Original Article

Heterogeneity in resource competition covaries with individual variation in long-term social relationships

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Resource competition among conspecifics is central to social evolution, as it serves as one of the primary selective pressures of group living. This is because the degree of competition for resources impacts the costs and benefits of social interactions. Despite this, how heterogeneity in resource competition drives variation in the type and quantity of long-term social relationships individuals foster has been overlooked. By measuring male mating competition and female foraging competition in a highly social, long-lived mammal, we demonstrate that individual variation in long-term intrasexual social relationships covaries with preferred habitat and experienced resource competition, and this effect differs based on the sex of the individual. Specifically, greater resource competition resulted in fewer social preferences, but the magnitude of the effect varied by both habitat and sex, whereas for social avoidances, both the directionality and magnitude of the effect of resource competition varied by habitat and sex. Together our work shows how fine-scale variation in individual socioecological niches (i.e., unique physical and social environments) can drive extensive variation in individual social behavior (here long-term relationships) within a population, thereby broadening current theories of social evolution.

Key words: **bottlenose dolphins, foraging competition, mating competition, social avoidances, social behavior, social evolution, social preferences.**

INTRODUCTION

Investigating the drivers of social bond formation is key to identifying the selective pressures involved in the evolution of group living. One such selective pressure is resource competition, as competition for food, space, mates, etc. modulates the costs and benefits of group living (Crook 1972; Moore et al. 1997; West-Eberhard 1983). As such, determining how resource competition might affect group living (e.g., group size, composition, cohesion, and pairwise interactions) has been a central endeavor (Crook 1965; Crook and Gartlan 1966; Schradin et al. 2010; Port et al. 2017). Ultimately, however, every group is made up of individuals, whose fitness is largely determined by their unique physical and social environment (i.e., their socioecological niche) (Webber and Vander Wal 2018). Individuals may therefore experience different fitness outcomes due to the variation in both the types and quantity of relationships they foster with conspecifics in their environment (Frère et al. 2010; McFarland et al. 2017; Snyder-Mackler et al. 2020) and theory posits that this variation should be influenced by the individuals' ecology (Emlen and Oring 1977; Wrangham 1980; van Schaik 1989; Sterck et al. 1997; Kappeler and van Schaik 2002).

Resource competition became a central focus in understanding the evolution of social relationships in the 1970's, when researchers developed socioecological models to understand affiliative and cooperative social relationships (Emlen and Oring 1977; Wrangham 1980; van Schaik 1989; Kappeler and van Schaik 2002). Specifically, theories regarding how resource competition drives the evolution of affiliative social behavior in mammals predict that female-female affiliation (e.g., through co-operative defense, co-operative hunting, dominance hierarchies) is primarily driven by food competition due to the high energetic demand of gestation and lactation (Sterck et al. 1997; Clutton-Brock and Huchard 2013a), while male-male affiliation is dictated by mating competition and the distribution of females (van Schaik 1996;

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Clutton-Brock and Huchard 2013b). That is, the distribution of and competition for resources causes variation in requirements and therefore shapes patterns of aggregation and social relationships. Consequently, these theories were developed to help explain the evolution of pairwise and group-level social dynamics, such as social hierarchies; yet if and how resource competition drives variation in the type (e.g., preferences and avoidances) and quantity of social relationships individuals foster has yet to be uncovered, especially in the context of long-term social relationships.

Societies with fission-fusion dynamics provide a natural experiment for identifying the role of resource competition in shaping individual long-term relationships (Webber and Vander Wal 2018). This is because the presence of stable long-term individual relationships despite frequent splitting and merging in groups of variable composition (e.g., (Kerth et al. 2011), may have evolved to cope with environments where resources vary spatially and temporally (Aureli et al. 2008; Webber and Vander Wal 2018). For example, across several delphinid species that exhibit high fission-fusion dynamics, foraging tactics, resource abundance, and competition contribute to the social structure of populations (Foster et al. 2012; Mann et al. 2012; Cantor et al. 2018; Machado et al. 2019). For instance, dolphins in Laguna, Brazil and in Shark Bay, Australia preferentially associate with conspecifics using similar specialized foraging tactics (Mann et al. 2012; Machado et al. 2019). Here, we capitalize on a long-term study of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) to ask whether individual differences in the level of resource competition experienced explains variation in long-term social relationships: both affiliative (e.g., long-term preferences/friendships; (Rubenstein 1986; Smolker et al. 1992; Wittemyer et al. 2005; Silk et al. 2006; Mitani 2009; Kerth et al. 2011; Carter et al. 2013; Rose and Croft 2020) and nonaffiliative (e.g., long-term social avoidances; (Strickland et al. 2017, 2018; Piza-Roca et al. 2018).

