Population density, cooperation, and the evolution of toothed whale societies

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Abstract

Odontocete societies come in two primary forms: stable matrilineally-based groups, often with bonds between groups, and labile associations among related and unrelated females in a 'fission-fusion' grouping pattern. There is no general theory to explain why these differing strategies evolved. Primate models of social bond evolution, based on cooperation in food competition, lack utility for highly mobile odontocetes, who live in a three-dimensional environment where food defense is impractical, and the group is often the only refuge against predators. Here we offer a general model of odontocete social evolution, illustrated by agent-based simulation. In our model, individuals (or subgroups) must disperse to forage, exposing them to danger from predators or rivals; a danger they may mitigate by investing in additional social bonds. This model can explain the evolution of labile versus stable matrilineal societies, as well as social

bonds between groups. Variation in local population densities, movement patterns, predation risk, and food distribution will be key for testing the predictions of our model.

Keywords: Social evolution; toothed whale; cooperation; kinship; social network

Introduction

The toothed whales (Odontoceti) are a diverse group of large and large-brained mammals found in marine habitats worldwide. In general, odontocetes live for decades; females invest heavily in single offspring and males appear to offer no parental care (Rendell et al. 2019). The social systems of several odontocetes have been described in some detail, including variation between and even within populations, ranging from the relatively small 2m Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) to the 10-18m sperm whale (*Physeter macrocephalus*). With the incorporation of new technology, the social structure and behavior of other species is increasingly coming into view (e.g. Hartman et al. 2020; O'Corry-Crowe et al. 2020; Ramos et al. 2023).

Social bonds and cooperation are widespread in odontocetes. Odontocetes large and small have preferred, often strongly bonded associates, engage in extensive prosocial behavior, hunt and defend against predators cooperatively, help others acquire mates, help distressed individuals, engage in baby-sitting and help support calves after birth (Würsig & Würsig 1980; Connor et al. 1992a, 2022; Whitehead 1996; Connor 2000; Pitman et al. 2001; Gazda et al. 2005; Benoit-Bird and Au 2009; Pitman & Durban 2012; De Stephanis et al. 2015; Kuczaj et al. 2015; Park et al. 2013; Augusto et al. 2017, Konrad et al. 2019; Torres Ortiz et al. 2021; Danaher-Garcia et al. 2022; Weiss et al. 2021b; Friedman et al. 2023, Maalouf et al. 2026). Odontocete studies have revealed striking instances of convergence with large brained terrestrial mammals, including the social system and life history of sperm whales and elephants (Weilgart et al. 1996) as well as traits that are otherwise distinguishing attributes of humans (multi-level male alliances in Indo-pacific bottlenose dolphins, menopause in killer whales (*Orcinus orca*), and symbolic

52 marking and large scale social structures in sperm whales; Connor et al. 1992a, 2011, 2022;
53 Brent et al. 2015; Croft et al. 2017; Hersh et al. 2022; Whitehead 2024). Equally striking
54 characteristics that are rare or unknown in terrestrial mammals have been found in some of these
55 same species, such as Indo-Pacific dolphins living in an open rather than a bounded society
56 typical of social terrestrial mammals (e.g. a wolf 'pack', a chimpanzee 'community', a baboon
57 'troop'; Randić et al. 2012), cultural evolution leading to sympatric populations with distinct
58 foraging specializations in killer whales, and bisexual philopatry in both species (Bigg et
59 al.1990; Ford et al. 1998; Connor et al. 2000, Saulitis et al. 2000; Riesch et al. 2012; Tsai et al.
60 2013; Foote et al. 2016).
61 There are two general types of social system in odontocetes, based on the stability and
62 cohesion of female associations: stable matrilineal groups, and societies characterized as having
63 a 'fission-fusion' grouping pattern at the individual level, which is a reflection of females
64 associating with a varying combination of maternal relatives and non-relatives (Frère et al. 2010;
65 Wells 2014). From here we refer to these female social modes as 'stable' and 'labile',
66 respectively. Matrilineal societies may include bisexual philopatry with strong mother son bonds
67 and bonds between matrilineal groups, and labile societies may include male alliances and bonds
68 between male alliances (e.g. Baird 2000; Ford 2019; Connor et al. 1992a, Connor et al. 2022,
69 Whitehead 2003, Whitehead et al. 2012). This divergence in social structure appears to have
70 coevolved with life history traits, with stable groups promoting the evolution of larger body size
71 and extended lifespans (Walmsley et al., 2026a). Given that these modes also often covary with
72 movement patterns, with stable groups moving collectively, we can also think of these modes as
73 socio-spatial strategies.

74 Why do females in some, generally larger, species remain in stable matrilineal groups
75 while in others they form social bonds with a wider range of related and unrelated females, but
76 none are constant associates? Whether there is continuous variation or a "tipping point" between
77 these modes, understanding the basis for this variation is a significant challenge (Rendell et al.
78 2019). Here we develop a model for the evolution of labile and stable societies based on changes
79 in local population density with body size in the context of predator risk during dispersed
80 foraging. We then generalize our model to explain the evolution of multilevel odontocete
81 societies, including social bonds between male alliances and matrilineal groups. We compare our
82 model with other ideas that have been offered to explain the evolution of stable and labile groups
83 and discuss avenues to test the model.
84 As Kappeler and van Schaik (2002) stated, we need "a theoretical framework that relates
85 fitness-relevant behavior of individuals, such as foraging, predator avoidance, mating and
86 parental care, to the defining characters of a social system". The Standard Ecological Model
87 (SEM) uses variation in key ecological variables to understand variation in social systems
88 (Crook and Gartlan 1966; Wrangham 1980, van Schaik 1983; Sterck et al. 1997, van Schaik and
89 Kappeler 1997; Isbell and Young 2002; Schülke and Ostner 2012; Rendell et al. 2019). Koenig
90 et al. (2013) point out that SEM models have been of two general types, models to explain
91 grouping patterns and mating systems, and models to explain grouping patterns and female social
92 structure.
93 Social structure is the pattern of social relationships, which includes affiliative and
94 agonistic social relationships (Hinde 1976). Social bonds, the topic of interest here, are enduring
95 affiliative social relationships based on frequent and generally affiliative interactions (Silk 2002;
96 Massen et al. 2010; Seyfarth & Cheney 2012, Ostner & Schülke 2014; SM).

If we look broadly at other large mammals with a range of social systems, we find differences in the application of these two types of SEM models. Models of ungulate social systems, for example, have focused more on grouping patterns and mating systems (Jarman 1974; Rubenstein 2010; Hex et al. 2021; Szemán et al. 2021). In contrast, primatologists have focused on patterns of grouping and social bonds, developing sophisticated verbal, and more recently, quantitative socio-ecological models seeking to understand the extraordinary diversity of primate social systems (Wrangham 1980, van Schaik 1983, Sterck et al. 1997, Schülke & Ostner 2012, Port et al. 2020, Isbell 2024). These models seek to explain the formation of primate social groups, as well the nature of social relationships within and between groups, and sex-specific patterns of dispersal.

