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Abstract

Males in polygamous species often engage in intra-sexual competition for mates. If females actively evade mating attempts, it may benefit males to cooperate to restrict female movement, as has been found in some mammals. We tested if male dusky dolphins (*Lagenorhynchus obscurus* (Gray, 1828)) cooperate or compete during group mating chases. If they cooperate, the per-male probability of copulating should increase with group size and if they compete, the probability should decrease. We followed mating groups by boat during the breeding season (Oct. 2013 – Jan. 2014) off Kaikoura, New Zealand. The copulation rate per male decreased with increasing group size and with the number of non-copulating males in proximity to a copulating female. Male dusky dolphins have multiple mates and appear to use sperm and exploitative scramble competition. Males may remain in mating groups despite competition because there are alliances within the groups, they are unable to exclude rivals from joining a group, the time and energy costs of searching for unescorted females exceed the costs of reduced mating opportunities in a group, they receive other direct or indirect benefits that offset the costs of reduced mating opportunities, or they are in the group largely for social learning rather than procreation.

Keywords

Cooperation, copulation, intra-sexual competition, scramble competition, dusky dolphin, *Lagenorhynchus obscurus*

44 Introduction

45 Intra-sexual competition among males for access to sexually mature females has been
46 documented in many species with polygynous (one male and multiple females) and
47 polygynandrous (multiple males and multiple females) mating systems (reviewed in Andersson
48 1994; Oliveira et al. 2008). The mating tactics used by males are largely dependent on their
49 ability to monopolize females (Emlen and Oring 1977; Clutton-Brock 1989). Males that
50 monopolize females often have higher reproductive success when they have few rivals (e.g.
51 Reichard et al. 2004). However, in some species and populations, males have higher
52 reproductive success when they cooperate instead of compete (e.g. lions, *Panthera leo* L., 1758;
53 Bygott et al. 1979; long-tailed manakins, *Chiroxiphia linearis* (Bonaparte, 1838); McDonald
54 1989; wild turkeys, *Meleagris gallopavo* L., 1758; Krakauer 2005), including circumstances
55 where males are unrelated and/or fertilizations are not sharable (e.g. reviewed in Díaz-Muñoz et
56 al. 2014; chimpanzees, *Pan troglodytes* (Blumenbach, 1775); Watts 1998; Camargue horses,
57 *Equus caballus* L., 1758; Feh 1999; fish, reviewed in Taborsky 2009; ungulates, reviewed in
58 Bro-Jørgensen 2011). For example, some male Indo-Pacific bottlenose dolphins (*Tursiops*
59 *aduncus* (Ehrenberg, 1832)) in Shark Bay, Western Australia, form stable first-order alliances
60 with one or two other males and cooperate to herd reproductive females (Connor et al. 1992;
61 Connor et al. 1996; reviewed in Connor and Krützen 2015). Males have been observed
62 coordinating movements and directing aggression towards evasive females (Connor and Smolker
63 1996). Cooperation between male Indo-Pacific bottlenose dolphins restricts female movements
64 (Connor and Smolker 1996). Adult males have higher reproductive success when they are part of
65 an alliance (Krützen et al. 2004).

Dusky dolphins (*Lagenorhynchus obscurus* (Gray, 1828)) off Kaikoura, New Zealand, also form mating groups with several males chasing one sexually mature female (Markowitz et al. 2010; Orbach et al. 2014). The modal mating group size consists of four adult males and one adult female (Orbach et al. 2014). Only one third of males in mating groups copulate with a female (Markowitz et al. 2010) and only one offspring results per fertilization. Orbach et al. (2014) observed that males were positioned directly beneath and in close proximity to a copulating pair, and engaged in immediate copulations with the female when the initial copulating male stopped mating. Markowitz et al. (2010) observed the longest copulation duration and highest copulation rate in a small group of dusky dolphins with synchronous male behaviors. They hypothesized that males form long-term cooperative alliances, as has been observed with some Indo-Pacific bottlenose dolphins (Connor et al. 1992; Connor et al. 1996; Connor et al. 2000b). We tested whether male dusky dolphins cooperate or compete during group mating chases. If males collectively cooperate, the per-male probability of copulation should increase with group size until a certain threshold is reached where costs exceed benefits. If they collectively compete, the per-male probability of copulation should decrease with increasing group size.