Bottlenose dolphins serve as an excellent model species because they live in societies characterized by high fission-fusion dynamics (Galezo et al. 2018), have long lifespans (Wells 2014; Karniski et al. 2018), and are highly social mammals that exhibit substantial individual variation in their social behavior (Connor et al. 1992; Smolker et al. 1992; Mann et al. 2012). In addition, the Shark Bay bottlenose dolphins are resident and bisexually philopatric meaning both sexes remain in their natal area (Tsai and Mann 2013), allowing for lifetime monitoring. Males and females exhibit both long-term social preferences and avoidances (Strickland et al. 2017), stable social traits across their lifespan (Evans et al. 2021), and relationships that can last decades (Connor and Krützen 2015; Miketa 2018; Gerber et al. 2020). Bottlenose dolphins also live in highly heterogeneous habitats, with diverse foraging tactics (Heithaus and Dill 2002; Mann and Sargeant 2003) and within Shark Bay, they have both stable home ranges across their lifespan (Tsai and Mann 2013) and are repeatable in their maternally inherited habitat use (Strickland et al. 2021). Finally, dolphins, unlike most social-living mammals (Clutton-Brock 2009; Lukas and Clutton-Brock 2018), have the ability to choose their associates freely without the constraint of kin groups or forced natal dispersal, allowing for the disentangling of sex-specific drivers of long-term social relationships.

METHODS

Study site and population

The main study site includes ~300 km² of the eastern gulf of Shark Bay, Western Australia (25° 47'S, 113° 43'E) where over

1700 residential and bisexually philopatric (Tsai and Mann 2013) Indo-Pacific bottlenose dolphins (*T. aduncus*) have been systematically studied since 1984. Group composition (10m chain rule, (Smolker et al. 1992), predominant activity (forage, rest, travel, social, or other) (Karniski et al. 2015), demographic, reproductive, ecological, and genetic data have been collected using boat-based opportunistic surveys. Individuals were identified using standard dorsal fin identification techniques (Würsig and Würsig 1977) and other distinctive features (Bichell et al. 2018). The identified proportion of the population used in this study was 93%. Sexes for the dolphins were determined by views of the genital area, presence of a dependent calf (Smolker et al. 1992; Mann et al. 2000), and/or genetics (Krützen et al. 2002). Ages (based on birth year information) were known for most dolphins (~88% of the population) born since 1982 but when the mother's identity was not known, age was estimated using size and ventral speckling information (Krzyszczyk and Mann 2012; van Aswegen et al. 2019). The current study used 16 886 surveys collected annually from 1988 to 2017 (average ± s.d. surveys per year, 562.9 ± 319.3).

All dependent calves, as well as any individual under four years of age (average weaning age, (Mann et al. 2000; Karniski et al. 2018) were omitted from analyses. If an individual was sighted more than once in a day, the last survey in which it was sighted was used to reduce spatial and temporal autocorrelation (Tsai and Mann 2013). Only individuals with ≥70 sightings across the 30 years were used in downstream analyses (average ± s.d. surveys per dolphin, 178.9 ± 130.9; $\mathcal{N}$ = 191, 90 females, 101 males out of 1057 individually identified adult and/or juveniles observed during this 30 year period) as this number of sightings has previously been found to estimate home ranges and social relationships accurately (Strickland et al. 2017).

Social metrics

To determine the type and number of long-term relationships individuals' foster, we first identified pairwise intrasexual social preferences and avoidances using data collected across their monitored lifespan within the 30-year study period (average ± s.d. years in the study, 23 ± 6.3 years). Social preferences are defined as instances where the strength of dyadic association is significantly stronger than expected by chance. Social avoidances are defined as instances where that strength of association is significantly weaker than expected by chance. As social interactions are highly correlated with association in this population, association is a good indicator of underlying social relationships (Foroughirad 2019; Leu et al. 2020).

We measured the strength of observed pairwise associations using the half-weight association index (HWI), calculated using the following formula:

$$HWI = \frac{X_{ab}}{X_{ab} + Y_{ab} + 0.5(Y_a + Y_b)}$$

where X_{ab} is the number of times that individuals a and b were seen associated together, Y_{ab} is the number of times that individuals a and b were seen on the same day, but not seen together, Y_a is the number of times that individual a was sighted but not individual b, and Y_b is the number of times that individual b was sighted but not individual a. HWI was used over other association indices as not every animal is reliably recorded in a sampling period or within a group, nor is every group located in every sampling period at our study site (Hoppitt and Farine 2018; Weko 2018). Additionally, as HWI is the most common association index used in animal

behavior, we used HWI for comparative purposes. To account for demographic turnover, caused by births and deaths (as migration has never been documented), within our 30-year dataset, we calculated the HWIs by only including the time period in which each dyad was available to associate (i.e., temporally overlapped). We then compared these observed values to a null model that measured the strength of random pairwise associations using HWI (see below).