In general, the information used to construct the early primate models is lacking for odontocetes (Wrangham 1980; van Schaik 1983). For example, the existence and importance of dominance relationships within groups, and contest competition between groups, has not been established for any odontocete society. For most, we know little about the nature of sex specific social bonds, or the nature and even existence of a core group structure (especially for most fission-fusion species) and dispersal from those core groups. However, in addition to those species whose societies have been reasonably well described (e.g. bottlenose dolphins, killer whales, sperm whales) we have grouping patterns, sometimes with information on sex and kinship, for a larger number of species. With the 'gambit of the group,' which assumes that associated individuals are interacting (Whitehead & Dufault 1999, Danaher-Garcia et al. 2022), we can develop explanations for variation in odontocete societies (e.g. see Gowans et al. 2007, Möller 2012; Weiss et al. 2021a; Walmsley et al., 2026a).

Since primates and odontocetes share important features like extensive parental

120 investment in single offspring, complex social relationships, a long lifespan and large brains,
121 should we attempt to superimpose primate models on odontocetes? We think not. Even if we had
122 the information used to construct the first primate socio-ecological models, it is unclear that such
123 an approach would be productive. Gowans et al. (2007) remarked that the delphinid family had
124 "the social intelligence/ thought processing capabilities of primates, the foraging requirements of
125 carnivores and the predation pressures of ungulates". Other characteristics distinguish
126 odontocetes from all terrestrial mammals (Connor 2000).
127 Cooperative defense of food plays a key role in all ecological models of primate social
128 evolution, whether it is considered the reason female-bonded groups form (Wrangham 1980) or
129 why female bonded groups defend areas against other groups and form nepotistic alliances
130 within groups (van Schaik 1983, Sterck et al. 1997, but see Isbell 2024). Cooperative defense of
131 food plays a less important role in structuring odontocete societies (Gowans et al. 2007, Rendell
132 et al. 2019). Odontocetes pursue prey that are often highly mobile in a fluid three-dimensional
133 habitat. While this is true of other mammals (e.g., bats or seals), toothed whales differ in their
134 lack of protected refuges like nests or haul-out areas (see Connor 2007). They are streamlined for
135 efficient movement and do not have to overcome gravity, so experience low costs of locomotion
136 at slow speeds and have concomitantly very large day and home ranges compared to terrestrial
137 mammals (Connor et al. 1998; Connor 2000). Their low cost of locomotion will also lower the
138 costs of forming and leaving groups in odontocetes (Connor 2000). Territoriality has not been
139 described in any odontocete and, given their large ranges and often deep three-dimensional
140 habitat, is likely to be rare. We do not discount a kind of 'area defense,' when different groups
141 are in the same vicinity (e.g., Wilson et al. 1997) or usurpation of prey by conspecifics or even
142 other species (Clua & Grosvalet 2001). However, in general the food related benefits of being in

143 groups in odontocetes are based less on defense compared to terrestrial mammals, and especially
144 primates, which rarely engage in cooperative food acquisition (but see Boesch 1994, Mine et al.
145 2022).

146 The same factors that favor scramble over contest competition in the sea, mobile prey
147 moving in three dimensions, also promotes cooperative food acquisition. Odontocetes often
148 cooperate to detect or corral mobile groups or aggregations of prey, or in some cases to capture
149 single large prey (Würsig & Würsig 1980; Connor 2000; Benoit-Bird and Au 2009; Gazda et al.
150 2005; Pitman and Durban 2012; De Stephanis et al. 2015; Vaughn-Hirshorn 2019; Torres Ortiz
151 et al. 2021). Here, cooperation may be as simple as forming groups that travel in spread
152 formation to increase the likelihood of prey patch detection, to active herding of prey schools.
153 Sharing of larger prey has also been recorded in several species (e.g., Baird 2000; Pitman &
154 Stinchcomb 2002; Wright et al. 2016; Ramos et al. 2021). The evolution of adaptations to
155 acquire and rapidly process the considerable energy available in fish schools, including
156 cooperative feeding, may have fueled the expansion of the delphinid brain (Connor 2007).

157 Following the SEM, the distribution of female odontocetes will be determined primarily
158 by access to resources and safety from predators, parasites and conspecifics, and the distribution
159 of females will then influence male distribution and mating tactics. Our model focuses on
160 predation risk (noting that infanticide risk may also be significant (Connor et al. 2000b, Möller
161 2012). Predation risk, and especially the risk of predation on infants, has long been considered as
162 the key factor favoring group formation in odontocetes (Best 1979, Norris & Dohl 1980, Connor
163 2000). Calf mortality in odontocetes is typically high and a major element in the population
164 dynamics of odontocete species (e.g. Olesiuk et al. 2005; Chiquet et al. 2013; Manlik et al.
165 2016). In open aquatic habitats, odontocetes cannot hide behind a rock, climb a tree or scurry

166 down a burrow to escape predators. In some cases, they can hide acoustically in the surf zone or
167 in silence; pygmy sperm whales (*Kogia breviceps*) can hide briefly in clouds of excreta that
168 function like squid ink, and some species are thought to use depth as an effective burrow, diving
169 to depths their pursuers (e.g. killer whales) cannot reach (Jefferson et al. 1991; Connor 2000;
170 Aguilar de Soto et al. 2020).

171 The most common hiding place for odontocetes is in a group, which at minimum dilutes
172 predation risk (Connor 2000). One of the earliest observations of cooperation against sharks was
173 McBride & Hebb's (1948) description of captive bottlenose dolphins attacking and killing
174 immature tiger sharks and herding sandbar sharks away from a mother at the moment of birth. In
175 the wild groups of dolphins have been observed chasing or attacking sharks and cooperative
176 defense has been observed in sperm whales, who form coordinated defensive formations during
177 killer whale attacks (Saayman & Tayler 1979; Corkeron et al. 1987, Wood et al. 1970,
178 Srinivasan & Markowitz 2010; Pitman et al. 2001). Indo-Pacific bottlenose dolphins rely on
179 larger groups in areas of increased shark density (Heithaus and Dill 2002). Even with these social
180 defense strategies, predation can still have a large impact on fitness in odontocete populations;
181 for example, 74% of adult dolphins in Shark Bay, Western Australia, had evidence of shark bites
182 (Heithaus 2001). However, foraging requirements often force individual odontocetes to leave the
183 safe confines of the group. In many species individuals must spread out to avoid competing for
184 single food items or, as mentioned above, to more efficiently locate food patches upon which the
185 group can feed. An odontocete apart from its group is especially vulnerable. This conflict
186 between the threat from predation and the potential benefits of foraging alone forms the basis for
187 our model (Figure 1). When an individual is alone and a predator threatens her or her calf, who
188 will help?