Materials and Methods

Dusky dolphin mating groups were followed off Kaikoura, New Zealand (42°25'S 173°41'E) from October 2013 through January 2014. Mating groups were sighted by three researchers scanning the horizon while travelling parallel to the shoreline. Dolphins were approached from a 6 m rigid-hull inflatable vessel with an 80 Hp 4-stroke outboard engine. To reduce the behavioral disturbance to the dolphins, we travelled parallel to the groups (Markowitz et al. 2009). Strict adherence to the operating rules in New Zealand's Marine Mammals Protection Act 1978,

Marine Mammals Protection Regulations 1992, and local dolphin conservation guidelines were maintained at all times (Childerhouse and Baxter 2010). No permit was required for our observational study.

Mating groups were identified by observed attempted copulation events or by males swimming inverted with their penises everted (Markowitz 2004; Orbach et al. 2014). Because it was not possible to confirm if ejaculation occurred, all ventral contacts with body alignment between males and females were classified as copulation events (Orbach et al. 2014). We considered dolphins within 10 m of each other as part of the same mating group (Smolker et al. 1992). If the group size and composition changed, we terminated the follow. Males were identified as individuals swimming venter-up during attempted venter-to-venter copulations and/or by the exposure of their penises (Markowitz et al. 2010). Females were identified as individuals swimming venter-down during attempted venter-to-venter copulations (Markowitz et al. 2010). As tissue collecting techniques can elicit short-term behavioral responses and disrupt the natural behaviors of dolphins (Bilgmann et al. 2007), we did not genetically-confirm the sexes of the animals. It was not possible to determine which males copulated with a female as their individually-distinctive dorsal fins were not visible when they were inverted beneath a female.

When a mating group was sighted, groups were approached within ~5 m and we started a follow of that mating group. The corresponding time, GPS coordinates (Garmin GPSMAP 76 GPS), group size, and group composition were documented at the beginning and end of mating group follows. Detailed *ad libitum* narrations and continuous video recordings were collected on a video camera (Sony Handycam HDR-XR550V). The group size was confirmed every 2-5 minutes. Copulation events and the corresponding group size and number of individuals within

one body-width of the copulating female were recorded. Follows terminated when the group size changed, mating behaviors ceased, or boating conditions became unsafe.

Analysis

Mating videos were analyzed using the software Transana (v. 2.51). The videos were transcribed in one minute time intervals. Due to the challenges of capturing all behaviors and individuals on video simultaneously, preference was given to the *ad libitum* narrations when there was conflict between the observable data on the videos and the narrations.

For each mating group follow, the total number of copulation events was scaled by the duration of the video. To calculate the per-male probability of copulation, the number of copulation events per minute was divided by the number of males in the group. The mean number of males within one body-width of a female during a copulation event was calculated for each mating video. We compared the copulation rate ($\text{male}^{-1}\text{minute}^{-1}$) per group size and per the mean number of males within one body-width of a copulating female using simple linear regressions in JMP (v. 11.0.0).

Results

Forty-nine mating group videos were analyzed, amounting to 505 hours of video recordings. Dolphins in mating groups spent 91% of the time at or near the surface of the water within our visibility. The mean follow duration was 10.30 minutes (S.E. = ± 1.12). The modal and median group sizes were 5 dolphins and the mean was 5.9 dolphins (S.E. = ± 0.49). One mating group contained two dolphins in the female body position while all other mating groups appeared to consist of one female and multiple males. One mating video was excluded from subsequent analysis because no copulation events were observed. A total of 514 copulation events were

recorded. During these copulation events, a mode of 1 male was within one body-width of a copulating female (S.E. = ± 0.12). The copulation rate ($\text{male}^{-1}\text{minute}^{-1}$) decreased with increasing group size ($R^2 = 0.18$, $F(1, 48) = 10.09$, $P = 0.0027$; Fig. 1) and decreased with an increasing number of non-copulating males within one body-width of a copulating female ($R^2 = 0.12$, $F(1, 48) = 6.29$, $P = 0.0158$; Fig. 2).

