Global reproductive strategies of *Tursiops* and *Stenella* (family Delphinidae)

Introduction

Generally, females make a larger investment toward future generations than males. Not only is production of eggs more expensive than production of sperm, but males essentially have an unlimited supply of sperm while females are born with a limited number of eggs (Campbell and Reece 2002). In placental mammals, the female carries the offspring in her uterus until it is ready to be born, at a great cost to her. If parental care is involved, the male is not involved. Therefore, the limiting factor for the fitness of mammalian females is expected to be the number of pregnancies they can successfully carry and the number of offspring they can successfully raise. The fitness of mammalian males, who, in contrast to females, expend very little energy on reproduction, is expected to be limited by the number of females they can successfully mate with. Females, therefore, should be choosy about which males they mate with and males should compete over opportunities to mate with the females (Freeman and Herron 2004).

The different limiting factors for males and females usually results in either promiscuous or polygynous mating systems. In a promiscuous mating system, males attempt to mate with as many females as possible and do not form any sort of bond with the female. Females also try to mate with as many males as possible. Different males will have very different degrees of success. In a polygynous mating system, one male mates with many different females, but forms a longer bond with the females than in a promiscuous system (Ricklefs 2001). In both of these systems, males compete for access to females, and females mate with the male that can best compete.

Members of the family delphinidae, which includes dolphins, killer whales, pilot whales, and many other species, are viviparous mammals. Therefore, it is expected that females will generally be choosy, males will be competitive, and the mating systems will probably be either promiscuous or polygynous. Delphinids are usually sexually dimorphic—males are generally larger than the females and may have a different shape (Animal Diversity Web, 1999 and Tolley et al. 1995). In general, males may be larger than females if male-male competition is an important selecting factor in reproduction. If males combat for access to the females, larger males will have an advantage, and be more likely to pass their genes that code for large size on to the next generation. However, because delphinidae encompasses so many genera and has a worldwide distribution (Animal Diversity Web, 1999), different mating strategies exist and male-male competition is not the sole determining factor for a successful mating for *Stenella* and *Tursiops*. The mating systems of the genus *Tursiops* (which includes bottlenose dolphins) and the genus *Stenella* (which includes spinner dolphins) have been studied more than many other genera, due to their tolerance of people and relatively easier access. Therefore, the focus of this review will be only on those two genera.

Delphinids use different reproductive strategies in different parts of the world. Major studies of the delphinid mating system have been done in Shark Bay, Western Australia (Connor et al. 1996 and Krützen et al. 2003); Sarasota, Florida (Owen at al. 2002 and Tolley et al. 1995); and in the eastern Pacific, along the coasts of Mexico and South America (Perrin and Mesnick 2003). Globally, males and females preferentially associate together when the females are reproductively active (Connor et al. 1996 and Owen et al. 2002), although males may interact with females even if the female is pregnant or not in estrous (Connor et al. 1996 and Owen et al. 2002). Dolphins in Western Australia were mostly polygynous, although the males exhibited two alternative strategies of controlling females. Dolphins in the eastern Pacific showed a gradient of polygyny in the eastern spinner population to promiscuity in the whitebelly spinner population. Dolphins in Sarasota may either be polygynous or promiscuous. A major limitation is that all of the studies focused mainly on the male reproductive strategy. Female choice may also be important in dolphins, and further study focusing on females is necessary.

Western Australia

The mating system of dolphins in Shark Bay seems to be polygynous because a few males mate with a group of females in a semi-long term bond. Male bottlenose dolphins interact aggressively with females using a herding technique to form consortships. Females are generally unreceptive to this herding, even if they are reproductively active. In order to capture a female, males will accelerate toward her, and control her using vocal popping noises and aggressive actions such as striking her with their flukes, charging at her, and jerking their heads at her. The females will usually try to escape, but are generally recaptured. Males use two alternative reproductive strategies in order to herd females: 1) Males form long-term first order alliances with 1-2 other males in order to herd females (Connor et al. 1996). Two of these alliances may combine (a second order alliance), forming groups of 4-6 males, which gives those males a better chance to "steal" females away from another alliance and to protect the females they have from theft by other male alliances (Krützen et al. 2003). 2) Alternatively, males may

combine into "super-alliances" of up to 14 males, which makes them even more effective at both stealing and guarding females (Krützen et al. 2003).

In the first reproductive strategy, males in either first or second order alliances were more closely related than would be expected by chance (Krützen et al. 2003). Males may form alliances not only to increase their chances of successfully subduing females, but also because these alliances increase their inclusive fitness. By helping a close relative monopolize a single female, a male dolphin will benefit indirectly if his relative mates with the female. Although one male dolphin may not mate with the female, some of his genes will be passed on to the next generation if a close relative mates with her. According to Hamilton's law, altruistic behavior will spread if the cost to the actor is low, the benefit to the recipient is high, and the actor and recipient are closely related (Freeman and Herron 2004). The cost to male dolphins for guarding a female can be high because males may fight viciously over females (Animal Diversity Web, 1999). However, because these altruistic alleles exist, the benefit of producing related offspring is apparently high enough to overcome the cost of fighting for females.

