

Sociogenetic structure, kin associations and bonding in delphinids

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Abstract

Social systems are the outcomes of natural and sexual selection on individuals' efforts to maximize reproductive success. Ecological conditions, life history, demography traits and social aspects have been recognized as important factors shaping social systems. Delphinids show a wide range of social structures and large variation in life history traits and inhabit several aquatic environments. They are therefore an excellent group in which to investigate the interplay of ecological and intrinsic factors on the evolution of mammalian social systems in these environments. Here I synthesize results from genetic studies on dispersal patterns, genetic relatedness, kin associations and mating patterns and combine with ecological, life history and phylogenetic data to predict the formation of kin associations and bonding in these animals. I show that environment type impacts upon dispersal tendencies, with small delphinids generally exhibiting female-biased philopatry in inshore waters and bisexual dispersal in coastal and pelagic waters. When female philopatry occurs, they develop moderate social bonds with related females. Male bonding occurs in species with small male-biased sexual size dimorphism and male-biased operational sex ratio, and it is independent of dispersal tendencies. By contrast, large delphinids, which live in coastal and pelagic waters, show bisexual philopatry and live in matrilineal societies. I propose that sexual conflict favoured the formation of these stable societies and in turn facilitated the development of kin-biased behaviours. Studies on populations of the same species inhabiting disparate environments, and of less related species living in similar habitats, would contribute towards a comprehensive framework for the evolution of delphinid social systems.

Keywords: dispersal, dolphins, genetic relatedness, social evolution, toothed whales

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Introduction

Social systems epitomize the outcomes of natural and sexual selection on the attempts of individuals to maximize their inclusive fitness. In mammals, because of differences in the potential rate of reproduction (PRR) of males and females, the lifetime reproductive success of females is generally limited by food resources, while that of males is mainly constrained by access to mates (Trivers 1972; Emlen & Oring 1977; Clutton-Brock & Parker 1992). Female distribution is therefore mainly influenced by food abundance and distribution, while the distribution and number of females, and the presence and behaviour of other males, are expected to

affect male distribution (Wrangham 1980). Ecological factors, primarily food distribution and predation risk, have been identified as the major causes of variation in mammalian social organization and structure (Rubenstein & Wrangham 1986).

In addition to ecological conditions, life history traits, demography and social factors related to intra-sexual competition and inter-sexual conflict are recognized as key factors shaping social systems (e.g. Bekoff *et al.* 1981; Sterck *et al.* 1997; Kappeler 1999; Clutton-Brock 2007; Bro-Jørgensen 2011), and these may also associate with phylogenetic signals (e.g. Di Fiore & Rendall 1994; Linklater 2000; Chapman & Rothman 2009). Among demographic factors, dispersal patterns have an important effect on social structure and social relationships. In mammals that live in social groups, females generally remain in their natal group or range, while males

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disperse before breeding (Greenwood 1980; Clutton-Brock & Lucas 2011). Because of their PRR, females benefit more than males from a high degree of familiarity with food resources, and this may be best attained by philopatry (Pusey & Packer 1987; Clutton-Brock & Lucas 2011). For males, sex differences in parental investment generally lead to a bias in the ratio of sexually receptive females to sexually mature males (the operational sex ratio, OSR), which in turn generates intensive competition among males for mates (Trivers 1972; Emlen & Oring 1977; Clutton-Brock & Parker 1992, 1995). Sexual conflict between females and males may then lead to sexual coercion of females by males (Van Schaik & Kappeler 1997; Kappeler 1999), which in turn promotes counter-strategies by females (Agrell & Wolff 1998). The interplay of social structure, dispersal patterns and mating tactics has important effects on the genetic structure of populations (Sugg *et al.* 1996; Dobson *et al.* 1998; Storz 1999), and in turn genetic relationships between individuals within populations are expected to influence their cooperative behaviours (Dobson *et al.* 1998).

Delphinid cetaceans are long-lived mammals that show a wide range of social structures, display large variation in life history traits and inhabit numerous marine, estuarine and freshwater environments (Wells *et al.* 1980, 1999; Connor 2000; Gowans *et al.* 2008). Some species of delphinids exhibit extremely complex social groupings matched only by other long-lived, large-brained mammals, such as primates and elephants (Connor *et al.* 1998). Delphinids are therefore an excellent group in which to investigate the interplay of ecological and intrinsic factors on the evolution of mammalian social systems in aquatic environments.

Recently, Gowans *et al.* (2008) proposed a socio-ecological model that considered the effects of food distribution, predation risk and ranging patterns on the evolution of delphinid social structure. This framework only considered the effects of ecological factors on social strategies, without taking into account the potential impacts of phylogeny, demography, life history traits and social factors on delphinid sociality. In this study I synthesize results from recent genetic studies on dispersal patterns, genetic relatedness, kin associations and mating patterns in delphinids and combine with ecological, life history and phylogenetic data to make predictions about the formation of kin associations and bonding in these animals. This represents an important step towards a more comprehensive framework for the evolution of social systems in delphinids.

The social structure of delphinids

Delphinids live in schools of a few individuals to thousands of animals, and these can range from very fluid

schools of small delphinids to highly stable matrilineal pods of toothed whales that join up to form social groups at higher hierarchical levels (Table 1). Here I synthesize some of this variation with examples from the most studied species with different life histories and inhabiting disparate environments. Environments are classified according to Wells *et al.* (1999). 'Inshore' environments include enclosed bays and estuaries, and their associated coastal waters; 'coastal' as habitats along an open shoreline; and 'pelagic' as offshore deep-water habitats, including continental shelf waters, unbounded by shorelines.

Small delphinids inhabiting inshore and coastal shallow waters are generally found in small schools, where school size and composition can change frequently (e.g. Wells *et al.* 1987; Smolker *et al.* 1992; Slooten *et al.* 1993; Bräger 1999). Depending on the availability of food resources, these dolphins may exhibit small home ranges and show year-round site fidelity, or larger range patterns and seasonal or weak site fidelity (e.g. Wells *et al.* 1987; Karczmarski 1999; Möller *et al.* 2002; Bräger *et al.* 2003). Sex and age segregation in small delphinids appears to repeatedly occur either between schools or within schools, depending on school size and activity, and the reproductive status of individuals (e.g. Wells *et al.* 1987; Smolker *et al.* 1992; Karczmarski 2000; Möller & Harcourt 2008). In all delphinids studied so far, the strongest social bonds are found between mothers and their calves. Apart from those, associations between some individuals persist more than with others. Strong and long-term social bonds have been particularly observed between male bottlenose dolphins (*Tursiops* spp.) and moderate bonds between females (Wells *et al.* 1987; Connor *et al.* 1992; Smolker *et al.* 1992; Möller *et al.* 2001, 2006; Wiszniewski *et al.* accepted). Other small delphinids, such as humpback dolphins (*Sousa chinensis*) and Hector's dolphins (*Cephalorhynchus hectori*) living in coastal environments, appear to mainly exhibit casual and short-lasting affiliations between individuals (other than mother-calf pairs; Slooten *et al.* 1993; Bräger 1999; Karczmarski 1999; Karczmarski *et al.* 2000).