Multiple null models (see Supplementary Table S1) are currently available to assess nonrandom patterns of associations (Manly 1995; Bejder et al. 1998; Whitehead and Dufault 1999; Whitehead 2008; Carter et al. 2009; Farine et al. 2015; Whitehead and James 2015; Spiegel et al. 2016; Strickland et al. 2017). Here, we used the digiroo null model to classify social preferences and avoidances (Carter et al. 2009; Strickland et al. 2017) using the *digiroo2* package (Dwyer et al. 2013) in R version 3.2.1 (R Development Core Team 2010). We selected this model as it efficiently accounts for spatial overlap by incorporating the heterogeneity of individuals' space use. This, therefore, allows researchers to predict random patterns of associations caused solely by space and habitat use. Similar to other null models, the digiroo model aims to retain properties of the observed dataset in the following three ways: (1) subjects retain their individually-specific space use, (2) spatial proximity to assign group members was selected to reproduce observed mean sociality (i.e., observed rate of gregariousness measured as the average HWI across our population), and (3) individual sighting probability was maintained by sampling randomized data with the same spatiotemporal observation biases found in our real data (Strickland et al. 2017). This is explained in detail in the Supplementary Materials (Text S1).

The HWIs from observed pairs were compared to a distribution ($n = 1000$) of predicted HWIs generated using the null model which incorporated individual space use (UD), highlighting instances where pairs associated more (preference), less (avoidance), or as expected (casual acquaintances) (Whitehead et al. 1991) (assuming a 95% confidence interval). On average, our dolphins had 91 ± 10 total relationships, 13 ± 13 avoidances, 12 ± 7 preferences, and 66 ± 15 casual acquaintances (see Supplementary Figure S1). As we were interested in testing the extreme (i.e., nonrandom) relationships that individuals foster, where active social choice is most likely driving these relationships, we focused our analyses on individual preferences and avoidances. As is the case with HWI, dyadic relationships (i.e., preferences and avoidances) were nondirectional and, therefore, we were unable to determine who is avoiding or preferring whom, but rather that the pair shares a social preference or avoidance relationship.

To measure individual variation in social preferences and avoidances, we then measured the average number of preferences and avoidances an individual had per year. That is, we calculated a single measure of preferences and avoidances per individual across the study period. Shark Bay dolphins exhibit highly stable social behavioral syndromes over their lifetimes (Evans et al. 2021) and the affiliative relationships of both sexes (i.e., male alliances and female social bonds) often last decades (i.e., 20 years for males; (Connor and Krützen 2015; Gerber et al. 2020) and > 18 years or more for females; (Miketa 2018). However, stability and repeatability among preference and avoidance relationships are not yet known. As such, we aimed to account for potential temporal variability within preference and avoidance relationships by measuring individuals' preferences and avoidances per year. However, identifying these relationships requires a minimum of 70 sightings (see above)

and was not possible to obtain in a single year or even across a few years, making measuring the number of preferences and avoidances an individual has per year impossible. As such, we instead opted to measure the average number of preferences and avoidances an individual had per year. To do this we first calculated the number of social preferences and avoidances per individual across the entire study period (average ± s.d. preferences (P) and avoidances (A) for females (F) and males (M), FP = 11.42 ± 6.68, FA = 13.71 ± 13.19, MP = 12.77 ± 6.49, MA = 12.48 ± 11.95, see further details in Supplementary Figure S1). Then, we added the years that each preference and avoidance of an individual was present in the study and divided that by the number of years the focal individual was monitored in the study. For example, if focal individual A is alive during 30 years of the study and has 3 preferences (individual B, C, and D) who are alive 30, 30, and 15 years respectively, then focal individual A would have on average 2.5 preferences (i.e., $(30 * 2 + 15)/30$) per year across the 30-year study. This resulted in a single per year average of preferences and avoidances across an individual's lifetime within the 30-year study. It is worth acknowledging the limitations of this approach, in that although averages account for more temporal variability than taking a single summed lifetime measure, not all variability will be accounted for.

Resource competition

Direct measures of resource competition are challenging to determine and quantify reliably in marine environments, due to the highly dynamic spatiotemporal distribution of resources (Link and Auster 2013; Fossette et al. 2017). As a result, proxies are necessary. Here, we measured the potential degree of sex-specific resource competition per individual using proximate measures of competition. For males, we measured the degree of mating competition each male experienced. For females, we measured the degree of foraging competition each female experienced.