In the second reproductive strategy, males were not closely related. Some males form "super-alliances" of about 14 individuals. The males will form first order alliances with other males of this super alliance. In contrast to the first strategy, where the alliances were stable and long term, first order alliances in the second strategy are transient and constantly changing. The males in a super-alliance are not any more closely related than would be expected by chance. The males may form these larger alliances in order to steal females away from first and second order alliances, and then compete among themselves for the opportunity to mate with the female (Krützen et al. 2003). The males in super 4

alliances do not gain any indirect fitness benefits by being in the alliance. The only benefit seems to be that the larger the alliance is, the more successful it will be at both taking and keeping females.

However, the reproductive strategies of the females have not been thoroughly studied and are still only mostly speculation. Due to the fact that males can monopolize females, it appears that intrasexual selection among males is occurring in this population of dolphins (Freeman and Herron 2004). Males that can most successfully control females are most likely to mate, and pass their genes on to the next generation. However, the mating system may be more complicated than simply the male who wins the fight has the opportunity to mate with the female. There is evidence that female choice may also be a selective factor. Females may use their escape behavior as a means to test the physical fitness of the males (Connor et al. 1996). By forcing the male to chase after her, she may be effectively selecting to only mate with healthy, strong males. There is also evidence that females may directly choose a mate. Researchers have observed elaborate displays by males around consorted females that suggest that females may use those displays to directly choose a mate among the males that are herding them (Connor et al. 1996). In addition, there is also evidence that females willingly socialize with an alliance of males, without any agonistic behavior (Connor et al. 1996). Some males may attempt to form relationships with females in order to increase their chances of being chosen by the female, also suggesting that female choice is an important factor.

The mating system is further complicated by the fact that females are not entirely monopolized by a few males. Females go into estrous several times a year, and so mate with many different males. It is unclear why females would be polyestrous, 5

which increases the number of times they will be harassed by males. Herding of females is costly and dangerous to the females because it decreases the amount of time the female can spend foraging for food and the males can be very aggressive. A possible explanation is that, if a female is monopolized by a less desirable male during one cycle, she will have the opportunity to mate with a more desirable male during a second cycle (Connor et al. 1996). It seems as if looking for the best genes is not a satisfactory explanation, especially because females may not even have a choice of mates. Females seem to usually mate with the group of males that manages to successfully capture her, which may or may not be males with the best genes. There is no guarantee that a female will be captured by a group of males with better genes during her next cycle.

An alternative explanation may be that mating with many males decreases the risk of infanticide. In some primate species, the risk of infanticide by a male is less if the female has copulated with that male. The male presumably realizes that the infant may be his, and so is less aggressive towards it. It is possible that by mating with many different males, female dolphins decrease the risk of aggression by males towards their infants (Connor et al. 1996). However, there are large differences between primates and cetaceans, so it may not be accurate to describe dolphin behavior using primate studies.

Both the study by Connor et al. (1996) and Krützen et al. (2003) focused largely on the reproductive strategies of the males. Further study of female dolphins is necessary to fully understand the complex mating system. Studies of female sociality are necessary to see if female choice is an important part of the mating system. If female choice is important, then what kind of males do females prefer? Paternity tests of calves would reveal which males are most successful, either through male-male competition or female choice. Further studies may also answer the question of why females are polyestrous even though it is detrimental to their health.

Eastern Pacific

In contrast to the studies conducted in Shark Bay, Perrin and Mesnick (2003) did not directly observe dolphin behavior. Spinner dolphins live offshore, so it is difficult to study them directly. The study was instead conducted using incidentally killed spinner dolphins that had been caught in tuna nets. The weight of the epididymis + testis was compared between the eastern spinner dolphin and the whitebelly spinner dolphin, which is a hybrid of the eastern spinner and a Hawaiian spinner. The range of the whitebelly spinner is larger than the range of the eastern spinner, but the ranges of these two populations greatly overlap (Fig. 1).