Small delphinids inhabiting deeper coastal waters are generally found in larger and more fluid schools than those found in inshore and shallow coastal waters. They also appear to have larger home ranges and show either little or seasonal site fidelity to local areas. In pelagic waters, they are found in medium-sized to extremely large schools reaching up to thousands of individuals; schools are dynamic in size and composition and are believed to range over vast areas (e.g. spotted and spinner dolphins in the eastern tropical Pacific; Scott & Cattanach 1998; Scott & Chivers 2009). Some degree of sex segregation within the large pelagic schools has also

Table 1 Social structure in delphinids[†]

| Subfamily [†] | Species | Social structure | Association patterns | General bonds | Sex-specific bonds | Mean group size | Environment | Ocean region | References |
|------------------------|------------------------------------|-------------------|----------------------|--|---|-------------------------------|---|---|---|
| Lissodelphininae | <i>Cephalorhynchus commersonii</i> | Fission–fusion | Fluid | Weak to moderate ^s Weak | | 2 | Coastal | Southwest Atlantic South Pacific | Cocarella <i>et al.</i> (2010, 2011) Slooten & Dawson (1988), Slooten <i>et al.</i> (1993) and Bräger (1999) |
| | <i>Cephalorhynchus hectori</i> | Fission–fusion | Fluid | Weak | | 2 to 8 | Coastal | South Pacific | Slooten & Dawson (1988), Slooten <i>et al.</i> (1993) and Bräger (1999) |
| | <i>Lagenorhynchus obscurus</i> | Fission–fusion | Fluid | Weak with a few strong | | 7 to 10 | Coastal and pelagic | Southwest Atlantic and South Pacific | Würsig & Würsig (1980) and Pearson (2009) |
| Delphininae | <i>Sotalia guianensis</i> | Fission–fusion | Fluid | Weak | | 12 | Inshore | Southwest Atlantic | Santos & Rosso (2008) |
| | <i>Stenella longirostris</i> | Fission–fusion | Fluid | Weak with a few strong | Possibly male coalitions | 35 to >100 | Pelagic (inshore for resting) | North Pacific | Würsig <i>et al.</i> (1994) and Norris & Johnson (1994) |
| | <i>Tursiops aduncus</i> | Bisexually bonded | Stable | Strong, long term | | 211 | Pelagic (inshore for resting) ^{††} | North Pacific | Karczmarski <i>et al.</i> (2005) |
| | | Fission–fusion | Fluid | Weak with some moderate and strong | Male alliances/coalitions, female networks/clusters | 4 to 7 | Inshore | East Indian and Southwest Pacific | Smolker <i>et al.</i> (1992), Connor <i>et al.</i> (1992, 1999, 2011), Möller <i>et al.</i> (2001, 2002, 2006) and Wiszniewski <i>et al.</i> (2010, accepted) |
| | <i>Tursiops truncatus</i> | Fission–fusion | Fluid | Weak with some moderate and strong | Male alliances, female bands | 5 | Inshore | Gulf of Mexico | Wells <i>et al.</i> (1987), Wells (1991) and Bouveroux & Mallefet (2010) |
| | | Fission–fusion | Fluid | Weak with some moderate and strong | Male alliances, moderate female bonds | 3 to 5 | Coastal | North Atlantic | Rosbach & Herzog (1999) and Rogers <i>et al.</i> (2004) |
| | Fission–fusion | Fluid | Weak | Weak | 20 | Coastal | Northeast Pacific | Defran & Weller (1999) | |
| | Bisexually bonded | Stable | Strong, long term | Bisexual bonds, possibly male coalitions | 17 | Inshore (Fjord) ^{††} | South Pacific | Lusseau <i>et al.</i> (2003) and Lusseau (2007) | |

Table 1 Continued

| Subfamily [†] | Species | Social structure | Association patterns | General bonds | Sex-specific bonds | Mean group size | Environment | Ocean region | References |
|------------------------|-----------------------------|---------------------|----------------------|--------------------------------|-----------------------------------|------------------|---------------------|--|--|
| | <i>Sousa chinensis</i> | Fission–fusion | Fluid | Weak | | 4 to 7 | Coastal and inshore | Southwest Pacific and Southwest Indian | Karczmarski (1999) and Parra <i>et al.</i> (2011) |
| | <i>Steno bredamensis</i> | Fission–fusion | Fluid | Weak to moderate ^{‡‡} | | 7 ^{§§} | Pelagic | North Pacific | Baird <i>et al.</i> (2008b) |
| | <i>Orcaella heinsolmi</i> | Fission–fusion | Stable | Strong, long term | | 5 | Coastal and inshore | Southwest Pacific | Parra <i>et al.</i> (2011) |
| Globicephalinae | <i>Grampus griseus</i> | Sexually stratified | Stable/Stratified | Strong, long term | Male clusters and female clusters | 13 | Pelagic | North Atlantic | Hartman <i>et al.</i> (2008) |
| | <i>Feresa attenuata</i> | Bisexually bonded | Stable | Strong, long term | Bisexual bonds | 13 ^{§§} | Pelagic | North Pacific | McSweeney <i>et al.</i> (2009) |
| | <i>Globicephala melas</i> | Matrifocal | Stable/hierarchical | Strong, long term | Bisexual bonds | 14 to 20 | Pelagic | North Atlantic and Strait of Gibraltar | Amos <i>et al.</i> (1991, 1993), Ottensmeyer & Whitehead (2003) and de Stephanis <i>et al.</i> (2008) |
| | <i>Pseudorca crassidens</i> | | Stable | Strong, long term | | 15 ^{§§} | Pelagic | North Pacific | Baird <i>et al.</i> (2008a) |
| | <i>Orcinus orca</i> | Matrifocal | Stable/hierarchical | Strong, long term | Bisexual bonds | 2 to 9 | Coastal and pelagic | Northeast and northwest Pacific | Bigg <i>et al.</i> (1990), Baird & Dill (1996), Baird (2000), Ivkovich <i>et al.</i> (2009) and Parsons <i>et al.</i> (2009) |

[†]Studies were included if provided information on social structure, association patterns and group size of a particular population(s).

[‡]Following McGowen (2011).

[§]Individuals sighted ≥ 2 times were used for calculating association indices.

[¶]Midway and Kure atolls, geographically isolated.

^{**}Doubtful Sound, New Zealand, geographically isolated.

[#]Individuals sighted ≥ 3 times were used for calculating association indices.

^{§§}Median group size.

been proposed (e.g. Dohl *et al.* 1986; Pryor & Kang Schallenberg 1991).

In contrast, large delphinids, such as killer whales and long-finned pilot whales, living in coastal and offshore waters are found in smaller and more stable schools than those of small delphinids living in comparable environments and form hierarchically structured, matrilineal societies (Bigg *et al.* 1990; Amos *et al.* 1993). In addition, the Risso's dolphin (*Grampus griseus*), a medium-sized delphinid that inhabits pelagic waters, appears to have a unique social structure, with stable long-term bonds organized in pairs or small clusters stratified by age and sex classes (Hartman *et al.* 2008).

