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# Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*)

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## Abstract

**In most mammals males usually disperse before breeding, while females remain in their natal group or area. However, in odontocete cetaceans behavioural and/or genetic evidence from populations of four species indicate that both males and females remain in their natal group or site. For coastal resident bottlenose dolphins field data suggest that both sexes are philopatric to their natal site. Assignment tests and analyses of relatedness based on microsatellite markers were used to investigate this hypothesis in resident bottlenose dolphins, *Tursiops aduncus*, from two small coastal populations of southeastern Australia. Mean corrected assignment and mean relatedness were higher for resident females than for resident males. Only 8% of resident females had a lower probability than average of being born locally compared to 33% of resident males. Our genetic data contradict the hypothesis of bisexual philopatry to natal site and suggest that these bottlenose dolphins are not unusual amongst mammals, with females being the more philopatric and males the more dispersing sex.**

*Keywords*: assignment tests, bottlenose dolphins, dispersal, microsatellites, philopatry, relatedness

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## Introduction

In higher vertebrates most members of one sex usually disperse before breeding, while members of the opposite sex remain in their natal group or area (Greenwood 1980). In mammals females are usually philopatric while males tend to disperse. Evolutionary explanations for sex-biased dispersal include local mate competition (Dobson 1982), inbreeding avoidance (Greenwood 1980; Wolff 1993) and resource competition (Greenwood 1980).

In cetaceans some molecular studies support the notion of male-biased dispersal (e.g. in belugas, O'Corry-Crowe *et al*. 1997; in sperm whales, Lyrholm *et al*. 1999; and in Dall's porpoises, Escorza-Trevino & Dizon 2000), but behavioural and /or genetic evidence from populations of four species suggest that both sexes may remain philopatric to their natal group or site. In the fish-eating resident killer whales (*Orcinus orca*), off British Columbia and Washington Strait, individuals are found in stable kin-based groups, where no dispersal appears to occur by either sex (Bigg *et al*. 1987). Similar to resident killer whales, long-finned pilot whales (*Globicephala melas*), caught in the drive fishery of the Faeroe Islands, displayed a social pattern in which neither males nor females dispersed from their natal group (Amos *et al*. 1993). Another potential case of bisexual philopatry in cetaceans has been proposed for coastal resident populations of bottlenose dolphins (genus *Tursiops*), where both males and females appear to display natal site philopatry (Connor *et al*. 2000).

Coastal bottlenose dolphins live in fission–fusion societies, where groups frequently change in size and composition but associations between certain individuals persist (Wells 1991; Smolker *et al*. 1992). Males usually show strong, long–term associations with a few other males within alliances (Wells 1991; Connor *et al*. 2000; Möller *et al*. 2001), while females associate at moderate level with several other females within bands or cliques (Wells 1991; Smolker *et al*. 1992; Möller 2001). For these animals natal site philopatry has been inferred for two populations based on field data (Wells 1991; Connor *et al*. 2000). In a resident *T. truncatus* community inhabiting Sarasota Bay, FL, where most individuals can be recognized by natural or artificial markings, both male and female calves tend to remain in their natal site when adults, with low annual rates of immigration and emigration (Wells & Scott 1990; Wells 1991). In Shark Bay, Western Australia, observations from birth to adulthood of naturally marked *T. aduncus* also

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suggest natal area philopatry for both sexes (Connor *et al*. 2000).

Dispersal patterns in bottlenose dolphins, as with many other cetaceans, are very difficult to document because these animals are long-lived (*c*. 45 years), they may move widely, and deployment of radio and satellite telemetry can be problematic (e.g. Wells 1991). Alternative methods to investigate dispersal patterns include the use of genetic markers, in particular microsatellites, and statistical analyses that estimate relatedness between animals (e.g. Queller & Goodnight 1989) and identify migrants, such as assignment tests (e.g. Favre *et al*. 1997; Rannala & Mountain 1997). Assignment tests are based on multilocus genetic data and use both individual genotypes and population level allele frequencies to identify migrants and recent gene flow, without relying on assumptions of equilibrium which are commonly violated in many populations (reviewed in Davies *et al*. 1999). Furthermore, differences in log-likelihood distributions of assignments between sexes can be used to infer sex-biased dispersal (Favre *et al*. 1997; Mossman & Waser 1999; Goudet *et al*. 2002).

In this paper assignment tests and analyses of relatedness based on microsatellite markers were used to investigate dispersal patterns in coastal resident bottlenose dolphins (*T. aduncus*) from southeastern Australia and to test the hypothesis of natal site philopatry for both sexes.