For males, the degree of mating competition per individual was measured as the number of adult males relative to adult females observed in the individual's home range averaged across years (N = 775, 382 adult males, 393 adult females across the 30-year study period). We defined the adult period from age 10 onwards for both males and females. This was because, in Shark Bay, virtually all first pregnancies occur at age 10 or later (Karniski et al. 2018; Mann 2019) and male bottlenose dolphins in captivity tend to be fertile by age 10 based on testosterone levels (Brook et al. 2000; Yeun 2007). We included all adult males as competitors, because although Shark Bay males form alliances to gain access to and sequester females for mating purposes (Connor et al. 1992; Connor and Krützen 2015), only one male can sire the offspring. Furthermore, although males within an alliance can be related (Krützen et al. 2004), most male alliances are not driven by kinship; i.e., inclusive fitness benefits are likely minimal (Gerber et al. 2020, 2021). We did not calculate an operational sex ratio due to the difficulties in determining female reproductive state in our population. While we can account for cycling females posthoc when calves are observed, fetal and early post-natal loss are not always accounted for, and while cycling overlaps with the latter stages of lactation, the extent of this overlap is not known, especially given that weaning ages vary (2–8 years; Mann et al. 2000; Karniski et al. 2018). Given this variation, we used a simple socionomic sex ratio estimate for mating competition. We note that the demographic composition in Shark Bay is stable (Manlik et al. 2016) and female reproductive success is similar across habitats and ecological factors (Mann and Watson-Capps

2005; Strickland et al. 2021), so at any given time point the proportions of reproductively available and unavailable females are expected to be similar. However, it is worth noting that female reproduction and calf survival can change as a function of ecological conditions. In Shark Bay, this has been recently detected following an extreme heatwave event (Mann et al. 2021), but this time period was not included in the dataset used for this analysis (see below for more details).

For females, we calculated the degree of foraging competition each female experienced. We first measured the size of a female's foraging home range in km² using a subset of each female's observations where they were observed foraging (average ± s.d. percentage of female observations foraging = 29.5% ± 12.3%). We then measured the amount of intrasexual competition for resources that each female experienced in their foraging home range per year as the average number of females present in each female's foraging home range (N = 437 adult and juvenile females across the 30-year study period). Although cooperative foraging is common in some cetacean populations, in Shark Bay foraging is a primarily solitary enterprise and cooperative foraging has not been documented (Galezo et al. 2018). Therefore, we can be confident that the presence of conspecifics is indeed a source of competition. Density of competitors was estimated as the average number of females (per year) divided by the size of a female's foraging home range. However, resources may not be evenly distributed throughout the study area, and so the availability of prey in the foraging sites of females may differ according to habitat characteristics. For instance, in Shark Bay, estimated dolphin prey biomass is on average 5 times higher (range = 3–8 times higher) in shallow, vegetated habitats (i.e., seagrasses) than in deep, unvegetated habitats (Heithaus and Dill 2002). This estimate is based on the ratio of dolphin prey biomass (g) caught per benthic trap set in shallow versus deep habitats across 3 years (1997–1999, see Figure 2 in (Heithaus and Dill 2002). It is also important to note that dolphin prey availability did not significantly vary between seasons and was only significantly influenced by habitat, where biomass was consistently higher in shallow habitat across the three measured years (Heithaus and Dill 2002). While these estimates might not account for prey variation in the water column or changes through time, they are the only available estimates of dolphin prey biomass by habitat currently available for Shark Bay. These estimates likely reflect stable prey biomass as schooling mid-water fish might be more ephemeral. Therefore, we scaled the size of the home ranges to incorporate this potential variation in prey biomass as a proxy for prey availability. To do this, we multiplied the size of the seagrass area in each female's foraging home range (estimated as the intersection of the seagrass with the 95% kernel contour of each female's foraging home range) by 5, thus adjusting our estimates of foraging resource availability for the observed prey biomass difference in vegetated vs. unvegetated habitats. To ensure our metric of resource competition was robust to error in our prey biomass estimate we also calculated the measure of female resource competition using the upper (8) and lower (3) ratio range of the reported habitat prey biomass ratio across multiple seasons from Heithaus and Dill (2002). This was also analyzed in the same way as our female resource competition measure calculated using the average prey biomass ratio measure (5, see details below) and no changes to the results were observed for either range (Supplementary Table S2). We measured the density of competitors in female resource competition in multiple ways (i.e., males and females, only females, only foraging females, foraging males and females) and all measures correlated highly (R^2 = 0.983–0.997,