The delphinid socio-ecological model

The risk of predation has long been suggested as one of the most important driving forces in the evolution of delphinid social organization (Norris & Dohl 1980; Norris & Schilt 1988), with school size generally associated with habitat openness, which in turn is correlated with the risk of predation (Wells *et al.* 1999). It is also well recognized that the distribution and abundance of food resources influence delphinid ranging patterns and school sizes and that cooperative foraging possibly played a role in the evolution of social organization in several species (Würsig 1986; Wells *et al.* 1999; Connor 2000). Detailed reviews of the potential benefits and costs of group living in odontocetes can be found in Wells *et al.* (1980, 1999), Connor (2000) and Gowans *et al.* (2008).

The delphinid socio-ecological model of Gowans *et al.* (2008) predicts that temporally and spatially predictable resources, which generally occur in complex inshore environments, should lead to high site fidelity, small home ranges and small school sizes. It further predicts the formation of female nursery groups for calf protection from predators, loose social networks of females based on reproductive status and long-term bonds between males for sequestering individual females for mating. By contrast, the framework envisages that when resources are unpredictable, delphinids will show larger home ranges and associate in larger bisexual schools for predator avoidance and cooperative foraging. This in turn may facilitate the formation of long-term social bonds between females if cooperation for offspring care is beneficial, but few long-term bonds between males are likely to form because males are unable to sequester individual females. It also predicts that because resource availability occurs in a range of complex distributions, in some circumstances, intermediate ranging patterns may emerge, where dolphins form medium-sized schools as a way of balanc-

ing intra-group competition for food and predation protection.

Delphinid life history traits

Delphinids are long-lived animals, with delayed maturity, low lifetime reproductive rates and high level of maternal investment, although considerable variation exists in these traits within the family (Table 2).

The smaller delphinids appear to live to just under 20 years of age, while medium-sized to larger delphinids can live for over 60 years (Table 2). In cetaceans, longevity is closely related to body size (Whitehead & Mann 2000). Delphinids range in length from about 1.3 to 1.8 m in the smallest species (e.g. genera *Cephalorhynchus* and *Sotalia*) to the large killer whales, which can reach lengths of almost 10 m (Table 2). There is also significant variation in sexual size dimorphism (SSD; Table 2), which is correlated with body size (Connor *et al.* 2000). Females attain slightly larger size than males in a few of the smaller delphinids, males attain slightly larger size than females in most of the small species, and greater male-biased SSD is seen in the larger delphinids (Table 2). Larger males also generally have larger propulsion structures and weapons, which are probably involved in male-male competition (Wells *et al.* 1999).

There are also differences in the age delphinids reach sexual maturity, with males and females reaching sexual maturity at a similar young age in Lissodelphininae and females generally maturing at a younger age than males in Delphininae and Globicephalinae (Table 2). Gestation, age at weaning and inter-birth interval also vary within delphinids (Table 2). Inter-birth interval generally increases with body size and correlates with gestational time and the duration of lactation (Whitehead & Mann 2000). Large delphinids of the genera *Globicephala*, *Pesudorca* and *Orcinus* show the lowest rates of prenatal growth (length at birth/gestation period) among cetaceans, suggesting very low prenatal energetic effort (Huang *et al.* 2011).

Additional information on reproductive parameters in delphinids, male reproductive strategies and female reproductive strategies and life histories in cetaceans is available in Perrin & Reilly (1984), Wells *et al.* (1999), Connor *et al.* (2000) and Whitehead & Mann (2000).

Dispersal patterns in delphinids and kin availability

Female philopatry is likely to be favoured when resources are spatially and temporally predictable, which in the case of delphinids is more likely to occur in inshore and coastal areas compared to pelagic environments.

Table 2 Summary of life history parameters in delphinids

| Subfamily | Species | Length (m) | | SSD (length) | Longevity (years) | Age at sexual maturity (years) | | Gestation (months) | Age at weaning (years) | IBI (years) | |
|-----------------------------------|------------------------------------|------------------------------|---------------------|---------------------|-------------------|--------------------------------|------|--------------------|------------------------|-------------|-----|
| | | M | F | | | M | F | | | | |
| Lissodelphininae | <i>Cephalorhynchus commersonii</i> | 1.30 | 1.34 | 0.97 | ≥18 | 5-9 | 5-9 | 12 | | | |
| | <i>Cephalorhynchus hectori</i> | 1.46 | 1.63 | 0.90 | ≥20 | 6-9 | 7-9 | 10-11 | | 2-4 | |
| | <i>Cephalorhynchus heavisidii</i> | ~1.70 | | | | | | | | | |
| | <i>Cephalorhynchus eutropia</i> | ~1.70 | | | | | | | | | |
| | <i>Lagenorhynchus obscurus</i> | 1.88 [†] | 1.91 [†] | 0.98 [†] | | 5-9 | 4-6 | 12 | 1 | 2.5 | |
| | <i>Lagenorhynchus cruciger</i> | 1.90 | 1.80 | 1.06 | | | | | | | |
| | <i>Lagenorhynchus obliquidens</i> | 1.90 [†] | 1.92 [†] | 0.99 [†] | | 10 | 8-11 | 11 | | | |
| | <i>Lissodelphis borealis</i> | 2.63 [†] | 2.17 [†] | 1.21 [†] | ≥42 | 10 | 10 | 12 | | 2 | |
| | <i>Lagenorhynchus australis</i> | 2.20 | 2.10 | 1.05 | | | | | | | |
| | <i>Lissodelphis peronii</i> | ~3.00 | | | | | | | | | |
| | <i>Sotalia guianensis</i> | 1.70 | 1.87 | 0.91 | 30-35 | 7 | 5-8 | 12 | | 2 | |
| | <i>Sotalia fluviatilis</i> | 1.87 | 2.06 | 0.98 | 30-35 | | | | | | |
| | <i>Stenella longirostris</i> | 1.92 [§] | 1.89 [§] | 1.02 [§] | 20 | 7-10 | 4-7 | 10 | 1-2 | 3 | |
| | <i>Stenella clymene</i> | 1.97 | 1.90 | 1.04 | | | | | | | |
| | <i>Stenella attenuata</i> | 2.28 [¶] | 2.09 [¶] | 1.09 [¶] | 46 | 12-15 | 9-11 | 11.5 | 1.7 | 2.5-4 | |
| | Delphininae | <i>Stenella frontalis</i> | 2.30 | 2.30 | 1.00 [?] | | | | | ≤5 | 1-5 |
| <i>Stenella coeruleoalba</i> | | 2.35 ^{††} | 2.18 ^{††} | 1.08 ^{††} | | | | 12-13 | 1.1 | 4 | |
| <i>Lagenodelphis hosei</i> | | 2.36 | 2.35 | 1.00 | ≥18 | 7-10 | 5-8 | | | | |
| <i>Tursiops aduncus</i> | | 2.38 | 2.35 | 1.01 | | ≥12 | ≥12 | 12 | 2.6-5.3 | 3-6 | |
| <i>Delphinus delphis</i> | | 2.42 ^{††} | 2.12 ^{††} | 1.14 ^{††} | ≥25 | 3-12 | 2-7 | 11.5 | 0.5 | 1-3 | |
| <i>Delphinus capensis</i> | | 2.54 | 2.22 | 1.14 | | | | | | | |
| <i>Tursiops truncatus</i> | | 2.61 | 2.51 | 1.04 | 40-50 | 9-14 | 5-13 | | 1.5-2 | 3-6 | |
| <i>Sousa chinensis</i> | | 2.80 | 2.60 | 1.08 | | | | | | | |
| <i>Sousa teuszii</i> | | ~2.80 | | | | | | | | | |
| <i>Lagenorhynchus acutus</i> | | 2.50 ^{§§} | 2.24 ^{§§} | 1.12 ^{§§} | ≥22 | 6-12 | 6-12 | 11 | 0.9 | 2.5 | |
| <i>Steno bredanensis</i> | | 2.32 [§] | 2.31 [§] | 1.004 [§] | ≥36 | 14 | 10 | | | | |
| <i>Lagenorhynchus albirostris</i> | | 2.60 ^{††} | 2.59 ^{††} | 1.003 ^{††} | | 13 | 16 | 10 | | | |
| <i>Orcaella heinsolmi</i> | | ~2.70 | | | ≥30 | | | | | | |
| <i>Orcaella brevistors</i> | | ~2.75 | | | ~30 | | | | | | |
| Globicephalinae | | <i>Peponocephala electra</i> | 2.68 | 2.60 | 1.03 | | 16.5 | 11.5 | 14 | | |
| | | <i>Feresa attenuata</i> | ~2.70 | | | | | | | | |
| | <i>Grampus griseus</i> | 3.80 | 3.80 | 1.00 | ≥35 | | | | | | |
| | <i>Globicephala macrorhynchus</i> | 4.53 ^{††} | 3.58 ^{††} | 1.27 ^{††} | ≥63 | 13-17 | 8-9 | 14.5-16 | | 2-2.8 | |
| | <i>Globicephala melas</i> | 5.45 ^{†††} | 3.81 ^{†††} | 1.43 ^{†††} | 35-45 (M) >60 (F) | 12 | 8 | 12 | | 3.7 | |