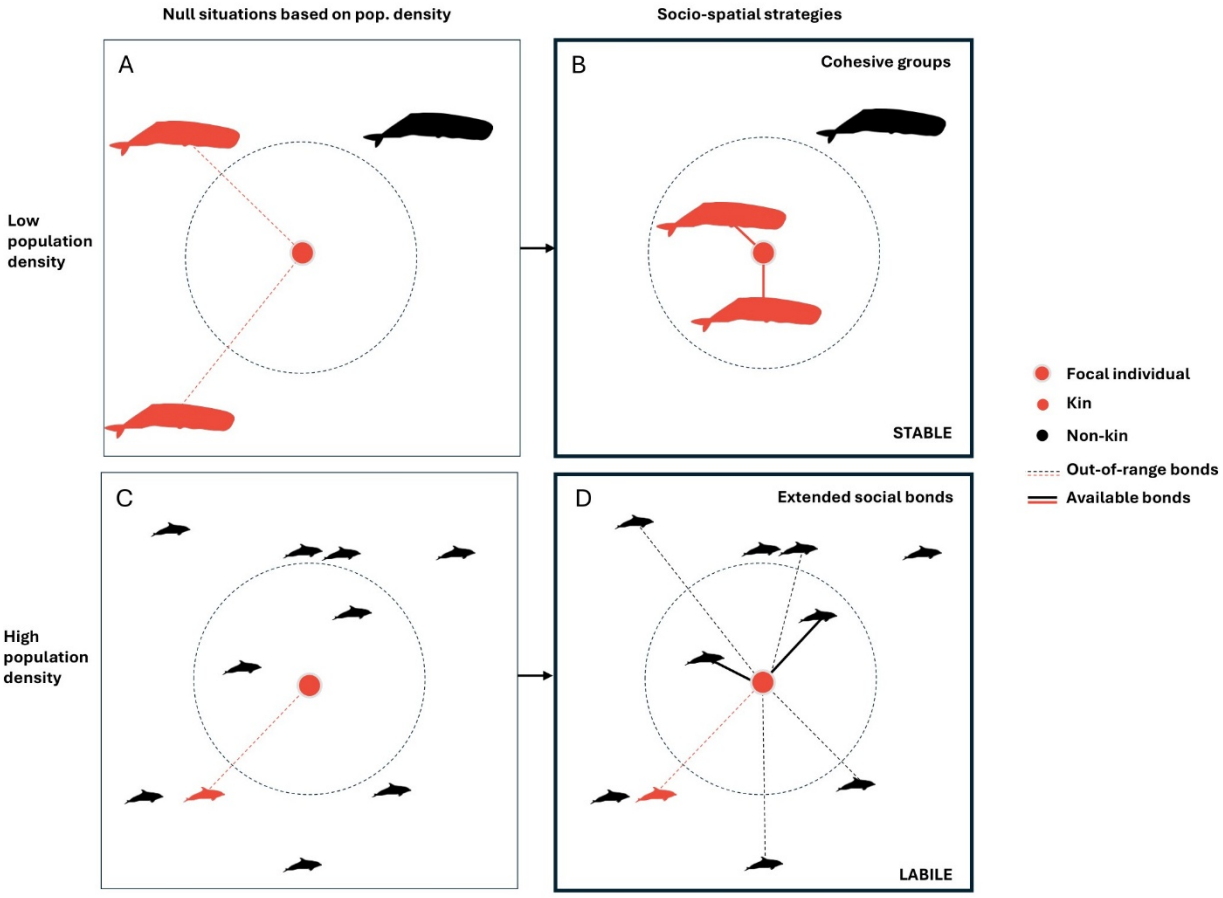

Figure 1 – Population density sets the stage for two alternate socio-spatial strategies. (A) Populations with low density are unlikely to have any social support if individuals spread out to forage. (B) Instead, these populations may form cohesive groups that move collectively. These groups are typically based on female kinship but see exceptions in later discussion on optimal group size. (C) Populations with high density may find themselves closer to non-kin when spreading out to forage. (D) Here, developing affiliative relationships with non-kin can be beneficial, hedging against the possibility of needing help and having no kin nearby. Silhouettes depicting typical species for each socio-spatial strategy (*Physeter macrocephalus* for A, B;

Tursiops aduncus for C, D) are modified versions of images available at phylopic.org (Chris Huh, license: creativecommons.org/licenses/by-sa/3.0/). To extend the model to bonds between social groups; e.g., those between female sperm whale units or male Indo-Pacific bottlenose dolphin alliances, silhouettes may represent stable social groups.

Illustrating our model with agent-based simulation

We developed an agent-based model to illustrate how variation in local density and the predictable availability of non-kin can shape the social structure of toothed whales. We simulated toroidal 2-dimensional surfaces (with no edges) wherein 40 agents representing female odontocetes move, form relationships, and are exposed to threats. We primarily conceive of these threats as predators or harassing conspecific males, but this could also represent any situation in which urgent social support is beneficial. These 40 whales are divided into 10 matrilines, each consisting of 4 individuals, within which social support is assumed given shared kinship.

We begin by assuming that animals must disperse to forage, either to avoid scramble competition for non-sharable resource patches or to increase the probability that a patch will be located upon which the entire group can feed (see Whitehead et al. 2026). Individuals that do not spread out will pay a foraging cost in increased scramble competition or reduced success at patch detection. These two situations are equivalent for our model but we proceed with the scramble competition case, in which individuals must spread out and will pay a foraging success cost relative to the local density of nearby conspecifics. This creates pressure to disperse from others.

This need to disperse is held in tension with a need to maintain proximity to conspecifics that can provide social support. When a threat emerges, an animal's degree of received social support is determined by the *availability* and *willingness* of social partners. Kin (members of the

same “matriline”) are assumed to help automatically in our model, i.e., no social cost is required to make them willing helpers. Spreading out away from these automatic helpers is thus costly but may be necessary for foraging requirements.

We simulate our whales with two evolved traits, each of which are inherited with some variation (i.e., mutation). The first is *kin cohesion*, a continuous measure of the probability that an individual will remain with its matriline rather than foraging in a randomly selected part of the simulated habitat on a given day. For example, an individual with a cohesion trait value of 0.3 will remain with its matriline during 30% of timesteps or “days”. The second trait is *non-kin investment*, which represents the probability that a simulated whale will pay a cost to develop social relationships with non-kin conspecifics they encounter. These encounters emerge naturally in our model from the tendency for individuals to disperse at random to enhance foraging returns. Each trait is initialized across the population using a uniform distribution spanning 0-1.

Social relationships are assumed to be symmetric and are solely built up if both members of a non-kin dyad pay an investment cost. Relationships are represented by dyadic “scores” ranging from 0-6, which increase by 1 each day that a mutual investment occurs, and decay by a small amount (0.05) on days without investment. Partners with a relationship score greater than or equal to 3 are considered to have formed a social bond and will provide social support when help is needed.

The crux of our model is that paying costs to invest in social relationships emerges if repeated encounters with the same non-kin individuals are adequately high. Each whale has a variable energy or resource value that accumulates proportional to their foraging success (capped at 150). Energy accumulates based on foraging returns and declines a small amount each timestep and when paying to form social relationships. Energy also declines a large amount in

the event of a threat without social support (e.g., predation event). If this value reaches 0, the whale dies.

For each run of the model, a simulated population of whales progresses through each of the following steps 12,000 times:

1. **Movement** – The central position of each matriline shifts to a new randomly selected location in the simulated environment. Individuals either stay with their kin group or move to a separate randomly selected location, based on their *kin cohesion* trait value. Each individual pays a daily metabolic cost from their energy reserves (0.5).
2. **Foraging** – Whales forage to accumulate energy in a density-dependent manner that is inversely proportional to the number of nearby whales.

$$F = \frac{K}{K + n}$$

Here, foraging intake (F) is a function of constant K (set to 3.25 for the main figures) and the number of individuals (n) within a given spatial range, set to 350 m (see Figure S1 for the effects of variation in these and other parameters). K can be interpreted as the number of nearby whales at which an individual experiences a 50% reduction in foraging gains. An individual with no nearby whales maximizes their intake (1), whereas an individual with 4 nearby whales (typical matriline size) receives approximately 45% of maximum possible intake.