see Supplementary Figure S3). Therefore, we selected the average number of females to best parallel the metric used to estimate male mating competition and to remain consistent with the socioecological models which typically focus on same-sex resource competition. Furthermore, in Shark Bay, females tend to specialize more than males(Mann and Sargeant 2003; Sargeant et al. 2007) and males tend to spend less (up to half as much) time foraging, at least for some tactics (Mann and Patterson 2013), as females have significant energetic demands from gestation and lactation, and males and females are not sexually dimorphic (van Aswegen et al. 2019). As such females are more likely to be each other's competitor. We also ran two alternative models estimating female resource competition: one solely using her absolute home range size and the second using the ratio of her absolute home range size to the number of her female competitors. Our initial measure of female resource competition garnered the most support for predicting social relationships (i.e., had the lowest AIC value, see Supplementary Table S3) and as such was subsequently used hereafter.

Individual home ranges (95% kernel contours) were measured using sightings per individual across the study period. This is because individual home ranges tend to be relatively stable across time (Tsai and Mann 2013; Mann et al. 2021) and a large sightings dataset (≥45 sightings) per individual is necessary for accuracy (Patterson 2012; Strickland et al. 2017). However, similar to our social measure, we measured resource competition as a yearly average, using the monitored lifetime of an individual across the 30 years. That is, we calculated resource competition per-year, and used the average of those yearly estimates to represent the average level of competition experienced by an individual.

As with our measures of social relationships, calculating a lifetime average allows an investigation into long-term trends, while accounting for the possibility of variation within years. This is pertinent since the degree of competition could be dynamic as density, resource availability, and habitat use can vary with time (Heithaus and Dill 2002; Heithaus 2004; Patterson 2012). Furthermore, although our metrics of habitat use (Strickland et al. 2021), as well as our sex-specific measures of resource competition (see Supplementary Figures S4 & S5), show varying degrees of repeatability across years, repeatability for male resource competition is not particularly high (see Supplementary Figure S4), which suggests using average measures would be better suited than those across a lifetime. As such, we used the number of males or females per year averaged across each individual's monitored lifespan over the 30-year study period as a component of our measure of resource competition. We measured resource competition this way, as opposed to a single life-time summed measure (across all 30 years), to attempt to account for temporal changes in competitors. Finer scale measurements of biomass/seagrass were not possible, and therefore a single averaged lifetime measure was used. Periodic surveys of seagrass coverage have shown that cover was largely stable between 1988 and 2010, before declining in some areas following a severe marine heatwave from 2010 to 2011 (Thomson et al. 2015; Strydom et al. 2020). However, recent studies suggest that the effects of the seagrass shift did not significantly impact the dolphins' home ranges or behavior until about five years after the marine heatwave (i.e., until 2016) (Miketa ML. 2018. Social and behavioral responses to environmental stressors in bottlenose dolphins in Shark Bay, Australia. Washington, D.C.: Georgetown University; Nowicki et al. 2019; Mann et al. 2021) and as such should not have substantially impacted our analyses.

The degree of resource competition individuals experience also depends on the physical features and the ecology of the habitat they occupy. This is because habitat can (1) affect the accessibility of resources (e.g., females or prey), (2) influence information transfer (e.g., via eavesdropping) regarding resource competition, and (3) affect the ability to aggregate and its benefits and trade-offs (e.g., due to predation risk). For instance, in-channel habitats, some prey species tend to burrow in the rubble-littered substrate and lack swim bladders which otherwise enhance prey detection via echolocation (Foote 1980; Patterson and Mann 2011). This means that prey accessibility is decreased in this habitat without the use of specialized foraging tactics (Mann et al. 2008; Patterson and Mann 2011). Furthermore, acoustic signals propagate further in deeper waters because there is less energy loss (i.e., sound absorption) than in shallow waters (Urick 1983; Bradbury and Vehrencamp 1998; Quintana-Rizzo et al. 2006). Consequently, dolphins are likely to detect competitors more readily in some habitats (such as deep open waters) than others. Finally, predation pressure by sharks is known to be most severe in shallow waters (Heithaus and Dill 2002) affecting conspecific density and ultimately competition. We, therefore, accounted for habitat type to determine how it could affect the amount of resource competition dolphins' experience.