Table 2 Continued

| Subfamily | Species | Length (m) | | SSD (length) | Longevity (years) | Age at sexual maturity (years) | | Gestation (months) | Age at weaning (years) | IBI (years) |
|-----------|-----------------------------|--------------------|--------------------|--------------------|---------------------|--------------------------------|-------|--------------------|------------------------|-------------|
| | | M | F | | | M | F | | | |
| | <i>Pseudorca crassidens</i> | 5.32 ^{SS} | 4.47 ^{SS} | 1.19 ^{SS} | 57 (M) 62 (F) | 8–14 | 8–14 | 15.5 | 1.8 | |
| | <i>Orcinus orca</i> | 9.45 ^{SS} | 5.66 ^{SS} | 1.67 ^{SS} | 50–60 (M) 80–90 (F) | 15 | 10–15 | 15–18 | 1–2 | 5 |

SSD, sexual size dimorphism; M, male; F, female; IBI, inter-birth interval.

[†]Southeastern Atlantic.

[‡]Northeastern Pacific.

[§]Gulf of Mexico.

[¶]Eastern tropical Pacific (coastal).

^{‡‡}Southwestern Indian.

^{##}Northwestern Pacific.

^{SS}Northeastern Atlantic.

⁺⁺⁺Northwestern Atlantic.

Data sourced from Perrin & Reilly (1984), Barros (1991), Slooten (1991), Hai *et al.* (1996), Lockyer *et al.* (1988), Reynolds & Rommel (1999), Jefferson (2000), Mann *et al.* (2000), Hale *et al.* (2000), Rosas & Monteiro (2002) and Jefferson *et al.* (2008).

Recent genetic studies have demonstrated female-biased philopatry for several inshore and coastal populations of small delphinids (Table 3). In these philopatric populations, females have the potential to spend their lives in close association or spatial proximity with their maternal kin, thus creating opportunities for the development of kin-biased affiliations and behaviours (e.g. Möller *et al.* 2006; Frere *et al.* 2010b). In at least two Indo-Pacific bottlenose dolphin (*T. aduncus*) populations, males also show a moderate degree of philopatry (Krützen *et al.* 2004; Möller & Beheregaray 2004). Based on long-term behavioural data, Connor *et al.* (2000) suggested the possibility of locational bisexual philopatry for bottlenose dolphins, by which males would include their natal home range into their adult home ranges. The availability of male kin in these populations could then lead to the presence of male relatives in cooperative alliances (e.g. Krützen *et al.* 2003) and associations between male and female kin (e.g. Wiszniewski *et al.* 2010).

By contrast, in pelagic waters where resources are likely to be less predictable, genetic analyses of several populations of small delphinids suggest that both males and females are likely to disperse, with no significant sex bias in dispersal (Table 3). Opportunities for association between kin in populations exhibiting bisexual dispersal, or among individuals of the dispersing sex, however, may still arise if there is dispersal of paternally related cohorts, if kin of different cohorts disperse together or if individuals disperse into groups already containing genetic relatives.

Evidence for an exception to the above-mentioned patterns comes from long-term behavioural studies and genetic data from killer whales (*Orcinus orca*) and long-finned pilot whales (*Globicephala melas*), where neither males nor females appear to disperse from their natal groups (Table 3). This is challenging to explain as the balance between benefits of kin cooperation and the costs of inbreeding is predicted to increase the magnitude of sex-biased dispersal with an increase in social complexity (Perrin & Goudet 2001). This unusual pattern among mammals, which was first demonstrated based on long-term behavioural data (Bigg *et al.* 1987, 1990), was recently genetically confirmed for several populations of killer whales from the North Pacific and North Atlantic (Pilot *et al.* 2010; Table 3). Connor (2000) suggested that the lower costs of locomotion for cetaceans in the aquatic environment could reduce the cost of philopatry for odontocetes compared to terrestrial mammals, as observed for the killer and pilot whales. The most extreme case is the fish-eating killer whales of British Columbia and Washington Strait. These killer whales are found in stable matrilineal groups, with no dispersal observed by either sex (Bigg