## Materials and methods

### Study areas and populations

This study was conducted in Port Stephens (PS) (32°42′ S, 152°06′ E) and Jervis Bay (JB) (35°07′ S, 150°42′ E), which are located in New South Wales, southeastern Australia, approximately 400 km apart. Boat surveys were conducted in PS (*n* = 43, December 1998 to April 2000) and JB (*n* = 86, May 1997 to May 1999) to identify bottlenose dolphins photographically, based on natural marks in their dorsal fins (photo-identification; Würsig & Jefferson 1990), and to assess individual site fidelity. In PS and JB, respectively, 149 and 116 individuals (excluding calves) were photo-identified during the period (Möller *et al*. 2002). The number of individuals considered residents, based on the dolphin's sighting rates and presence across seasons in the areas, was 87 in PS and 57 in JB (Möller *et al*. 2002). Resident animals were those photographically identified in more than 10% of surveys and that were also present in multiple seasons. There were no photographic matches of individuals between areas during the 4 years of photo-identification surveys, suggesting that JB and PS dolphins may be part of two different populations (Möller *et al*. 2002). However, significant but moderate genetic differentiation at nuclear microsatellite DNA ($F_{ST}$ = 0.07) suggests a certain extent of gene flow between populations (Möller 2001).

### Biopsy surveys and sampling

Biopsy sampling was conducted in PS (*n* = 28 boat surveys) and JB (*n* = 40) between March 1998 and June 2000. Biopsy samples were collected from dolphins from a distance of approximately 10 m from the research boat, using a rifle modified to deliver biopsy darts (details in Krützen *et al*. 2002). Samples were preserved in 20% dimethyl sulphoxide saturated with sodium chloride (Amos & Hoelzel 1991). Dolphins were identified during sampling by photo-identification as they were biopsied or through visual recognition by one of the authors (L.M.M.). Sampling effort was directed towards individuals from various social groupings (i.e. male alliances, Möller *et al*. 2001; female bands, Möller 2001) to avoid sampling bias. In addition, no samples from dependent calves were included.

### Genetic methods

DNA was extracted using a salting-out protocol (Sunnucks & Hales 1996). The sex of sampled dolphins was determined by amplification through the polymerase chain reaction (PCR) of the genes *ZFX* and *SRY* (Gilson *et al*. 1998).

Nine cetacean microsatellite loci were amplified by PCR: *EV1* and *EV37* (Valsecchi & Amos 1996); *MK5*, *MK6*, *MK8* and *MK9* (Krützen *et al*. 2001); *D8* (Shinohara *et al*. 1997); and *KW2* and *KW12* (Hoelzel *et al*. 1998). All loci were amplified in 10 µl radiolabelled reactions starting with 94 °C for 3 min, followed by a 32-cycle 'touchdown' (94 °C for 20 s, 59–51 °C for 45 s and 72 °C for 60 s), and 72 °C for 4 min (details in Beheregaray & Sunnucks 2000); except *D8* and *MK8* (63–53 °C touchdown) and *MK5* and *MK6* (60–50 °C). PCR products from five selected individuals were independently amplified three times across all loci to check the reliability of the genotyping protocol.

### Data analysis

*Microsatellite variability.* Allele frequencies and expected ($H_E$) and observed ($H_O$) heterozygosities were estimated with the program GENEPOP (Raymond & Rousset 1995). This program was also used to conduct tests for linkage disequilibrium and Hardy–Weinberg equilibrium employing the Markov chain method.

*Assignment tests.* Assignment tests were computed with the program GENECLASS (Cornuet *et al*. 1999), using the Bayesian method (Rannala & Mountain 1997). To avoid biases when estimating population allelic frequencies, the 'leave one out' procedure was used as it excludes the current individual being assigned from its sampled population (Cornuet *et al*. 1999).

The approach of Favre *et al*. (1997) was used to examine the sex differences in assignment values of resident individuals from both populations. This approach corrects assignment indices (*AI*) for population effects by subtracting population means after log-transformation. Corrected assignment (*AIc*) values average zero for each population, and negative values characterize individuals with a lower probability than average of being born locally. Thus, a cumulative distribution of *AIc* values for each sex can be obtained across populations. *AIc* values of male dolphins were compared with those of females using a two-tailed *t*-test. In the case of sex-biased dispersal, the more dispersing sex is predicted to show a lower mean *AIc* than the more philopatric sex (Favre *et al*. 1997; Mossman & Waser 1999). This genetic test has been shown to perform well even with species that do not have extreme sex-biased dispersal tendencies (Mossman & Waser 1999).