Habitats were defined and classified into three types based on Patterson (2012) (see also (Wallen et al. 2016)): (1) channel (rock, shell, and coral debris substrate with relatively deep depths averaging –7.1m and strong currents), (2) deep open (a mixed sand, silt, and clay substrate with deep depths averaging –6.6m but weaker currents), and (3) shallow habitats with an average of –1.1m depths (see Supplementary Figure S6). Shallow habitats consisted of both sand flats (sand substrate with extremely shallow depths averaging –0.11m and little current) and seagrasses (continuous seagrass coverage in moderate to shallow depths averaging –2.0m with little current). These two were grouped together due to their shallower depths and acoustically similar structural properties (e.g., sand flats are shallower and coastal, while seagrasses, though in slightly deeper water, can interfere with sound travel), likely enabling similar levels of sound travel. For each individual, we identified their number of sightings in each habitat by spatially intersecting each individual's sightings with the three habitat classifications. Individual preferred habitat use was then determined by calculating selection ratios per individual for each habitat (Manly et al. 2002). Selection ratios measure an individual's proportional use of each habitat relative to the proportional availability of that habitat in an individual's home range (Manly's type III design). A value of one signifies habitat use equal to availability, while values greater or less than one indicate positive or negative selection respectively. For males, sightings and habitat availability were based on the full (95%) home range; however, for females, proportional use was calculated based only on sightings in which the female was foraging, while availability was based on the full (95%) home range.

Due to high collinearity between habitat selection ratios and to identify the patterns of preferred habitat use by each individual, correlations between selection ratios for each habitat per individual were evaluated using a principal component analysis (PCA). This was done separately by sex (see Supplementary Figure S7), as we measured selection ratios differently for males and females (i.e., using sightings based on full home range for males and foraging home range for females), and the sexes are known to use space differently (Randić et al. 2012; Wallen et al. 2016). For both males and females, two PCA components were extracted and interpreted based on similar coefficient loadings. These components did vary by sex. For males, habitat PCA 1 grouped males that use the channel over the deep open and shallow habitats (i.e., sand flats and seagrass). Habitat PCA 2 loaded males using the shallow habitats over the deep open. For females, habitat PCA 1 split the deep habitats and explained females that preferentially used the channel over the deep open. Habitat PCA 2 then loaded females using the shallow habitats over the deep habitats (i.e., channel and deep open, that were split in PCA 1 above) (see Supplementary Table S4). It is important to note that habitat use in this population of dolphins is consistent through time and the PCA dimensions used in the analyses hereafter reflect the actualized habitat use of our population (Strickland et al. 2021). We also note that although some aspects of resource availability, such as home range size, covary with habitat (average foraging home range size of dolphins who preferred the shallow habitats = 81.5km², preferred channel habitat = 92.1km², and preferred deep open habitat 124.7km²), correlations between PCA axis values and home range sizes were generally low (R^2 = –0.156 PCA 1 and 0.120 PCA), and all predictor variables satisfied our thresholds for variance inflation factors (see below).

Analyses

We implemented generalized linear models (GLMs) in R version 4.0.2 (R Development Core Team 2010) to determine how the heterogeneity of resource competition shapes variation in the type and number of relationships individuals foster. Our response variables (i.e., average intrasexual social preferences and avoidances) and our predictor variable (average resource competition) were each one single averaged yearly measure, ascertained using data across all years. Using *a priori* modeling, we tested and compared four statistical models and one null model (of no effect, i.e., intercept and sightings) for each sex (Table 1). We tested whether (1) habitat use (i.e., PCA1 and PCA2 scores), (2) resource competition (mating competition for males, foraging competition for females), (3) habitat use and resource competition (additive model), and (4) the interaction of habitat use and resource competition (multiplicative model) best explained variation in the number of male and female intrasexual social preferences and avoidances. Due to our interest in how the patterns between these two relationships differed, we analyzed social preferences and avoidances separately.

Prior to running all GLMs, variance inflation factors (VIFs) were calculated using the *usdm* package in R (Naimi et al. 2014) on all predictor variables in each model. VIFs assess explanatory variables for collinearity (Zuur et al. 2009). We chose to use a conservative cut-off value of three (Zuur et al. 2009). All predictor variables fell within our cut-off range and, therefore, all variables were included in our analyses. All models were initially fit as Poisson GLMs to handle count data; however, due to large overdispersion in our data, models were further fitted as Negative Binomial GLMs with log link to account for this overdispersion (McCullagh and Nelder 1989; White and Bennetts 1996; Lindén and Mäntyniemi 2011). To control for variation in the availability of associates across space and time (i.e., adjust our counts for conspecific availability and yearly turnover), we included an offset term with the average number of intrasexual associates that shared at least 5% home range overlap (UD ≥ 0.05) and temporally overlapped for more than one year with the focal animal (average ± s.d. of the average female (F) and male (M) associates, F = 65.0 ± 5.4, M = 82.7 ± 4.1, Supplementary Figure S2). The minimum amount of home range overlap (volume of intersection) assigned to a preference or avoidance relationship was 0.05, therefore we considered only those associates as having