Table 3 Dispersal tendencies in delphinid populations inferred based on genetic data

| Species | Ocean region | Environment | Dispersal tendencies | Statistical tests | Number of samples | References |
|--------------------------------|--|-------------------------------|----------------------|---------------------------------------|-------------------|--|
| <i>Tursiops aduncus</i> | Southwestern Pacific | Inshore | MB | mAIC, r | 54, 35 | Möller & Behergaray (2004) and Möller <i>et al.</i> (2007) |
| <i>Tursiops aduncus</i> | Southeastern Indian | Inshore | MB | F_{ST} , Φ_{ST} , Nm | 302 | Krützen <i>et al.</i> (2004) |
| <i>Tursiops truncatus</i> | Gulf of Mexico | Inshore | MB | F_{ST} | 56 | Sellas <i>et al.</i> (2005) |
| <i>Tursiops aduncus</i> | Southwestern Indian | Coastal | MB | mAIC, vAIC, F_{ST} | 142 | Natoli <i>et al.</i> (2008b) |
| <i>Tursiops truncatus</i> | Northwestern Atlantic | Pelagic | MB [†] | mAIC, vAIC, r , F_{ST} , F_{IS} | 404 | Rosel <i>et al.</i> (2009) |
| <i>Tursiops</i> sp. | Southern Indian | Inshore | MB | mAIC, r , F_{ST} | 50 | Bilgmann <i>et al.</i> (2007) |
| <i>Stenella coeruleoalba</i> | Mediterranean Sea and Northeastern Atlantic | Pelagic | MB | r | 165 | Gaspari <i>et al.</i> (2007) |
| <i>Stenella frontalis</i> | Northwestern Atlantic, including Gulf of Mexico | Coastal and pelagic | MB [†] | F_{ST} , Φ_{ST} | 199 | Adams & Rosel (2006) |
| <i>Stenella longirostris</i> | South Pacific Ocean | Pelagic (inshore for resting) | MB | F_{ST} and Φ_{ST} , vAIC | 154 | Oremus <i>et al.</i> (2007) |
| <i>Lagenorhynchus obscurus</i> | Southeastern Pacific, Southwestern Atlantic, Southwestern Pacific | Coastal and pelagic | MB | vAIC, F_{ST} | 120 | Cassens <i>et al.</i> (2005) |
| <i>Tursiops truncatus</i> | Northwestern Atlantic | Coastal | BD | F_{ST} | 58 | Parsons <i>et al.</i> (2006) |
| <i>Tursiops truncatus</i> | Gulf of Mexico | Coastal | BD | F_{ST} | 185 | Sellas <i>et al.</i> (2005) |
| <i>Tursiops truncatus</i> | Mediterranean Sea, Black Sea and Northeastern Atlantic | Pelagic | BD | mAIC, vAIC, r , F_{ST} , F_{IS} | 145 | Natoli <i>et al.</i> (2005) |
| <i>Tursiops truncatus</i> | North Atlantic | Pelagic | BD | mAIC, vAIC, r , F_{ST} , F_{IS} | 112 | Querouil <i>et al.</i> (2007) |
| <i>Tursiops aduncus</i> | Southwestern Pacific | Coastal | BD | mAIC, r , F_{ST} | 51, 131 | Möller <i>et al.</i> (2007) and Wiszniewski <i>et al.</i> (2010) |
| <i>Tursiops</i> sp. | Southern Indian | Coastal | BD | mAIC, r , F_{ST} | 34 | Bilgmann <i>et al.</i> (2007) |
| <i>Delphinus delphis</i> | Southern Indian | Coastal and pelagic | BD | mAIC, r , F_{ST} | 72 | Bilgmann <i>et al.</i> (2009) |
| <i>Delphinus delphis</i> | Southwestern Pacific | Pelagic | BD | mAIC, F_{ST} | 115 | Möller <i>et al.</i> (2011) |
| <i>Delphinus delphis</i> | Black Sea, Mediterranean Sea and Northeastern Atlantic | Pelagic | BD [§] | mAIC, vAIC, r , F_{ST} , F_{IS} | 118 | Natoli <i>et al.</i> (2008a) |
| <i>Delphinus delphis</i> | North Atlantic | Pelagic | BD | mAIC, vAIC, r , F_{ST} , F_{IS} | 424 | Mirimin <i>et al.</i> (2009) |
| <i>Delphinus delphis</i> | Northeast Atlantic | Pelagic | BD | F_{ST} | 150 | Querouil <i>et al.</i> (2010) |
| <i>Delphinus delphis</i> | Northeastern Atlantic, Eastern Atlantic, Northwestern Atlantic, South Atlantic | Pelagic | BD | mAIC, F_{ST} , F_{IS} | 156 | Natoli <i>et al.</i> (2006) |
| <i>Delphinus capensis</i> | Southwestern Indian | Pelagic | BD | mAIC, F_{ST} , F_{IS} | 43 | Natoli <i>et al.</i> (2006) |
| <i>Stenella attenuata</i> | Eastern tropical Pacific | Coastal and pelagic | BD [†] | F_{ST} | 225 | Escorza-Trevino <i>et al.</i> (2005) |
| <i>Stenella frontalis</i> | Northeastern Atlantic | Pelagic | BD | F_{ST} | 193 | Querouil <i>et al.</i> (2010) |
| <i>Stenella longirostris</i> | North Pacific | Pelagic (inshore for resting) | BD | mAIC, vAIC, r , F_{ST} , F_{IS} | 505 | Andrews <i>et al.</i> (2010) |
| <i>Lagenorhynchus acutus</i> | North Atlantic | Pelagic | BD | r | 42 | Mirimin <i>et al.</i> (2011) |

Table 3 Continued

| Species | Ocean region | Environment | Dispersal tendencies | Statistical tests | Number of samples | References |
|---------------------------|----------------------------------|---------------------|----------------------|-------------------|-------------------|----------------------------|
| <i>Globicephala melas</i> | North Atlantic | Pelagic | BP | r | 193 | Amos <i>et al.</i> (1993) |
| <i>Orcinus orca</i> | North Atlantic and North Pacific | Coastal and pelagic | BP | r | 213 | Pilot <i>et al.</i> (2010) |

FB, female-biased; MB, male-biased; BD, bisexual dispersal; BP, bisexual philopatry. F_{ST} , Φ_{ST} , fixation indices; mAIC, mean of corrected assignment index; vAIC, variance of corrected assignment index; r , relatedness; F_{IS} , inbreeding coefficient.

[†]MB suggested based on higher values for female comparisons, although nonsignificant test results.

[‡]MB suggested based on significant Φ_{ST} differences between males and females.

[§]BD suggested but F_{IS} significantly greater for females.

^{*}BD suggested but significant F_{ST} differences between males and females for localities with small sample sizes.

et al. 1987, 1990). This dispersal pattern is in contrast to the sympatric marine mammal-eating killer whale, despite extensive geographic overlap. Mammal-eating whales are generally found in smaller groups and appear to be composed of only a single matriline with up to two generations. From these groups, females may disperse when their first calf is born, or males, other than the firstborn, before sexual maturity (Baird 1994; Baird & Dill 1995; Baird 2000). Smaller groups appear to be optimal for foraging their main prey, harbour seals (Baird & Dill 1995), suggesting that dispersal in these animals is related to foraging efficiency. Long-finned pilot whales also appear to display a pattern of bisexual philopatry, with molecular typing revealing that large pods of pilot whales caught in a drive fishery consisted of single extended families (Amos *et al.* 1991, 1993). Differences in philopatric and dispersal patterns impact on the kinship structure of groups and in turn will affect social relationships among individuals (Clutton-Brock & Lucas 2011). Therefore, among the delphinids, the prospects for association and potentially cooperation with a large number of relatives appear to be highest among these bisexually philopatric toothed whales.