*Relatedness estimates.* Multi-locus genotypes from all nine microsatellites were used to estimate relatedness in each population using the index of Queller & Goodnight (1989) within RELATEDNESS 5.04 (Goodnight & Queller 1998). This index calculates relatedness between any two individuals by comparing the alleles shared by these individuals with the allele frequency of the population, with relatedness coefficients (*R*) ranging from −1 to 1 (Queller & Goodnight 1989). Standard errors of *R* estimates were obtained by jackknifing over all loci (Queller & Goodnight 1989).

Mean relatedness between males (*MM*), females (*FF*), and opposite-sex pairs (*MF*) was estimated in each population for resident dolphins. Differences in the mean relatedness between categories were evaluated using a two-sample randomization test with the program RT 2.1 (Manly 1997). If there is sex-biased dispersal, a lower mean relatedness is expected between dolphins of the dispersing sex than between individuals of the more philopatric sex, and also between opposite-sex pairs than between members of the more philopatric sex. If there is bisexual philopatry or no bias in dispersal, no significant differences between sexes are expected in the mean relatedness of individuals (*FF* vs. *MM*), and between same-sex and opposite sex comparisons (*FF* vs. *MF*, *MM* vs. *MF*).

## Results

### Sampling and microsatellite variability

A total of 125 bottlenose dolphins were biopsied, genetically sexed and typed at the nine microsatellite loci. Three replicate PCRs consistently yielded identical genotypes, strengthening the reliability of the genotyping protocol. After genetic analyses, it appeared that seven individuals had been sampled twice and one three times in Port Stephens, as samples showed identical genotypes at all microsatellite loci and were from the same sex. Since the probabilities that full siblings would match those microsatellite genotypes were less than 1/1000 (Möller 2001), samples were considered duplicates and triplicates and were excluded from the analyses. Hence, relatedness estimates and assignment tests were based on 116 individuals (PS, $n = 87$; JB, $n = 29$). From these 116 dolphins, 73 were identified at the time of sampling (55 by photo and 18 by eye only). From these 73 animals, 57 were residents and were used for the sex comparisons. Between one and four of these samples were obtained from each of 14 male alliances and between four and seven samples were obtained from each of five female bands (Möller 2001; Möller *et al*. 2001). Analysis for the Port Stephens dolphin population showed that, in general, kinship is not a factor influencing either male alliance formation or band membership (Möller 2001; Möller *et al*. 2001) and therefore sampling regime is unlikely to have biased the results. Table 1 gives information on the number of resident individuals sampled in each of the areas by sex.

**Table 1** Number of genetically sampled resident bottlenose dolphins, by sex, in each of the study areas in southeastern Australia; all individuals are adults

| Study area | Number of dolphins |
|---|---|
| Port Stephens | |
| females | 20 |
| males | 22 |
| Jervis Bay | |
| females | 4 |
| males | 11 |
| Total | 57 |

The average number of alleles per locus was 6.6 ± 0.6 in PS and 5.1 ± 0.6 in JB, and mean $H_E$ was 0.55 ± 0.05 and 0.60 ± 0.06, respectively. Exact tests for linkage disequilibrium revealed no significant locus comparison at the 5% level, none of the loci showed significant departures from Hardy–Weinberg equilibrium, and probability tests did not detect excess or deficiency of heterozygotes at any locus.

### Assignment tests

Corrected assignment (*AIc*) values ranged between −2.9 and 2.1 for resident males and between −2.2 and 2.3 for resident females. Mean *AIc* was higher for these females than for these males and this difference was marginally significant (females, mean = 1.054; males, mean = 0.36, $t = 2.080$, $P = 0.042$) (Fig. 1). Thirty-three per cent of the male genotypes were in the negative portion of the *AIc* distribution as against 8% of the females (Fig. 1).

### Relatedness

Mean relatedness in PS was significantly higher for *FF* than *MM* ($P = 0.009$) and for *MF* than *MM* ($P = 0.03$) (Table 2).

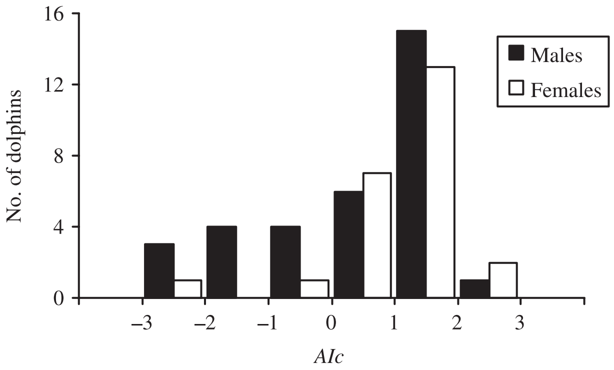

**Fig. 1** Frequency distribution of corrected assignment indices (*AIc*) for resident bottlenose dolphins sampled in Port Stephens and Jervis Bay, southeastern Australia. *AIc* values average zero for each population and negative values characterize individuals with a lower probability than average of being born locally.