The whitebelly spinner dolphin and the eastern spinner dolphin were found to have a gradient of mating systems, ranging from promiscuity in the whitebelly form to polygyny in the eastern form. The whitebelly population had a greater testis + epididymis weight than the eastern population. Increased testis size can evolve if the sperm must compete. If a female mates with several males, the male who can produce the most sperm (largest testis) is most likely to successfully fertilize the female. Therefore, a large testis size is expected in a promiscuous mating system, where the female mates with many males. The whitebelly population had larger testis + epidermis weights than the eastern population, suggesting that the whitebelly dolphin mating system is more promiscuous than the spinner population. The eastern spinner showed greater sexual dimorphism than the whitebelly spinner, suggesting that the mating system of the spinner dolphin is polygynous. Sexual dimorphism is usually a result of male-male competition, which may

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evolve when males can control access to females or resources the females need. The largest males can control access to females, resulting in several females mating with one male (polygyny). Because the male can directly control the female, she will not mate with many other males. There is less selective pressure for more competitive sperm, so it is expected that the eastern testis + epididymis would be smaller than the whitebelly (Perrin and Mesnick 2003).

However, because the dolphins were not studied directly, it is unknown how exactly the mating systems work and if the assignment of a promiscuous mating system to the whitebelly form and a polygynous mating system to the eastern form is correct. Sexual dimorphism can occur in both polygynous and promiscuous mating systems. Males in both mating systems compete to mate with as many females as possible. Competition between males facilitates the evolution of dimorphism in size, coloration, behavior, etc (Ricklefs 2001). Therefore, the conclusion by Perrin and Mesnick (2003) that the eastern spinner is polygynous because it shows greater sexual dimorphism is not necessarily true. Their argument is strengthened by the congruent data from epididymis + testis size that suggests the whitebelly form is more promiscuous than the eastern form. However, direct study of the dolphins would be the most convincing way to confirm that the mating system assignment is correct.

Perrin and Mesnick (2003) discuss and dismiss several alternative hypotheses and confounding factors that could account for the difference in epididymis + testis weight between the eastern form and the whitebelly form. Whitebelly dolphins are, on average, about 5 cm longer than eastern dolphins (Perrin and Mesnick 2003). Therefore, larger epididymis + testis weight of whitebelly dolphins may only be an incidental result of their larger overall size. However, size does not appear to be a confounding factor because whitebelly epididymis + testis weight was still larger than eastern epididymis + testis weight for dolphins of the same length (Perrin and Mesnick 2003). Another possible confounding factor could be that whitebelly and eastern dolphins reach sexual maturity at different ages or times of the year. Juvenile eastern dolphins—which would have a smaller epididymis + testis weight because they are not sexually mature—may have been compared against adult whitebelly dolphins in the study, leading to skewed results. Perrin and Mesnick (2003) controlled for this by limiting the study to adult males whose right testis + epididymis weight was at least 88g. Testis + epididymis weight is, on average, 88g at spermatogenesis, so all of the males should have been sexually mature. Samples were also collected over every month of the year, allowing for different reproductive seasons. Size and time of reproduction should therefore not be confounding factors, and it is probably an accurate conclusion that whitebelly epididymis + testis weight is larger than eastern epididymis + testis weight.

Another possible alternative explanation for the difference in epididymis + testis weight could be a greater chase-and-capture pressure from tuna fishermen on the eastern spinners. A greater chase-and-capture pressure may have a depressive effect on male reproductive function, thereby causing the epididymis + testis weight to be smaller. Perrin and Mesnick (2003) reject this possible explanation because annual pregnancy rates in the two populations are comparable, which would not be expected if the eastern spinner male reproductive system was depressed. They also found that a comparable percentage of whitebelly spinners (17%) and eastern spinners (22%) were accidentally

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captured in nets. It appears that there is not greater chase-and-capture pressure on the eastern spinner dolphin than on the whitebelly spinner dolphin.

Direct study of both the whitebelly and eastern spinner dolphins should be conducted in order to confirm Perrin and Mesnick's (2003) conclusions and to see how males and females interact. Are the spinner dolphins similar to the Shark Bay bottlenose dolphins? Shark Bay males form alliances that aggressively herd females. Are interactions between male and female spinner dolphins also agonistic? Do male spinner dolphins form alliances in order to herd females (especially in the polygynous eastern population), and if so, are they related to their fellow alliance members?

Sarasota

Male bottlenose dolphins in Sarasota normally bond with another male during their teens for a long-term, stable relationship, but rarely associate with other males. Owen et al. (2002) found no evidence of pair bonds combining to find second order alliances or super-alliances, as was found in Shark Bay dolphins (Connor et al. 1996 and Krützen et al. 2003). Dolphins in Shark Bay are smaller than dolphins in Sarasota (Tolley et al. 1995), and a social system of limited interaction between unpaired males may have evolved in order to lessen the occurrence of agonistic interactions between males (Owen et al. 2002). The larger a male is, the more potential he has to injure another male. Injuries between Sarasota males fighting over females may be more severe than injuries to Shark Bay males, facilitating the evolution of less interaction between Sarasota males.