the ability to regularly encounter one another and form a relationship. The use of this offset term also minimizes any loss of temporal overlap that may occur in a lifetime approach, by accounting for availability and therefore demographic turnover. The number of sightings per individual was also included in all GLMs to further account for sample size effect. To ensure our predictor variables were on a comparable scale, we standardized our competition measure by subtracting the mean and dividing by the standard deviation. We compared each model and selected the most appropriately fitted using the Akaike's information criterion with a correction for small sample sizes (AICc) (Akaike 1973; Sugiura 1978; Burnham and Anderson 1998). Model diagnostics including simulating residuals for visual inspection were done using the R package *DHARMa* (Hartig 2021) (Supplementary Figure S8). Heteroskedasticity was present in the data and was only made worse by the inclusion of potentially overlooked explanatory variables (e.g., foraging tactics, years in the study). Not wanting to overfit the models as well as ensure comparison across sex and behavior, we compared our models against the same models with log-transformed y-variables by examining significance and positive or negative estimate trends. Log-transforming is commonly used to improve the spread of data by pulling in more extreme values and reducing heteroskedasticity (Kaufman 2013). Due to both normal and log(y) models being in agreement (Supplementary Table S5 and S6), we report our initial analyses (nontransformed) below and graph all significant terms.

RESULTS

Social preferences

For both males and females, model four was the most parsimonious (Table 1), showing a significant interaction between habitat use and resource competition on the number of social preferences individuals had (Table 2). Specifically, there was always a negative effect of intrasexual resource competition on the number of social preferences, but the effect size varied in magnitude depending on habitat, and these trends differed by sex (Figures 1 and 2).

For example, the negative correlation between mating competition and the number of social preferences was greater for males who preferentially used the deep open over the shallow habitats (Table 2, Figure 1). This was similar for females where the negative correlation between foraging competition and the number of social preferences was greatest for those who preferentially used the deep habitats (i.e., deep open and channel) over the shallow habitats (Table 2, Figure 2A). When the deep habitats were separated, we found that the negative correlation between foraging competition and the number of social preferences was greatest for those who preferentially used the deep open over the channel habitat (Table 2, Figure 2B).

Social avoidances

For both males and females, heterogeneity in the degree of resource competition individuals experienced correlated with the number of intrasexual social avoidances they had. However, the direction and magnitude of the correlation between resource competition and the number of social avoidances in males and females differed between sexes and habitat.

For males, model four (the interaction of mating competition with habitat) was the most parsimonious (Table 1). Males who preferentially used the deep open and shallow habitats over the channel had more social avoidances when mating competition was high (Table 2, Figure 3A). Furthermore, males who utilized the shallow habitats over the deep open had fewer social avoidances when

Table 1

Hypothesis-based model comparison (in rank order) used to explore how heterogeneity in resource competition covaries with individual social preferences and avoidances

Response	Sex	Model	Predictors	AICc	R^2	ΔAICc
Social preferences	Male	4	Habitat use * Mating competition	581.0	0.511	0
		3	Habitat use + Mating competition	585.4	0.465	4.4
		1	Habitat use	592.6	0.411	11.6
		Null	Null	636.0	0.052	55.0
		2	Mating competition	636.9	0.064	55.9
	Female	4	Habitat use * Foraging competition	561.1	0.217	0
		3	Habitat use + Foraging competition	568.4	0.126	7.3
		2	Foraging competition	571.6	0.063	10.5
		1	Habitat use	573.1	0.069	12.0
		Null	Null	574.9	0.015	13.8
Social avoidances	Male	4	Habitat use * Mating competition	615.5	0.475	0
		3	Habitat use + Mating competition	644.7	0.287	29.2
		1	Habitat use	647.9	0.252	33.4
		2	Mating competition	663.9	0.121	48.4
		Null	Null	667.6	0.075	52.1
	Female	3	Habitat use + Foraging competition	579.8	0.436	0
		4	Habitat use * Foraging competition	583.7	0.441	3.9
		2	Foraging competition	591.4	0.332	11.6
		1	Habitat use	595.6	0.319	15.8
		Null	Null	604.7	0.220	24.9

All analyses were Negative Binomial generalized linear models (GLMs). Mating competition is measured as the ratio of adult males to adult females in a male's home range. Foraging competition is measured by the average number of females in a female's foraging home range per year divided by habitat area of that home range, where the seagrass area is multiplied by 5 (an average prey biomass factor). $N_M = 101$, $N_F = 90$ individuals. Model selection was done using Akaike's information criterion with a correction for small ample sizes (AICc). R^2 estimated as $1 - o$(Residual deviance/null deviance).