Discussion

Male dusky dolphins off Kaikoura, New Zealand, appear to compete in group mating chases. Each male's probability of copulation decreased when more males were in the group. In addition, each male's probability of copulation decreased as more males were in proximity to the female, indicating males were rivals. Male dusky dolphins have large testes-to-body-size ratios, suggesting intense sperm competition (Cipriano 1992). Males also appear to engage in exploitative scramble competition, during which they maneuver for a proximate position next to a (presumed) ovulatory female (Markowitz et al. 2010; Orbach et al. 2014). It is unlikely that physical proximity was a form of mate-guarding a female (e.g. Seychelles warblers, *Acrocephalus sechellensis* (Oustalet, 1877); Komdeur et al. 2007) as males within one body-width of a copulating female were not the ones engaged in copulation.

Males may remain in mating groups despite a decline in individual copulation rate for several non-mutually exclusive reasons:

1) Male alliances (e.g. pairs and trios) may exist within mating groups and larger groups may include competing alliances. Repeated and long-lasting associations between the same males who cooperate to obtain mates against other male groups are evidence for male reproductive alliances (Harcourt and de Waal 1992). Individual identification of all dolphins in mating groups

is necessary to distinguish between the alternative hypotheses of all males competing individually or alliance members competing against non-alliance members within a mating group. Dolphins can be individually identified by their distinctive dorsal fin marking patterns (Würsig and Jefferson 1990). Of the 275 dusky dolphins that could be identified in mating groups over two breeding seasons, only 14 individuals were re-sighted in mating groups across different days (D.N.O. pers. observ.). Ten of these individuals were re-sighted with at least one consistent group member, indicating preferred associations. However, some of these re-sighted individuals were females or of unconfirmed sex (D.N.O. pers. observ.). To assess if male dusky dolphins off Kaikoura form small stable alliances, further analyses of the strength of association patterns across activity states is necessary (e.g. Pearson 2008).

Our data do not support the hypothesis that some male dusky dolphins cooperate in mating groups. During copulation events, inverted male dusky dolphins pushed females up and appeared to use the surface of the water as a physical barrier to prevent the escape of females (Markowitz et al. 2010). Individuals did not use each other as physical barriers to curtail female movement, as has been observed among young Indo-Pacific bottlenose dolphins (D.N.O. pers. observ.). Furthermore, consorting male Indo-Pacific bottlenose dolphins that cooperate demonstrate synchronous movements (Connor et al. 2006), whereas male dusky dolphins in mating groups attempt to synchronize their behaviors with the female instead.

2) Males may not be able to exclude rivals from joining a group. The observed group size in nature often exceeds the predicted optimum group size when exclusion by group members is not possible (Sibly 1983; reviewed in Krause and Ruxton 2002). All dolphins in mating chases spent most of their time (> 91%) at the surface of the water where they could be observed. The lack of observed aggression among male dusky dolphins in this study and rare observations of agonistic

179 interactions in other studies (e.g. Markowitz et al. 2010; Orbach et al. 2015) support this
180 hypothesis.

181 3) The time and energy costs of searching for unescorted females exceed the reduced mating
182 opportunities in a group. One male mating strategy when females have asynchronous estrus
183 cycles is to rove in search of receptive females (e.g. sperm whales, *Physeter macrocephalus* L.,
184 1758; African elephants, *Loxodonta africana* (Blumenbach, 1797); lesser kudu, *Tragelaphus*
185 *imberbis* (Blyth 1869); reviewed in Whitehead 1990). Factors that contribute to a male's decision
186 to remain in or depart from a mating group include a female's duration of estrus and the distance
187 to other receptive females (Whitehead 1990). As dusky dolphins are gregarious animals and are
188 commonly found in large mixed-sex groups off Kaikoura (Markowitz 2004), the rates of
189 encountering solitary females in estrus are predicted to be low. Future studies that use unmanned
190 aerial vehicles to quantify the group size, composition, number, and distances between mating
191 groups can test the hypothesis that costs of searching for new mating opportunities exceed the
192 costs of remaining in current groups.