Genetic relatedness, kin associations and mating patterns in delphinids

Analysis of relatedness and parentage in delphinids is still in its infancy (Table 4). Kinship relationships in delphinid schools are best known from studies of bottlenose dolphins living in inshore environments, where strong female philopatry and moderate male philopatry were suggested (Möller & Beheregaray 2004; Krützen *et al.* 2004). Genetic studies in populations of Indo-Pacific bottlenose dolphins from Australia suggested that females form moderate social bonds with maternally and biparentally related females (Möller *et al.* 2006; Freire *et al.* 2010b; Table 4) but also associate closely with unrelated females, including those in similar reproductive status (Möller & Harcourt 2008). In addition, certain females in one population associated closely with related adult males (Wiszniewski *et al.* 2010; Table 4). Altogether, these results imply kin recognition in delphinids (Box 1).

Male bottlenose dolphins in some inshore populations associate strongly with other males forming alliances and coalitions that cooperate to gain access to receptive females for mating (Wells *et al.* 1987; Connor *et al.* 1992, 1999; Möller *et al.* 2001; Wiszniewski *et al.* accepted; Tables 4 and 5). Strong male bonds and the formation of coalitions have also been suggested for other members of the subfamily Delphininae (Atlantic spotted dolphins, *S. frontalis*, Herzing & Johnson 1997;

Table 4 Patterns of genetic relatedness within delphinid groups

| Species | Area | Dispersal tendencies | Relatedness patterns | Sample type | Number of samples | Reference |
|------------------------------|-----------------------------------|----------------------|---|--------------------------|--|------------------------------|
| <i>Tursiops</i> sp. | Shark Bay, Western Australia | MB | First-order and second-order allied males are more related than expected by chance; superallied males are randomly related Females associate preferentially with maternal and biparentally related females Females associate with maternal kin within bands | Biopsies | 162 m | Krützen <i>et al.</i> (2003) |
| <i>Tursiops truncatus</i> | Sarasota Bay, Florida | MB | Allied males are randomly related Associated and allied males are randomly related Females associate preferentially with maternally related females Females associate preferentially with genetic related females and males | Blood samples | 60 | Duffield & Wells (1991) |
| <i>Tursiops aduncus</i> | Port Stephens, eastern Australia | MB | Allied males are randomly related Associated and allied males are randomly related Females associate preferentially with maternally related females Females associate preferentially with genetic related females and males | Blood samples | 81 m | Owen (2003) |
| <i>Tursiops truncatus</i> | Little Bahamas Bank | BD | Allied males are more related than expected by chance Associated females in small groups are more related than expected by chance; associated males are randomly related | Biopsies, faecal samples | 21 m | Parsons <i>et al.</i> (2003) |
| <i>Stenella coeruleoalba</i> | Ligurian Sea | MB | Associated females in small groups are more related than expected by chance; associated males are randomly related | Biopsies and scrub pads | 33 f, 29 m | Gaspari <i>et al.</i> (2007) |
| <i>Delphinus delphis</i> | Bay of Biscay and English Channel | | Average relatedness within pods not significantly different than average relatedness between pods, but large mass stranding likely to include half sibships | Strandings | 51 f, 1 m ⁺ ; 24 f, 18 m ⁺ | Viricel <i>et al.</i> (2008) |
| <i>Lagenorhynchus acutus</i> | West Ireland | BD | Groups consisted of multiple maternal lineages, mostly unrelated adults and mother-offspring calves | Strandings | 15 f, 21 m | Mirimin <i>et al.</i> (2011) |

Table 4 Continued

| Species | Area | Dispersal tendencies | Relatedness patterns | Sample type | Number of samples | Reference |
|---------------------------|---|----------------------|--|-----------------------------------|-------------------|----------------------------|
| <i>Orcinus orca</i> | Washington State, southeast Alaska, Kamchatka Russia, Aleutians and Bering Sea, North Pacific offshore, California, southeast Iceland | BP | Average relatedness within pods was significantly higher than average relatedness within populations, but lower in 'transient' compared to 'resident' ecotypes; average relatedness of females higher than males in Washington State and Alaskan resident populations and the reverse pattern in transient offshore and Russian resident populations | Strandings, biopsies [§] | 87 f, 126 m | Pilot <i>et al.</i> (2010) |
| <i>Globicephala melas</i> | Faroe Islands, North Atlantic | BP | Pod members were from a single extended family | Drive fishery | 193 | Amos <i>et al.</i> (1991) |

MB, male-biased; BD, bisexual dispersal; BP, bisexual philopatry; m, males; f, females.

[†]Mass stranding.

[‡]Single strandings.

[§]Biopsies from captive and free-ranging animals.

spinner dolphins, *S. longirostris*, Norris & Johnson 1994). In bottlenose dolphins, male alliance formation has been documented in populations with male-biased and female-biased dispersal patterns (Table 5), and therefore, this cooperative behaviour appears to have evolved independently of dispersal tendencies. Members of stable alliances are closely related in some populations (Krützen *et al.* 2003; Parsons *et al.* 2003; Tables 4 and 5), but in other populations, allied males are on average only randomly related (Möller *et al.* 2001; Owen 2003; Wiszniewski *et al.* in press; Tables 4 and 5). In one population where males in stable alliances were on average more related than expected by chance (Krützen *et al.* 2003), the reproductive success of males within some of the alliances was significantly skewed (Krützen *et al.* 2004). Levels of inbreeding in this population were higher than expected by chance, with young, less experienced mothers producing earlier calves that are more inbred and less fit (Frere *et al.* 2010a). By contrast, in a population where allied males are on average randomly related, reproductive skew within alliances was not significantly different from random expectations, although there was a moderate degree of polygyny in the population with males in larger alliances fathering more calves per capita (Wiszniewski *et al.* 2011). In another species, the Atlantic spotted dolphin, age appears to have an effect on male reproductive success (Green *et al.* 2011).

