact with the female were scored as copulations due to difficulties confirming ejaculation. An ethogram of sex-specific mating behaviors was developed based on published descriptions [10] and direct observations of mating groups (Table 1). We focused on tracking females in mating groups as their ventrum-down body positioning provided visibility of their individually distinctive dorsal fins [13]. It was challenging to detect subtle behavioral changes in males when they swam inverted beneath a female because of distortion of the water and increased distance from the researchers. When males were ventrum-down at the surface of the water, we could not confirm their sex. There were several males in a mating group and it was not possible to track all their behaviors simultaneously. Accordingly, our ethogram may be biased towards detecting female behaviors.

Videos were analyzed post-hoc using the video analysis software Transana [14]. Video playback speed was reduced to up to 0.1x the original speed. The behaviors in the videos were transcribed and time-stamped, including start and end times of dives and copulation events. The number of animals within one body length of the copulating pair was noted for each copulation. Preference was given to the *ad libitum* narrations when there was conflict with observable data on video. The annotations were summarized in 1-minute time intervals to determine behavioral frequencies. Repeated occurrences of a single behavior were counted as separate events. The mean mating group follow duration was 13 minutes (S.E. \pm 1.15, $n=91$). Mating groups spent 92.6% of their time at the surface of the water, suggesting most of their mating behavior repertoire was observable. It is possible that different sex-specific mating behaviors occurred when the dolphins dove beyond our visibility range. Males and females copulated with several individuals in ventrum-to-ventrum contact. Males were inverted during all copulations and pushed the females against the surface of the water during 87% of all copulation events. Mating interactions generally consisted of five adult males chasing one adult female (S.E. \pm 0.33, $n=90$). Copulation events were brief, lasting 4.57 seconds in duration (S.E. \pm 0.26, $n=90$), and generally occurred once per minute (S.E. \pm 0.08, $n=91$) per group until the group broke apart or mating behaviors ceased. On average, 1.3 presumed males were within one body length of the copulating pair (S.E. \pm 0.09, $n=90$). These males could cooperate or compete with the copulating male. Males performed several behaviors to maintain a close spatial position near the female such as swimming directly beneath (3% of male behaviors) or physically blocking (2% of male behaviors) the pathway of a copulating pair. Females exhibited maneuvers such as reorientation leaps out of the water (31% of female behaviors), rolling onto their dorsa so their ano-genital regions were inaccessible to males (11% of female behaviors), changing directions of travel (17% of female behaviors), and slapping their tails to terminate physical contact with a male (32% of female behaviors).

Our study provides direct assessment of the behavioral components of mating strategies for a free-ranging cetacean population. We contribute to the broader understanding of sexual selection theory and evolutionary mechanisms in animals with complex social and group dynamics. The observed male behaviors indicate exploitative scramble competition. During scramble competition, the most maneuverable or proximate male dolphins gain copulation opportunities with a female [9-10]. The males that copulate with the female closest to her ovulation remove her from the resource pool of rival males. The mating tactics of male dusky dolphins vary from other dolphin species. For example, some bottlenose dolphins (*Tursiops* sp.) exhibit mate-guarding and aggression [15]. We did not observe male dusky dolphins exhibiting physically aggressive behaviors, such as biting. Physically aggressive behaviors are associated with male contest competition [1], and when directed towards a female, can constrain her ability to escape or select alternative mates [15].

The observed female behaviors indicate an overall evasive tactic that potentially enables them to exercise mate choice. Females may extend the duration or difficulty of the mating chase to evaluate the competitive abilities of potential mates [10]. However, some females may not exercise mate choice. For example, females close to ovulation may instead actively reject all males and thereby induce intense male intra-sexual competition. The techniques to measure dolphin mating behaviors and the ethogram developed in this study set the stage for sequence analyses of female behavioral responses to male sexual behaviors, such as first and second order Markov chain analyses. Subsequent sequence analysis will enable us to differentiate between female mate choice and male rivalry and to determine if the mating system of dusky dolphins is consistent with a promiscuous or polygynandrous definition.

Table 1. Ethogram of sex-specific mating behaviors of dusky dolphins off Kaikoura, New Zealand

Behavior	Sex	Description
Coordinated reorientation leap	Both	Simultaneous vertical leap out of the water by two or more dolphins followed by a head-first re-entry into the water. The whole dolphins' bodies clear the surface of the water
Reorientation leap of unknown sex	Unknown	A dolphin leaps vertically out of the water and re-enters head-first nearby. Its whole body clears the surface of the water. The sex of the dolphin is unknown
Tight circles	Both	Closely-spaced dolphins swim in a circle
Group dive	Both	All dolphins dive to depth and are no longer visible from the surface or an absence of surface behavior for at least 30 seconds duration
Inverted swim	Male	Male swims in a ventrum-up body position
Swim under leaping female	Male	Male swims inverted below a leaping female
Push female to surface	Male	Male pushes female up vertically while swimming ventrum-to-ventrum such that her dorsal region is above the surface of the water
Herd female against physical barrier	Male	Male pushes female against physical barrier (e.g. the keel of a vessel or the shore)
Swim under copulating pair	Male	Male swims inverted below and within one body-width of a copulating male
Interference	Male	Any movement by a male to directly break up a mating pair (e.g. positioning himself in the path of the copulating pair, rolling over the copulating pair, etc.)
Reorientation leap	Female	Female leaps vertically out of the water and re-enters head-first nearby. Her whole body clears the surface of the water
Tail slap	Female	Female raises her tail out of the water and strikes it against the surface of the water
Swerve	Female	Female quickly moves non-linearly through the water (e.g. small, fast changes

		in direction of travel)
Extreme directional change	Female	Female quickly changes her direction of travel 180° or more
Body roll	Female	Female rotates her body along her longitudinal axis (e.g. rolls onto her dorsum)
Caudal peduncle lift	Female	Female raises her caudal peduncle above the surface of the water during copulation
Spyhop	Female	Female positions herself vertically in the water with her head above the surface
Speed burst	Female	Female slices through the water at a high speed with minimal changes in direction

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