Sarasota dolphins are sexually dimorphic (Tolley et al. 1995) suggesting that the mating system is either polygynous or promiscuous. Males do not possess ornate secondary sexual characters; instead differences between the sexes are size related. Males

are larger than females, have larger locomotor muscles, and have larger flukes and dorsal fins. The increased size of the flukes and dorsal fins and locomotor muscles may give the males greater propulsion, better maneuvering, and better thermoregulation which could be used either to chase females or in fights with other males over females (Tolley et al. 1995). Tolley et al. (1995) cite a study by Trivers (1985), which suggests that Sarasota dolphins may be promiscuous. Trivers (1985) found that moderate sexual dimorphism suggests a mating system of males competing for access to dispersed females, instead of a more polygynous system where the largest males are able to monopolize females. The dolphins in Sarasota exhibited moderate sexual dimorphism, suggesting that the mating system may be promiscuous.

However, adult male dolphins associate with potentially reproductive females during the breeding season; subsequently, males and females may form long-term bonds, which are not seen in promiscuous mating systems (Ricklefs 2001). Compared to the Shark Bay male-female interactions, the interactions during the breeding season between males and females in Sarasota were shorter, less stable, and less agonistic. However, male interactions with potentially reproductive females during the non-breeding season were more stable than during the breeding season. Males may form affiliative relationships with females during the non-breeding season in order to increase their chance of being chosen by the female during the breeding season (Owen et al. 2002). However, Owen et al. (2002) did not report the nature of the interactions between males and females, only how often males associated with potentially reproductive and nonreproductive females. The time of interaction between males and females was shorter than for the Shark Bay dolphins, suggesting that males in Sarasota do not guard mates for long, so the relationship is probably less antagonistic. In addition, the fact that males attempt to form relationships with females when they are not reproductively active suggests that female choice, and not solely male-male competition, is important.

It is difficult to conclude from these two studies if the mating system of Sarasota dolphins is polygynous, promiscuous, or possibly something else. Evidence is supported for both a polygynous and a promiscuous mating system. It might be possible that two alternative strategies exist in this population, such as in the eastern Pacific spinner dolphins. Research comparing testis size for two different populations in Sarasota may be helpful in determining if the mating system is promiscuous.

Conclusion

The mating systems of *Tursiops* and *Stenella* are mostly either promiscuous or polygynous. Western Australia dolphins tend to be polygynous. Eastern Pacific dolphins may either be polygynous (the eastern form) or promiscuous (the whitebelly form). It is inconclusive whether Sarasota dolphins are promiscuous or polygynous. Male-male competition appeared to be an important selective factor globally; female choice may also be an important selecting factor, but further research focusing more on females needs to be conducted in order to fully understand the mating system.



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Fig 1. Distribution of the eastern spinner is shown in the top picture. Distribution of the whitebelly spinner is shown in the bottom picture. The eastern spinner's distribution is generally more northern than the whitebelly spinner's distribution, but the ranges overlap (Perrin and Mesnick 2003).

Literature Cited

- Campbell, N.A. and Reece, J.B. (2002). *Biology* (6th ed.). San Francisco, CA: Benjamin Cummings.
- Connor, R.C., Richards, A.F., Smolker, R.A., and Mann, J. 1996. Patterns of female attractiveness in Indian Ocean bottlenose dolphins. *Behaviour*. 133:37-69.
- 1999. "Delphinidae" (On-line), Animal Diversity Web. Accessed April 04, 2004 at http://animaldiversity.ummz.umich.edu/site/accounts/information/Delphinidae.ht ml.
- Freeman, S. and Herron, J.C. (2004). *Evolutionary analysis* (3rd ed.). Upper Saddle River, NJ: Prentice Hall.
- Krützen, M., Sherwin, W.B., Connor, R.C., Barré, L.M., de Casteele, T.V., Mann, J., and Brooks, R. 2003. Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different alliance strategies. *Proceedings of the Royal Society of London Series B-Biological Sciences*. 270(1514): 497-502.
- Owen, E.C.G., Wells, R.S., and Hofmann S. 2002. Ranging and association patterns of paired and unpaired adult male Atlantic bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative male strategies. *Canadian Journal of Zoology—Revue Canadienne de Zoologie*. 80(12): 2072-2089.
- Perrin, W.F. and Mesnick, S.L. 2003. Sexual ecology of the spinner dolphin, *Stenella longirostris*: Geographic variation in mating system. *Marine Mammal Science*. 19(3): 462-483.
- Ricklefs, R.E. (2001). *The economy of nature* (5th ed.). New York: W.H. Freeman and Company.
- Tolley, K.A., Read, A.J., Wells, R.S., Urian, K.W., Scott, M.D., Irvine, A.B., and Hohn, A.A. 1995. Sexual dimorphism in wild bottlenose dolphins (*Tursiops-truncatas*) from Sarasota, Florida. *Journal of Mammalogy*. 76(4): 1190-1198.