Information on the degree of genetic relatedness of delphinid schools living in coastal and pelagic waters, where bisexual dispersal is typical, is scarcer. In the striped dolphin, analysis of genetic relatedness showed higher average relatedness between adult females within small schools, suggesting that females preferentially associate with adult kin in these groups (Gaspari *et al.* 2007; Table 4). In some other dolphin species living in open environments and usually found in large schools, genetic relatedness has been investigated based on samples from stranded animals. Short-beaked common dolphins, for example, do not appear to associate preferentially with relatives, but sex, age and sexual maturity may influence associations in these animals (Viricel *et al.* 2008; Table 4). A similar pattern is also suggested for Atlantic white-sided dolphins where groups were mainly composed of unrelated adult individuals and calves, with juveniles absent from the groups studied (Mirimin *et al.* 2011; Table 4). Calves in the latter study were not closely related to each other, suggesting that the mating system was more likely to be promiscuous (Mirimin *et al.* 2011). Large group sizes and promiscuous mating systems, coupled with the bisexual dispersal patterns of pelagic dolphins, should lead to dilution of genetic relatedness

Table 5 Male alliance formation in populations of bottlenose dolphins (genus *Tursiops*) with available genetic data

| Species | Population | Alliance type | Alliance size | Relatedness | Dispersal | Sex ratio [†] | SSD (length) | IBI (years) | References |
|---------------------------|---------------|---------------|---------------|---------------------------------|-----------|------------------------|--------------------|-------------------|--|
| <i>Tursiops</i> sp. | Shark Bay | First order | 2–3 | Greater than expected by chance | MB | 0.8 | 1.004 [‡] | 3–6 | Smolker <i>et al.</i> (1992), Mann <i>et al.</i> (2000) and Krützen <i>et al.</i> (2003, 2004) |
| <i>Tursiops</i> sp. | Shark Bay | Second order | 5–6 | Greater than expected by chance | MB | 0.8 | 1.004 [‡] | 3–6 | Smolker <i>et al.</i> (1992) and Krützen <i>et al.</i> (2003, 2004) |
| <i>Tursiops</i> sp. | Shark Bay | Superalliance | 14 | Randomly related | MB | 0.8 | 1.004 [‡] | 3–6 | Smolker <i>et al.</i> (1992) and Krützen <i>et al.</i> (2003, 2004) |
| <i>Tursiops truncatus</i> | Sarasota Bay | First order | 2 | Randomly related | MB | 0.7 [§] | 1.060 | 3–6 | Wells <i>et al.</i> (1987), Wells (1991), Scott <i>et al.</i> (1990) and Tolley <i>et al.</i> (1995) |
| <i>Tursiops aduncus</i> | Port Stephens | First order | 2–4 | Randomly related | MB | 0.8 | 1.003 [¶] | 3–5 ^{††} | Möller <i>et al.</i> (2001) and Wiszniewski <i>et al.</i> (2009) |
| <i>Tursiops truncatus</i> | Bahamas | First order | 2 | Greater than expected by chance | BD | 0.9 | | | Parsons <i>et al.</i> (2006) |

MB, male-biased; BD, bisexual dispersal; SSD, sexual size dimorphism (body length); IBI, inter-birth interval.

[†]Estimated based on the proportion of biopsy sampled adult males and females.

[‡]Estimated based on 2 adult males and 2 adult females reported in Smolker *et al.* (1992).

[§]Based on capture-released animals.

[¶]Estimated based on measures from eastern Australian *T. aduncus* reported in Hale *et al.* (2000).

^{††}Möller (unpublished data).

values within schools (e.g. Lukas *et al.* 2005; Holekamp *et al.* 2011). By contrast, genetic analyses of several populations of killer whales in the North Pacific and North Atlantic demonstrated very high levels of genetic relatedness within pods, both within and between sexes (Pilot *et al.* 2010; Table 4). In these animals, gene flow appears to be mainly mediated by males during temporary associations of pods and temporary dispersal of males between pods, populations and ecotypes, with only a few cases of permanent dispersal genetically suggested (Pilot *et al.* 2010; Foote *et al.* 2011; Ford *et al.* 2011). As in the closed societies of bats, maternally inherited mtDNA should be highly conserved among group members, while biparentally inherited nuclear DNA should be less structured depending on the level of gene flow (Kerth & Van Schaik 2011). Recent paternity analyses in these animals revealed contrasting male reproductive behaviours, with low skew and half of the paternities assigned to males from different populations in one study (Pilot *et al.* 2010) and moderate skew and most matings occurring within pods in another (Ford *et al.* 2011).

Box 1 Potential mechanisms of kin recognition in delphinids

Kin recognition is the ability to distinguish between individuals of different degrees of genetic relatedness (Hepper 1991). In delphinids, kin recognition is likely to occur via social familiarity. In bottlenose dolphins, juveniles usually remain loosely associated with their mothers, but associate more closely with them when their siblings are born (Wells 1991). Therefore, young dolphins have opportunities to become familiar with at least maternal siblings of adjacent cohorts. Female bottlenose dolphins have also been observed to return to their natal band when their first calves were born (Wells 1991) and continued to associate with their mothers after conceiving calves (Smolker *et al.* 1992), suggesting that mother–daughter social bonds continue into adulthood.

Another mechanism for individual and possibly kin recognition is through vocal communication. Dolphins produce a large array of vocalizations, and among these are individually distinctive whistles, called signature whistles (Caldwell & Caldwell 1965; Caldwell *et al.* 1990). In bottlenose dolphins, there is strong evidence that these sounds play a role in individual recognition, including that of close kin (Sayigh *et al.* 1999; Janik *et al.* 2006). Playback

experiments have shown that bottlenose dolphins respond more strongly to whistles of closely related than to those of unrelated but familiar individuals (Sayigh *et al.* 1999). This has been also demonstrated in a similar experiment but using synthetic whistles from which all voice features were removed, suggesting that signature whistles may be used as referential signals similar to the use of names in humans (Janik *et al.* 2006). Signature whistles are also used for maintaining group cohesion (Janik & Slater 1998), including that between kin (Smolker *et al.* 1993). In captivity, dolphins were more likely to produce signature whistles when one of the group members voluntarily swam to a different pool (Janik & Slater 1998). In the wild bottlenose dolphin, calves whistled more often towards the end of mother–calf separations, just before reunions (Smolker *et al.* 1993). Allied male bottlenose dolphins also converge to similar whistles as social bonds strengthen (Watwood *et al.* 2004). While most studies on the function of signature whistles have been conducted in bottlenose dolphins, these whistles have also been reported in several other dolphin species, including short-beaked common dolphins (Caldwell & Caldwell 1968), Pacific white-sided dolphins (Caldwell & Caldwell 1971), Atlantic spotted dolphins (Caldwell & Caldwell 1973) and humpback dolphins (Van Parijs & Corkeron 2001).

Killer whales that live in highly stable matrilineal pods (Bigg *et al.* 1990) are known to have distinctive group-specific vocal repertoires (Riesch *et al.* 2006). Call structure is known to reflect both maternal relatedness and social affiliation, providing a mechanism for kin recognition, and also to facilitate social decisions (Deecke *et al.* 2010). Moreover, individuals within groups produce calls with different frequency contours, suggesting that these whales may also be able to distinguish between the highly similar shared calls of their matrilineal relatives (Nousek *et al.* 2006).