3. **Social investment** – Whales that have a non-kin conspecific in their vicinity (radius of 1 km) can opt to invest in developing social relationships, based on their *non-kin investment* trait value. Attempts to invest incur a small cost to a whale's energy reserves (0.03), regardless of whether the investment is reciprocated. If both whales opt to invest

in one another, their social relationship advances by one point (+1). Whales can invest in as many nearby non-kin in a day as they wish but will pay costs for each investment.

4. **Threats** – Each whale experiences a chance of a threat (or some other need for urgent social support) of 5% per day. Whales that have kin and/or a socially bonded non-kin whale within 1 km are assumed to receive support, and are alleviated from experiencing any cost from the threat. Whales caught alone in a time of need experience a large cost to their energy reserves (-12).
5. **Death** – Any whale whose energy reserves have declined below 0 die and are removed from the population. Furthermore, each whale experiences a very small chance of death at random, meant to capture senescence or other natural causes of death (1/3000 chance per timestep).
6. **Reproduction** – New whales are born to replace any individuals that have perished. These whales are born into the same matrilines, ensuring that matriline size and population density remain stable across the simulation. Trait inheritance is shaped by the net energy gain of surviving whales (i.e., total lifetime energy gain minus total lifetime losses, divided by the number of days the whale has persisted in the simulation). Most of the time (75%), traits are inherited with mutation from the most successful surviving member of that matriline (based on net energy gain). Otherwise, the newborn whale inherits traits from the whale with the highest net energy gain from a random sample of 8 whales across the entire population. This occurs 25% of the time and ensures genetic mixing between matrilines. Traits are inherited with an additional gaussian noise term (mean 0 and standard deviation 0.05), with any resulting values below 0 and above 1

assigned 0 and 1 respectively. Newborn individuals inherit no social relationships and start with the same initial energy reserves (30).

Every 100 timesteps, we created a binary social network whereby kin and bonded non-kin are assumed to have a social relationship while other dyads do not. This allowed us to calculate the modularity of the population over time, a measure of the stability and clique-ishness of social groups. We ran the model across 10 different "population densities", achieved by manipulating the size of the toroidal surface. We selected 10 densities spanning a range of observed densities for odontocete populations: sperm whale densities in the open ocean at the low end (0.0024 individuals/km^2) to the bottlenose dolphins of Shark Bay at the high end (0.92 individuals/km^2). We concentrated densities towards the higher end of this range, as it was only in these higher densities that relationships between non-kin began to form. All other rules and parameters remained constant, such that population density was the only factor that varied systematically across runs. We ran the model 100 times for each density level as replicates, resulting in a total of 1,000 model runs.

Finally, we assessed the sensitivity of these patterns to variation in several key parameters, varying in turn: the cost of being alone when social support is needed, the rate of threats or needs for social support, the rate at which social bonds decay, the intensity of foraging competition (K), and distance at which foraging competition takes place.

Results of the agent-based simulations

The results of the simulation showed that initial differences in local density alone are sufficient to replicate the two broad patterns of social structure in odontocetes (Figure 2). Simulations at lower density resulted in the evolution of social networks heavily shaped by matrilines, with few

interactions among non-kin. Simulations at higher density resulted in denser networks where whales had a range of social relationships with both kin and non-kin. The resulting average network modularity values were roughly consistent with those estimated from observed associations in various toothed whale species. There appeared to be some bimodality at higher densities, with some societies shifting towards very fluid social structures while others maintained higher levels of modularity and low levels of bonds among non-kin (Figure 3). In other words, high population density promoted the extension of bonds among non-kin, but was not always sufficient to do so.

Links between population density and social mode were reflected not only in the density-dependence of "evolved" social network structure, but also in the heritable behavioral traits of individuals. The tendency to maintain social cohesion with kin declined from over 90% to less than 50% across the range of population densities that we explored (Figure 3). Simultaneously, whales at higher population densities evolved a greater tendency to pay a cost to form relationships with non-kin. Interestingly, the lowest trait values for non-kin investment occurred at intermediate densities. Investment attempts always incurred a cost in our model, so we might expect the tendency to be eliminated except in higher-density simulations where meaningful social benefits can be gained. However, at very low densities encounters with non-kin are rare enough that their small cost is overwhelmed by genetic mutation. In other words, within our model moderate levels of tolerance towards non-kin were not selected against until encounter rates were high enough that costs were substantial (Figure 3).

As expected, when the benefits of social support were removed, investment into relationships with non-kin very rarely occurred, even at the highest densities. Similarly, individual tendencies to invest in non-kin declined as density increased, reflecting the costs of

attempts to form relationships with no ultimate benefit (these model runs are summarized in Figure S1).

Parameterizing our model required many assumptions which will capture the realities of toothed whale populations to varying degrees. Still, our results were robust to variation in several key parameters, with bonds among non-kin exclusively forming at relatively high densities (Figure S1). Exploring this parameter space also highlighted effects such as the importance of the rate of decay in social bonds as a key factor that could limit or facilitate the evolution of labile societies. Our model quantitatively illustrates the idea that predictable access to non-kin in higher-density populations can be a stepping stone for the extension of social bonds beyond kinship-based groups. This can be seen as an evolutionary instance of the social bet-hedging hypothesis, whereby uncertainty in access to kin (or other preferred partners) in a time of need promotes investment into a more diversified network of potential helpers (see Carter et. al. 2017).

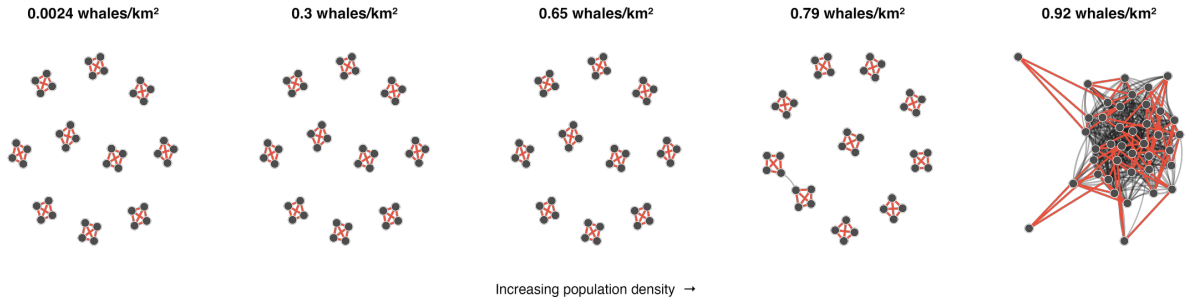

Figure 2 – Representative social networks resulting from simulated whales at varying population densities. Circles represent individuals, red lines represent relationships among kin, and grey lines represent bonds among non-kin. Here, edges between individuals imply that those individuals would help one another in a time of need. At very low densities (e.g., oceanic sperm whales; left), simulated whales remain within matrilineal groups. As density increases past a certain threshold, simulated whales expand their social investments towards non-kin, resulting in more densely connected networks.