193 4) Males in mating groups may receive other direct benefits that offset the costs of reduced
194 mating opportunities (reviewed in Acevedo-Gutiérrez 2008). For example, by remaining in
195 mating groups, males may reduce their risk of predation or expend less effort in predator
196 vigilance (reviewed in Roberts 1996), as has been found in bighorn sheep (*Ovis canadensis*
197 (Shaw, 1804); Berger 1978). Common predators of dusky dolphins off Kaikoura include sharks
198 and orcas (Srinivasan and Markowitz 2010). There is limited evidence that the benefits of
199 reduced predation pressure drive group living among cetaceans (Acevedo-Gutiérrez 2008). The
200 direct foraging benefits commonly associated with group living in many taxonomic groups
201 (reviewed in Giraldeau and Caraco 2000; reviewed in Krause and Ruxton 2002) are not

applicable to mating dusky dolphins off Kaikoura, as foraging is spatially and temporally separated from mating (Markowitz 2004).

5) Males in mating groups may receive indirect benefits that offset the costs of reduced mating opportunities. When males in mating groups are kin, a non-mating individual's inclusive fitness can increase when it helps a close relative to increase its reproductive success (Hamilton 1964). For example, subordinate male wild turkeys form coalitions with related males, increasing the mating success of their dominant relatives (Krakauer 2005). Data on dusky dolphin genetics does not support this kin selection hypothesis driving males to remain in mating groups. Genetic sampling of dusky dolphins off Kaikoura showed low mean relatedness within mating groups (Shelton et al. 2010).

6) Some males in mating groups may not try to inseminate females. Non-conceptive sexual behaviors are common among dolphins, primates, birds, and many taxonomic groups, and can strengthen relationships, establish hierarchies, and reduce tension, among other functions (reviewed in Sommer and Vasey 2006; reviewed in Furuichi et al. 2014). For example, copulation-like behaviors have been observed between sexually immature males and non-kin adult females in bonobos (*Pan paniscus* (Schwarz, 1929)) and chimpanzees (Furuichi et al. 2014). Sexual behaviors are often initiated by sexually immature male Indo-Pacific bottlenose dolphins and could be a form of practice for future courtship (Mann 2006). It is possible that some young male dusky dolphins remained in mating groups to learn successful copulation techniques. Our data do not strongly support this hypothesis. The age classes of dusky dolphins were determined *in situ* by body length estimates (Würsig and Würsig 1980), and only 5 of 49 mating groups contained sexually immature dolphins.

Behavioral plasticity to ecological conditions is apparent among the dolphin populations that have been observed mating or engaging in socio-sexual relationships (Gowans et al. 2008; Möller 2012). Male dusky dolphins appear to be unable to individually monopolize females (Markowitz et al. 2010; Orbach et al. 2014). Sexual size dimorphism is weak (Cipriano 1992). Prey is mobile and territory defense is unknown among cetaceans (Connor et al. 2000a). Dusky dolphins off Kaikoura form large mixed-sex aggregations ranging up to thousands of animals and have weak association patterns (Markowitz 2004). Predation pressure is reduced by the large aggregations of dolphins (Srinivasan and Markowitz 2010). The prey resources of the deep scattering layer are comparatively reliable (Dahood and Benoit-Bird 2010). In contrast, male Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia, compete for mates by coercive and aggressive mate herding (Connor et al. 2000b). Prey is patchily distributed and mobile, predation pressure is high, and small group sizes prevail that appear to reduce food competition and detection by predators (Connor et al. 2000b).

The decreased copulation rate per male as mating group size increased and more males were in close proximity to females indicate males compete rather than cooperate within mating groups. Males may remain in mating groups despite competition for several reasons. Our data most strongly support the hypothesis that males are unable to exclude rivals from joining a group. The reduced physical aggression levels in large aggregations of dusky dolphins compared to other small delphinid species (Orbach et al. 2015), observations of males in mating group sizes above the predicted optimum (Orbach et al. 2014), and constrained abilities of dusky dolphins to individually monopolize each other emphasize the complex dynamics of group living, with much more to be learned.

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390 **Figure Captions**

391 **Fig. 1** Simple linear regression of the copulation rate ($\text{male}^{-1}\text{minute}^{-1}$) per group size for dusky
392 dolphin (*Lagenorhynchus obscurus* (Gray, 1828)) mating groups off Kaikoura, New Zealand.

393 **Fig. 2** Simple linear regression of the copulation rate ($\text{male}^{-1}\text{minute}^{-1}$) per mean number of males
394 within one body-width of a copulating female for dusky dolphin (*Lagenorhynchus obscurus*
395 (Gray, 1828)) mating groups off Kaikoura, New Zealand.

Draft

35x25mm (300 x 300 DPI)