**Table 2** Mean relatedness between same-sex and opposite-sex pairs of identified resident adult dolphins in Port Stephens and Jervis Bay, southeastern Australia

| Study area | *FF* | *MM* | *MF* |
|---|---|---|---|
| Port Stephens | 0.1543<br>(0.0484) | 0.0943<br>(0.0388) | 0.1268<br>(0.0032) |
| Jervis Bay | 0.1709<br>(0.1537) | −0.0503<br>(0.0409) | −0.0721<br>(0.0531) |

Standard errors jackknifed over loci are shown in parentheses. *FF*, among females; *MM*, among males; *MF*, among male–female pairs.

Mean relatedness in JB was significantly higher for *FF* than *MM* ($P = 0.004$), and for *FF* than *MF* ($P = 0.012$) (Table 2). However, estimates of mean relatedness for females in JB are only tentative because of the small number of samples and the correspondingly large standard error.

## Discussion

Assignment tests showed that a larger proportion of resident females than resident males from two coastal populations of *Tursiops aduncus* from southeastern Australia had a higher probability than average of being born locally. In addition, relatedness estimates in both populations were higher among resident females than among resident males. These results indicate the occurrence of male-biased dispersal and contradict the hypothesis of natal site philopatry for both sexes in coastal resident bottlenose dolphins (Wells 1991; Connor *et al*. 2000). Our genetic evidence suggests that these dolphins are not unusual among mammals, with females being the more philopatric and males the more dispersing sex (Greenwood 1980; Dobson 1982).

A proposed explanation for male-biased dispersal in mammals is the resource–competition hypothesis. This predicts that females remain philopatric because they benefit more than males from familiarity with food resources (Greenwood 1980). In some coastal populations, female bottlenose dolphins range less than males, tend to concentrate their activities in small core areas (Wells 1991), and show specialized feeding strategies (Smolker *et al*. 1997), suggesting that familiarity to food resources may be important for these females. Female bottlenose dolphins may also gain from familiarity to other females. They associate at moderate levels with other females within bands or cliques (Wells 1991; Smolker *et al*. 1992) and groups are usually larger when calves are present (e.g. Möller *et al*. 2002). Shark predation on these animals seems to focus on females and calves (Corkeron *et al*. 1987), and male dolphins are known to harass females (Connor *et al*. 2000) and may even kill calves (e.g. Patterson *et al*. 1998). Therefore female philopatry in bottlenose dolphins may be advantageous for rearing offspring and defending themselves against predators and males.

Other hypotheses for male-biased dispersal in mammals include the local mate competition hypothesis, which predicts males disperse as a result of competition for mates among kin (Dobson 1982), and the inbreeding hypothesis, which suggests that males should disperse because they are at greater risk of inbreeding with close kin (Greenwood 1980; Wolff 1993). Male *T. aduncus* are known to form alliances that compete with other alliances over access to females (Connor *et al*. 2000; Möller *et al*. 2001). However, the presence of several genetically related male dolphins in opposite alliances in Port Stephens (Möller *et al*. 2001; but see Parsons *et al*. 2003 for kin-based alliances in male *T. truncatus*), the relatively high mean relatedness found for male–female pairs in the area (mean = 0.13), and several observations of males herding females which are related to them (Möller, unpublished data), conflict, to a certain extent, with the above two hypotheses. For both *T. aduncus* and *T. truncatus*, sporadic movements of individuals outside their core areas have been observed and assumed to promote genetic exchange between adjacent dolphin groups (Wells 1991; Möller *et al*. 2002). It is hypothesized that these movements may also serve to facilitate familiarization with new social environments. Males may be able to access social opportunities, such as available alliance partners, and mating opportunities, such as the likelihood of winning agonistic contexts over access to females. Since male reproductive success depends more on access to mates and less on familiarity to resources (Greenwood 1980), it might be advantageous for these males to disperse when their breeding prospects are greater in a new area.

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Luciana Möller has interests in behavioural ecology, social evolution and genetic structure of long-lived mammals, especially cetaceans. This publication is part of her PhD thesis on the social and genetic structure of southeastern Australian bottlenose dolphins. Luciano Beheregaray is the head of the Molecular Ecology Laboratory at Macquarie University and has broad interests in conservation genetics, phylogeography and speciation.

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