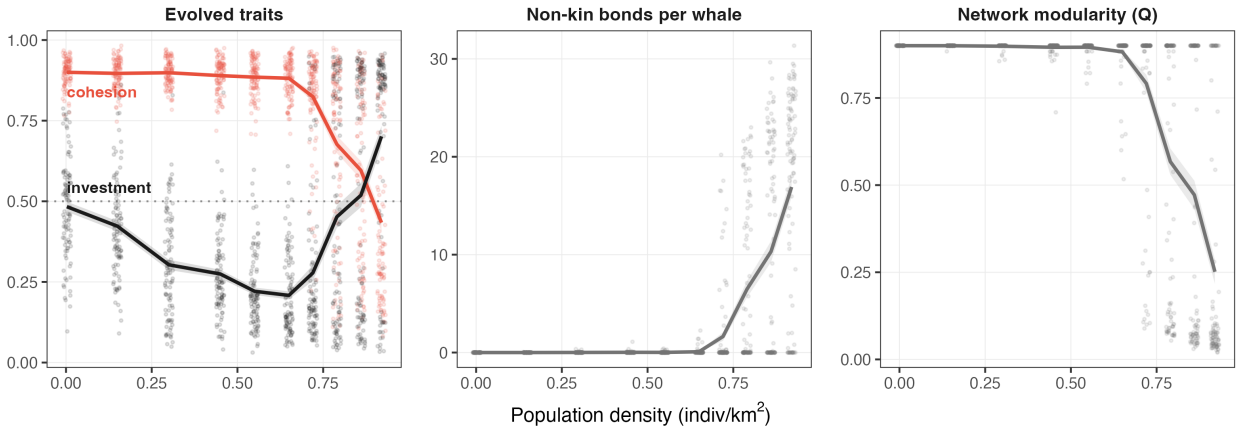

Figure 3 – Visual summary of results from simulations of whale social investment. Left: optimal values of heritable traits depend on population density. As density increases, individuals shed a strong bias to maintain social cohesion with kin (red line) and become more likely to invest in

social relationships with non-kin that they encounter (black line). Middle: Simulated whales developed increasingly large networks of non-kin social bonds as population density increased. Right: Overall, the modularity of the "help network" declined dramatically with increasing population density, as strict kinship-based modules are broken up and simulated whales received social support from non-kin.

Discussion

Socio-ecological models of animal social systems attempt to elucidate the key factors driving social variation within and between populations and species. Primate models have focused on female feeding competition (Sterck et al., 1997; Koenig et al., 2013; Wheeler et al. 2013; Kalbitzer & Chapman 2021, but see Isbell 2024, SM) which is unlikely to provide useful explanations for odontocetes, where competition is generally scramble rather than contest, food defense is impractical, and cooperation to find and capture food is common (Gowans et al. 2007). Instead, our model focuses on social bonds, not to cooperate in defense of food, but to help in defense against predators and other threats such as infanticide.

Our model suggests that variation in population density can contribute to the evolution of individual tendencies to associate with kin and non-kin, as well as the resulting social network structure. We interpret this as being driven by encounter rate, i.e., it is only in spatial and ecological contexts where there is a reasonable probability of re-encountering the same specific individuals that costly social investments pay off. It was only at relatively high densities that these non-kin relationships started to form, converging with the hypothesized "tipping point" between stable and labile social modes suggested by Rendell et al (2019).

We emphasize that in our simple model helping between kin is automatic, so we focus on

389 investment in social bonds to cultivate willing helpers among non-kin. Our model is another
390 example of a *social bet-hedging strategy* where individuals increase the number of social bonds
391 among non-relatives as a buffer against uncertainty in the availability of preferred partners such
392 as close kin (Carter et al. 2017; Pereira et al. 2023; and see Connor & Curry's 1995). As the
393 value of acquiring unrelated willing helpers increases, individuals should spend time away from
394 close relatives to cultivate and maintain such bonds.

395 The key difference between large and small species is the availability of unrelated
396 potential protectors (or sources of other types of social support). Larger species may expect to
397 have few or no such protectors within the range at which they could respond to a threat in time,
398 so animals maintain proximity to reliable, often related, partners. In contrast, individuals in
399 smaller species living at higher densities may form social bonds with unrelated potential helpers
400 who are more likely to be nearby when needed.

401 Below we discuss population density and other factors which may provide tests of our
402 model. These include variation in movement and ranging patterns, life history, predation,
403 foraging behavior, and phylogeny. We then compare our model to previous hypotheses for the
404 evolution of stable and labile odontocete societies. In the last section we address three larger
405 questions: (1) how predictions from our model intersect with variation in optimal group size, (2)
406 how social bonds with non-relatives might translate into help against predators, and (3) how the
407 model can apply to cooperative bonds between groups of odontocetes and terrestrial mammals,
408 including humans.

409 **Population density**

410 Our model is based on local densities. Our expectation that local densities will vary with body
411 size is an extrapolation from the general relationship between population density and body size.

There will, of course, be tremendous variation in local densities, in time and space, within a species range. This variation should present opportunities to test our model, along with temporal and spatial variation in predation risk and foraging behavior.

In at least three cases, medium to large odontocetes that were predicted to have a stable matrilineal social structure are now known to have a labile fission-fusion grouping structure. Northern bottlenose whales (*Hyperoodon ampullatus*) share a deep diving niche with sperm whales, so researchers expected to find matrilineal groups based on communal care of young, as in sperm whales, but instead found a fission-fusion grouping pattern with long-term social preferences among both males and females, more like bottlenose dolphins (Gowans et al., 2001; Walmsley et al., 2026b). More recently, a fission-fusion grouping pattern with some strong associations among males was described in the largest member of the Ziphiid family, Baird's beaked whale (*Berardius bairdii*) (Fedutin et al. 2015), also going against earlier predictions of a stable matrilineal social structure (Kasuya et al. 1997). Finally, Belugas (*Delphinapterus leucas*) are a medium-size odontocete (4-4.5m) that were thought to have a matrilineal social structure (Smith & Martin, 1994; Palsboll et al. 2002) but recent observations indicate a labile fission-fusion grouping pattern among females, with possible male alliances (O'Corry-Crowe et al. 2020 Aubin et al. 2026).

Northern bottlenose whales live at high densities in relatively small areas (about 0.2 whales/km^2; Hooker et al. 2002, Walmsley et al. 2026b). Mean densities were estimated at 0.1-1.2 whales/km^2 in Baird's beaked whales (Ferguson and Barlow 2001) and between 0.10-7.05 seasonally for belugas across four study areas (Luque and Ferguson 2010). In contrast, mean densities of sperm whales in all oceans are about 0.0024 whales/km^2 (Whitehead and Shin 2022). Based on these examples, we predict that population density may be a better predictor of

odontocete social strategies compared to body size alone. This may also operate on an intraspecific scale, e.g., if populations of dolphins at higher densities demonstrate more widely distributed social bonds (Connor et al. 2000a, Brightwell & Gibson 2023).