Towards a comprehensive framework for the evolution of delphinid social systems

Predictability of resources and dispersal patterns: female bonding in small delphinids

In this review I showed that in small delphinids, female-biased philopatry is primarily observed in populations residing in inshore waters (Table 3), where predictable resources are more likely to be found compared to other marine environments (e.g. Wells *et al.* 1999; Gowans *et al.* 2008). Female philopatry in

these areas is likely to occur because of differences in PRR of male and females, and females benefiting more than males from familiarity with food resources. Genetic studies further indicated that these females preferentially associated with female kin (Table 4). In addition, results from behavioural studies suggested that they also associate closely with other females in similar reproductive states (Wells *et al.* 1987; Möller & Harcourt 2008). Thus, under these circumstances, I propose that moderate female social bonds emerge between kin and nonkin, although long-term social bonds may preferentially occur between female kin. This conflicts with the prediction of loose social networks of females based on reproductive status, which was proposed by Gowans *et al.* (2008). Benefits for the formation of these bonds include calf protection from predators, male harassment and possibly infanticide, the latter two depending on the degree of sexual conflict between males and females, which relates to the bias in the OSR.

By contrast, the majority of genetic studies of small delphinids inhabiting coastal and pelagic environments revealed bisexual dispersal tendencies (Table 1). In these areas, dolphins generally exhibit large home ranges because of the unpredictability of food resources (Wells *et al.* 1999; Gowans *et al.* 2008). Therefore, in these environments, there may be no food-related advantages for females to remain philopatric, and both females and males will tend to disperse. Females may still associate preferentially with females in similar reproductive condition. Thus, under these circumstances, I predict that female associations and weak bonds occur irrespective of kinship. This also disagrees with the socio-ecological model, which suggested the formation of long-term social bonds between females if cooperation for offspring care was beneficial (Gowans *et al.* 2008). However, if there is between-group competition for critical resources (e.g. resting refuge for spinner dolphins in remote atolls; Karczmarski *et al.* 2005), geographic isolation (e.g. common bottlenose dolphins in Doubtful Sound, New Zealand; Lusseau *et al.* 2003) or sexual conflict, moderate to strong social bonds may emerge.

Life history and sexual conflict: male bonding in small delphinids

Here I showed that the formation of male bonding appears restricted to the Delphininae, in species with small male-biased sexual size dimorphism and moderate inter-birth interval, and occurs independently of dispersal tendencies (Tables 1 and 5). I suggest that male alliance formation is a mechanism for increasing the power of males for coercing females for mating and for male–male competition. Different relatedness patterns

in alliances of bottlenose dolphins (Table 5), and no alliance formation in some populations, support the existence of different male mating strategies within and between populations. Although nonkinship-related factors are probably involved in the choice of alliance partners (Möller *et al.* 2001), when related males are present within an alliance, kin selection may operate (Krützen *et al.* 2004). Thus, I propose that the formation of male social bonds as alliances or coalitions occurs independent of dispersal tendencies and kinship and will develop in species with small male-biased SSD and male-biased OSR. In the socio-ecological model, long-term bonds between males for sequestering individual females for mating were only proposed for males inhabiting inshore environments, where females generally associate in small groups. I further suggest that although promiscuity seems the most plausible mating system for small delphinids, the formation of male alliances may lead to a mating system characterized by moderate polygyny.

Life history and sexual conflict: bisexual kin bonding in large delphinids

I reviewed evidence for the unusual pattern of bisexual philopatry in large delphinids and the occurrence of matrilineal societies (Tables 1 and 3). Large body size appears to have evolved twice in the delphinid lineage (e.g. McGowen 2011), and this is also the case for matrilineal social structures, because it is represented in members of the subfamily Globicephalinae and in the genus *Orcinus*. Whales of these societies generally range over large distances because of the unpredictability of their food resources (e.g. Baird 2000), and therefore, bisexual kin bonds are unlikely to have arisen because of strong resource competition. However, kin bonds may facilitate cooperative foraging, food sharing and social learning of foraging techniques (e.g. Guinet 1991; Hoelzel 1991, 1993). Cultural transmission of foraging specializations and vocal sounds has been proposed for killer whales and bottlenose dolphins, but occurs both inside and outside the immediate kin group (e.g. Guinet 1991; Deecke *et al.* 2010; Watwood *et al.* 2004; Krützen *et al.* 2005; Sargeant *et al.* 2005).

I suggest that matrilineal societies in large delphinids have primarily evolved for protection of calves and females from potential male harassment and injuries. Bonds in turn may have facilitated the evolution of kin-biased behaviours. Females in these species show long gestation and lactation, probably leading to a male-biased OSR. In addition, there is a high potential risk of injury from males because of the high SSD between males and females. Although male coercion of females

and calves, and male–male competition, appears to be a rare event, the formation of matrilineal societies may be a successful strategy that led to low prospective for effectiveness in male coercion. In at least one killer whale population, units with large number of adult males rarely associate with other units, which could be related to the costs of foraging in larger groups (Ivkovich *et al.* 2009) or could represent avoidance by other units.

The formation of mother–sons bonds in these animals, although more difficult to explain, could also relate to protection of females and their calves, and this being best attained by the presence of protector male(s) because of the high SSD between females and males. Males on the other hand could benefit through inclusive fitness gains, and also from knowledge transfer of habitat and the location of food resources, particularly from the matriarch. In turn, ‘good sons’ could be preferentially chosen as mates by females. In killer whales, where some feeding specializations favour small groups (e.g. Baird 2000), matriarchs may prefer the primogenitor to remain philopatric because of preferential investment on the offspring with higher potential of reproductive output. Recent genetic studies on these animals showed that male reproductive success appears to increase with age and body size (Ford *et al.* 2011), and males do not breed with female kin (Pilot *et al.* 2010; Ford *et al.* 2011), suggesting the evolution of a mechanism for inbreeding avoidance in philopatry (see Box 1).

Conclusions

Ecological factors, particularly food distribution and predation risk, have been proposed as the main driving forces of delphinid sociality. Here, I showed that environment type, which relates to food predictability and delphinid ranging patterns, impacts upon dispersal tendencies, with small delphinids that live in fission–fusion societies generally exhibiting female-biased philopatry in inshore waters and bisexual dispersal in coastal and pelagic waters. When female philopatry occurs, females preferentially associate with kin and form moderate social bonds with them. Male bonding occurs in species of Delphininae with small male-biased SSD and male-biased OSR, and this behaviour is independent of dispersal tendencies. Males form alliances preferentially with genetically related males or irrespective of kinship, and this has an effect on reproductive skew within alliances.

By contrast, large delphinids, which live in coastal and pelagic waters, show bisexual philopatry and live in matrilineal societies (*Orcinus*, and possibly *Globicephala* and *Pseudorca*). Risk of predation and food competition are unlikely to explain these bisexual kin bonds. It is proposed that protection of calves and females

because of sexual conflict may have favoured the formation of these societies. In turn, kin bonds facilitated the evolution of kin-biased behaviours.

Only a few paternity studies have been conducted for delphinids so far, and these, combined with information of large testes relative to their body mass (Connor *et al.* 2000), point towards promiscuity and moderate polygyny as the most plausible mating systems. Studies on populations of the same species inhabiting disparate environments, and studies of less related species living in similar habitats, would contribute towards unravelling ecological and intrinsic factors shaping the evolution of delphinid social systems. Preferably, these studies would combine long-term behavioural observations, genetic information on relatedness and parentage, life history and demographic data towards building a comprehensive framework for the evolution of delphinid social systems.

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