Movement and ranging patterns

Movement patterns, such as home and day ranges, may also impact the rate that individual non-relatives are encountered, and thus the utility of forming social bonds to turn them into willing protectors. Available evidence indicates these factors change in the same direction as density, decreasing encounter rates with increasing body size. Larger terrestrial mammals have larger home and day ranges because of their greater energy needs and lower costs of locomotion (McNab 1963, Pontzer 2007, Carbone et al. 2005) and carnivores have larger home ranges than herbivores (Tucker et al. 2014). Home range size may also increase with body size in odontocetes (Tucker et al. 2014, but see Broekman et al. 2024, SM), which would further decrease encounter rates between non-relatives. Isbell (2024) recently developed a primate socio-ecological model that is based on home range overlap, rather than contest competition or predation but her model cannot explain labile versus stable odontocete societies (see SI).

An increase in velocity with body size might increase encounter rates, mitigating other factors, and increase the radius at which kin protectors suffice. In large mammals, however, normal traveling speed, maximal speed and acceleration increase only slightly or not at all with body size (Gough et al. 2019; Hirt et al. 2017, Cloyed et al. 2021; SM) and clearly scale at much lower exponents than population density (Cotgreave 1993; White et al. 2007). The maximum and normal speeds recorded for small and large odontocetes are similar (see Rohr et al. 2002, Aoki et al. 2007; Gough et al. 2019; Tanaka et al. 2019).

458

459 **Life history**

460 If the number of overlapping generations increases with body size, then larger species might
461 have more available female relatives, favoring stable societies. However, the population of
462 bottlenose dolphins (*Tursiops truncatus*) in Sarasota, Florida, has recorded four and even five
463 generations of females associating, the same as is found in matrilineal killer and sperm whales
464 (Wells 2014, Ford 2019; Konrad et al. 2018). Further, stable matrilineal groups are found in
465 species with (killer whales) and without (sperm whales) menopause and extended female
466 lifespans (Ellis et al. 2024).

467

468 **Predation**

469 Just as odontocete density is related to body size, the density and variety of their predators
470 should show a similar relationship. A small delphinid might be threatened by several kinds of
471 sharks as well as killer whales. Killer whales threaten every cetacean within their range but are
472 themselves relatively safe from predation, although their young may still be at risk from sharks,
473 infanticidal males, sympatric killer whale populations and even groups of potential prey species
474 such as pilot whales (e.g. Towers et al. 2018; De Stephanis et al. 2015; Selbmann et al. 2022).
475 Thus, in general, smaller odontocetes foraging alone should have a higher probability of being
476 attacked, so predation risk and density will work in concert favoring social bonds with potential
477 protectors.

478 We add two qualifying observations to this scenario. First, the need for protectors varies
479 with size *within* species so that dependent calves are much more vulnerable than their mothers,
480 but differences in calf size among species may not predict vulnerability. For example, adult

elephants are relatively invulnerable to predation but their offspring, who can neither run fast nor hide effectively like many other ungulate calves, are extremely vulnerable (see Connor 2007). A sperm whale calf may be in a similar predicament.

Second, being the victim of a successful predation attempt ends an individual's chance for further reproduction. So, the key to group and social bond formation might not be the rate of encounter with 'average' predators but the rare encounter with the most dangerous kind. A single adult dolphin might be sufficient to mitigate the threat posed by an approaching shark, but a single adult female sperm whale would likely be insufficient to ward off a pod of approaching killer whales, who hunt cooperatively in packs, favoring associations between sperm whale groups (see below).

It is worth noting that social defense strategies against aquatic predators may have been counterproductive against human whalers, who could take multiple individuals from defensive groups (e.g. Gray & Flower 1882). In fact, sperm whales may have learned to modify their tactics to reduce the risk from whalers (Whitehead et al. 2021).

Foraging

Our model is based on cooperation against threats, but as we noted in the introduction, cooperation to locate and capture prey is very common in odontocetes. Substituting availability of cooperative foraging partners for willing protectors in our population density model may achieve a similar outcome. At low population density it may be more efficient to remain with close kin as others are not readily available for cooperative foraging, while at high density other individuals are always nearby to cooperate for prey location and capture. However, a cooperative foraging efficiency model struggles to explain why dolphins are intensely prosocial, investing

504 extensively in social bonds with affiliative interactions (e.g. Danaher-Garcia et al. 2022,
505 Friedman et al. 2023). This is because cooperative foraging, including spread formations to
506 locate food patches and corralling schools of prey, are byproduct mutualisms that provide
507 immediate benefits for all participants and do not require social bonds (see Connor 1995). While
508 social bonds may be important where there is active food sharing (as in killer whales), and it is
509 possible that individuals that share a social bond forage cooperatively more effectively than
510 individuals that do not (see Connor 2010), we think that the threat from predators more readily
511 explains both social structure and bonds in odontocetes. Thus we think foraging efficiency
512 reinforces the predation model rather than social bonds emerging after individuals form groups
513 based on cooperative foraging efficiency (see Isbell 2024 for ideas about social structure and
514 foraging efficiency in primates).

515 The variety of prey and foraging tactics found in odontocetes guarantees variation in how
516 far individuals must separate during foraging. At one extreme we might find species that almost
517 always forage in groups (e.g. dusky dolphins, *Aethalodelphis obscurus,* Würsig & Würsig 2009)
518 while others might do so on an occasional basis or not at all. Just as we emphasized that group
519 formation might be based upon rare but dangerous predators, the 'average' foraging spread might
520 not lead to the correct prediction. Seasonal variation in foraging might produce critical periods
521 where the intersection between foraging spread and predation risk favors the formation of bonds
522 with available non-relatives.

523 We also emphasize that spread includes movement in three dimensions. Individuals may
524 spread out horizontally to forage but for deep diving species the vertical spread can be critical.
525 Despite having many physiological adaptations to facilitate diving, cetaceans may still need to
526 surface slowly to avoid decompression sickness (Lemaitre et al. 2009). This means that the time

it takes for a diving social partner to return to the surface will often be greater than expected based on vertical distance (i.e., depth) alone. Vertical spread may be eliminated by synchronizing dives, but calves cannot always follow adults who feed at depth. They would be completely exposed with this forced separation, but when adult sperm whales dive to forage a 'baby-sitter' often remains at the surface to protect the calf (Whitehead 1996).

Phylogeny

While our model finds a key role for population density in odontocete social systems, we do not mean to imply any specific sequence of evolutionary events. We expect that density, movement patterns, foraging behaviour, and life history traits like body size are both plastic within species, and likely influenced one another (i.e., co-evolved) across phylogenetic history (see Walmsley et al., 2026a). More broadly, an important role for phylogeny can explain why primate social systems often do not vary as expected in response to ecological variation. (Thierry 2008, 2013; Clutton-Brock & Janson 2012; Kappeler et al. 2013, Koenig et al. 2013). Comparing populations of the same species and/or applying comparative analyses that incorporate phylogenetic history will help to control for phylogenetic signals in odontocete social systems (e.g. Clutton-Brock & Janson 2012), whether direct (conserved social systems) or indirect (conserved physiological, ecological or other traits that influence social evolution).

Characteristics that impact social structure in primates, like intensity of aggression and the steepness of dominance ranks, may relate to overall tolerance levels (Thierry 2022). Given their high degree of mutual dependence and prosocial nature, odontocetes are obvious candidates to examine for evidence of high tolerance levels, self-control and even self-domestication (Hare 2017; Hare et al. 2012; Wilkins et al. 2014; Shilton et al. 2020). Human aggression can be

550 divided into reactive aggression, an immediate response associated with ‘anger,’ and proactive or
551 planned aggression (Wrangham 2018). Shark Bay male dolphins leaving a rival alliance with a
552 female to recruit their allies before returning to attack should be considered proactive aggression
553 (Connor et al. 1992b). Evidence that delphinids have low levels of reactive aggression compared
554 to typical mammals has been hiding in plain sight since the first dolphins, including killer
555 whales, the most formidable predator on the planet, were taken into captivity without violently
556 attacking their captors. In a greatly under-cited paper, (Pryor 1973) describes variation in
557 aggression and tolerance among dolphin species held in captivity that promises a productive
558 future examining how these ‘species personalities’ relate to phylogeny, social structure and
559 ecology.
560
561 **Other hypotheses**
562 Weiss et al. (2021a) reviewed previous ideas for the increase in stable, modular societies with
563 body size, which can be summarized as follows: stable groups in larger species are favored
564 because of (1) unpredictable resources in larger patches and greater predation risk in larger, open
565 water ranges, Gowans et al. (2007); (2) greater threats from males in larger species with higher
566 levels of sexual size dimorphism (Moller 2012); and (3) greater need for maternal investment
567 and cooperative care in larger species (Rendell et al. 2019). However, predation risk can be quite
568 high in small inshore species (contra Gowans et al. 2007), males in smaller species with reduced
569 dimorphism can cooperate to harass females (contra Moller 2012), and the degree of maternal
570 investment required can be as high or nearly so in small animals, and some populations of larger
571 species have been found to have more labile groups). Weiss et al. (2021a) made the intriguing
572 suggestion that larger species have greater resource uncertainty in their larger home ranges, due

to the longer scales of oceanographic processes over larger spatial scales. Older elephants matriarchs are important reservoirs of social and possibly ecological knowledge (McComb et al. 2001) and the same might be the case in sperm whales, whose social organization and brain size is remarkably convergent with elephants (Weilgart et al. 1996). The importance of older individuals as repositories of knowledge could help explain the extreme degree of support given to an older dying male false killer whale by members of its group (Porter 1979, reviewed in Connor 2000). The resource uncertainty hypothesis suggests that stable societies will be associated with larger ranges rather than population density. It will be informative to investigate the range size of some of the larger odontocetes that have labile societies (e.g. Baird's beaked whale).

Optimal group size and the number of kin in stable groups

Our model has contrasted relatives, from whom help is automatic, and non-relatives, from whom help is dependent upon prior investment in developing and maintaining a social bond. While this is obviously a simplification of the natural variation in social bond formation, our model can explain the transition from stable to labile groups and vice versa. What we have not addressed is the relationship between number of relatives and the optimal group size. What happens if stable kin groups grow beyond the optimal group size or if the number of close kin is less than the optimal group size? In resident killer whales, as stable kin groups grow beyond the optimal size; they fission into separate matrilines (Baird 2000, Stredulinsky et al. 2021). Once a resident killer whale 'pod' exceeds some optimal size (likely for foraging), more distantly related matrilines within the group begin traveling apart initially as 'sub-pods' eventually forming new pods (Baird 2000, Stredulinsky et al. 2021).

What happens if stable groups are favored but the number of available kin falls below the optimal group size? In this case individuals may form stable bonds with relatives or non-relatives that are also in need of or benefit from a larger group (Pereira et al. 2023, Shaw & Rubenstein 2023). There are fascinating precedents for unexpected fusions in primates, such as when two primate groups experiencing declining numbers after habitat degradation fused due to predation pressure (Isbell et al. 1991). Similarly, the fusion of two related sperm whale units off Dominica coincided with a size reduction in one unit (Konrad et al. 2018). Sperm whale group size might be optimized around the number of adults required to provide reliable babysitters when the mother is feeding at depth or to fight off killer whales (Whitehead 2003). The lack of a sufficient number of adults for these functions, in some cases owing to whalers, might explain why some sperm whale social units have more than one matriline (Whitehead et al. 2012).

Why should whales help each other?

The return on help provided to relatives includes the increased survival and reproduction of the relatives helped (Hamilton 1964), but may also include direct fitness benefits (below). The return on help provided to non-relatives must come back to the helper, usually from the one helped (Trivers 1971). Models of reciprocity have been as controversial as they are numerous, (e.g. Connor 1995, 2025; Leimar & McNamara 2023, Carter 2024). Recently, Leimar & Bshary (2024) showed that social bonds can promote cooperation, including reciprocity, and how investments in social bonds may translate into critical help when needed. Models aside, exchanges of help between socially bonded non-relatives is common in mammals (e.g. Wilkinson et al. 2016, Seyfarth & Cheney 2012). Likewise, dolphins have been known to cooperate with and help non-kin (Connor & Norris 1982, Connor 2010, Gerber et al. 2021).

While our model is based on dyadic bonds, helping based on kin selection and some form of dyadic reciprocity (among non-relatives), we point out that other factors may reinforce helping in stable and labile groups. First, members of stable groups and social bonds in labile groups may be hard to replace, favoring helping to preserve byproduct benefits derived from their presence (Carter 2024; Connor 1986, 2025, Kokko et al. 2001, Roberts 2005; Raihani & Bshary 2011, Barclay 2020). For example, mutual dependence is high in sperm whale groups and the oceans are not full of sperm whales looking for a new home. If sperm whales fail to come to the assistance of a non-related group member, thereby reducing the size of their group, each individual would suffer increased risk of predation from killer whales. Second, since the original suggestion that dolphins may have indirect reciprocity and/or generalized altruism (Connor & Norris 1982, see Trivers 1971, Alexander 1989), our much improved understanding of dolphin cognitive capacities and helping behavior has not diminished this possibility. For example, dolphins will help other groups without gaining immediate benefits and can copy the individual identity calls of others, raising the prospect of communicating about others in their absence (Connor 2010, Connor et al. 1992a, 2022).

Help may also derive more from harming the success of a predator and so reducing the chance they will hunt in the same area again, as in mobbing (see Carlson & Griesser 2022). Humpback whales interfere with predation attempts by killer whales on several species (Pitman et al. 2017) a behavior most likely explained by the 'move on' hypothesis so the killer whales will leave the area and not continue to threaten the mobbing individuals or their relatives (see Carlson & Griesser 2017). Our model assumes that selection for mobbing is not a sufficiently reliable substitute for individuals that need help, so they invest in social bonds.

642 **Bonds between groups**

643 In Shark Bay, Western Australia, male Indo-Pacific bottlenose dolphins use affiliative
644 interactions to form three levels of alliances (Connor & Krutzen 2015; Friedman et al. 2023).
645 The core male social unit is the second-order alliance of 4-14 mostly unrelated males which may
646 be stable for decades and whose members form intergroup (third-order) alliances with other
647 groups in contests over females (Connor & Krützen 2015; Gerber et al. 2020, 2021 Connor et al.
648 2011, 2022). Males cooperate with 1-2 other second-order allies to herd individual estrus females
649 (=first-order alliances, Connor et al. 1992a, 1996). Bottlenose dolphin populations vary from
650 having no alliances, to first-order alliances only, to the three alliance levels in Shark Bay.

651 Our model can explain the existence of 2nd and 3rd order alliances, as follows. Consider a
652 population with only stable 1st order alliances of 2-3 males with a female. Males often spread out
653 to forage, sometimes leaving a single male to guard the female, where he is vulnerable to attack
654 (King et al. 2019). A male that has invested in social bonds with 2nd-order allies is much more
655 likely to have a potential helper within range, should a competing group of males appear.
656 Second-order allies are also often widely dispersed in an area, so similarly, intergroup alliances
657 increase the probability that that help is nearby (Connor et al. 2011, 2022). In general, foraging
658 separation from size-constrained groups (so simply having larger alliances is not viable) favors
659 the formation of additional bonds outside of the group, if the risk of attack from other males is
660 sufficiently high. Indeed, the inter-population variation in bottlenose dolphin alliance complexity
661 has been linked to encounter rates that increase with density and the distance rivals are detected
662 (Connor et al. 2000a; Ermak et al. 2017; Brightwell & Gibson 2023; Sorenson et al. 2024).

663 Associations between sperm whale matrilineal social units are more pronounced in
664 regions where they are threatened more by killer whales (Whitehead et al. 2012), which are

665 exceptionally dangerous predators who hunt in packs and may inflict multiple fatalities on sperm
666 whale groups (Pitman et al. 2001). A single helper would be useless against a pack of killer
667 whales but we can apply the model to bonds between sperm whale social units rather than
668 individuals. The equivalent help of an *individual* dolphin warding off a shark might be assistance
669 from other sperm whale *social units* to ward off a pack of killer whales.
670 Finally, our model might apply to intergroup cooperation on land. Randić et al. (2012),
671 linked intergroup bonds in humans, dolphins and elephants with density and low travel costs, "at
672 a given population density, cheaper travel and concomitantly larger ranges would have increased
673 the rate that individuals and groups encountered each other in competitive contexts, favoring.
674 larger groups and alliances, and perhaps intergroup relationships that are sometimes cooperative
675 rather than hostile or merely tolerant".
676
677 **Conclusion**
678 Two very different social systems have been described in odontocetes: stable matrilineal groups
679 and labile groups where females associate with a range of relatives and non-relatives. The stable
680 matrilineal system is found in some larger species while labile systems prevail among smaller
681 odontocetes. Socio-ecological models that explain patterns of sex specific bond formation in
682 primates are of little utility for odontocetes, who live in a three-dimensional environment where
683 cooperative defense of food is contraindicated but cooperation to obtain food and thwart
684 predators is common. We developed a novel socio-ecological model which explains the
685 extension of social bonds to non-kin based on the availability of conspecifics when help is
686 needed. Our simulations illustrate that under a simple set of rules for investing in social
687 relationships, population density can be a difference maker in the evolution of social bonds.

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Supplementary Material

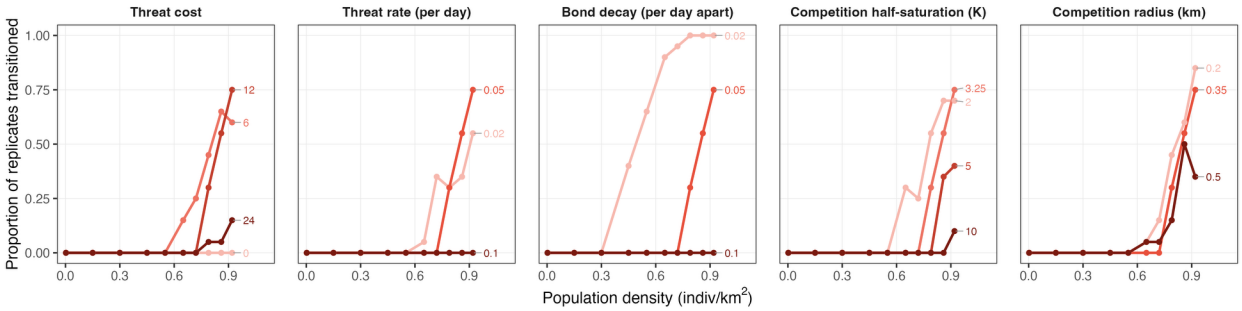

Figure S1 – Visual summary of sensitivity analysis. Points represent pooled results from 20 simulations of 12,000 timesteps each, reflecting change in one key model parameter along with density (x axis). The y-axis shows the proportion of model runs where simulated whales more than 5 non-kin bonds, on average. This provided an overall measure of the transition to "labile" societies. Our results were robust to variation in these key parameters, though the resulting propensity to evolve labile societies differed in predictable ways. **Threat cost**: an intermediate fitness cost to facing a threat (or other need for social support alone) was most predictive of labile societies. Without any fitness costs (0), individuals have no benefit from investing in relationships with non-kin, so maintain their matrilines. If fitness costs were too high (24), the risk of moving away from a matriline was likely too great. **Threat rate**: Similarly, an intermediate frequency of threats predicted the evolution of labile societies. If threats were too high (rate of 0.1 per timestep), movements away from the matriline were likely too costly, while very low rates (0.02) translated into reduced benefits of non-kin bonds compared to intermediate values (0.05). **Bond decay**: Some degree of memory or inertia for social bonds is essential for the evolution of labile societies. If affiliation or memory for partners declines very rapidly (0.1 per timestep), bonds fail to be maintained. **Foraging competition**: Lower levels of *K*, implying that it takes fewer individuals to experience a foraging cost, was associated with the evolution of

labile societies. This aligns with our attempt to model how foraging competition should push individuals to disperse and thus more regularly encounter non-kin. **Competition radius**: When foraging competition only occurs at finer levels of spatial overlap (e.g., 200 m rather than 500 m), non-kin experience reduced foraging competition from bonded partners that (may) be nearby. Individuals that stay with the matriline experience the same foraging competition regardless, so the benefits of being labile increase.

Isbell's ranging model for primates applied to odontocetes

Isbell (2024) recently developed a primate socio-ecological model that is based on home range overlap, rather than contest competition or predation. To summarize her model, the primary selective force on female primate social organization is foraging efficiency, leading to variable patterns of home range overlap between females that are, in turn, related to patterns of movement during foraging, (essentially, 'random' during opportunistic foraging vs direct movement between patches). Females who share their ranges with other females aggregate to monitor the feeding of others, and so avoid searching recently foraged space, only then leading to selection for social behavior and bonds. She groups female primates into seven categories, including two where females share their entire ranges with other females; relatives in one case and non-relatives in the other (as when unrelated females join an adult male silverback gorilla for protection). All of the odontocetes that we have considered would belong in a new category, where females share their entire home ranges with related and unrelated females. While it is possible that other categories exist among some odontocete species (that live in rivers for

example), it is clear that the degree of home range overlap cannot explain the size related labile vs stable social organizations we find in odontocetes.

References for Supplementary Material

Isbell, L.A., 2024. *Primate socioecology: shifting perspectives*. JHU Press.