Table 2

Model outputs for the most parsimonious models

Response	Sex	Model	Predictors	Estimate (95% CI)	SE	z
Social preferences	Male	4	Intercept	**−2.435 (−2.615 to −2.259)**	0.090	−27.156
			Habitat 1	**0.300 (0.227 to 0.373)**	0.037	8.142
			Habitat 2	−0.014 (−0.110 to 0.083)	0.050	−0.273
			Mating competition	**−0.254 (−0.391 to −0.124)**	0.068	−3.722
			Sightings	**0.002 (0.002 to 0.003)**	0.000	5.749
			Habitat 1 * Mating competition	−0.047 (−0.127 to 0.032)	0.041	−1.163
			Habitat 2 * Mating competition	**0.161 (0.048 to 0.275)**	0.058	2.774
	Female	4	Intercept	**−2.211 (−2.437 to −1.985)**	0.114	−19.483
			Habitat 1	−0.081 (−0.193 to 0.031)	0.055	−1.473
			Habitat 2	**−0.171 (−0.290 to −0.054)**	0.060	−2.872
			Foraging competition	**−0.323 (−0.490 to −0.159)**	0.083	−3.892
			Sightings	**0.001 (0.000 to 0.002)**	0.001	2.087
			Habitat 1 * Foraging competition	**0.126 (0.003 to 0.258)**	0.062	2.030
			Habitat 2 * Foraging competition	**−0.212 (−0.344 to −0.085)**	0.063	−3.394
Social avoidances	Male	4	Intercept	**−2.160 (−2.577 to −1.731)**	0.191	−11.319
			Habitat 1	**−0.435 (−0.626 to −0.250)**	0.090	−4.827
			Habitat 2	−0.168 (−0.432 to 0.092)	0.127	−1.312
			Mating competition	0.226 (−0.184 to 0.643)	0.156	1.448
			Sightings	0.002 (0.000 to 0.004)	0.001	1.936
			Habitat 1 * Mating competition	**−0.662 (−0.942 to −0.392)**	0.102	−6.528
			Habitat 2 * Mating competition	**−0.775 (−1.202 to −0.365)**	0.162	−4.784
	Female	3	Intercept	**−2.498 (−2.770 to −2.221)**	0.135	−18.519
			Habitat 1	0.074 (−0.043 to 0.193)	0.061	1.227
			Habitat 2	**0.274 (0.138 to 0.410)**	0.070	3.918
			Foraging competition	**0.399 (0.221 to 0.590)**	0.085	4.697
			Sightings	**0.003 (0.002 −0.004)**	0.001	4.797

All analyses were Negative Binomial generalized linear models (GLMs). Mating competition is measured as the ratio of adult males to adult females in a male's home range. Foraging competition is scaled and zero centered and measured by the average number of females in a female's foraging home range per year divided by habitat area of that foraging home range, where the seagrass area is multiplied by 5 (an average prey biomass factor). Habitat use varies by sex. For females, habitat 1 is a habitat PCA output that aligns females using the channel over the deep open. Habitat 2 is a habitat PCA output that groups females that choose the deep habitats (channel and deep open) over the shallow habitats (sand and seagrass). For males, habitat 1 is a habitat PCA output that aligns males using the channel over the deep open and shallow habitats. Habitat 2 is a habitat PCA output that groups males that choose the shallow habitats (sand and seagrass) over the deep open. For further habitat use details see Supplementary Materials. N_M = 101, N_F = 90 individuals. Significance was assessed against the 95% confidence intervals of the estimate (shown in parentheses). Significant values shown in bold. Model selection was done using Akaike's information criterion with a correction for small ample sizes (AICc).

mating competition was high (Table 2, Figure 3B). For females, model three (foraging competition and habitat) was the most parsimonious model (Table 1). Females who experienced high foraging competition had more social avoidances than those who experienced low competition (Table 2, Figure 4A). In addition, habitat use also significantly affected the number of social avoidances females had regardless of foraging competition (Table 2, Figure 4B). Specifically, females who preferentially used deep habitats (i.e., deep open and channel) had more social avoidances than those that preferred shallow habitats (Figure 4B).

DISCUSSION

Although resource competition has long been recognized as a pivotal driver of group formation (Emlen and Oring 1977; Wrangham 1980; van Schaik 1989), here we provide new empirical insight that intraspecific variation in resource competition and sociality will inherently be linked through the socioecological environment. This link has recently been suggested theoretically (Webber and Vander Wal 2018), however, our results illustrate these links by showing how variation in the long-term social relationships that individuals' foster covaries with their preferred habitat and degree of resource competition, depending on their sex. Taken together, our findings highlight how an individual's social behavior (here long-term relationships) is intrinsically tied to the individual's ecological niche;

showing that the ecology of individuals matters (Bolnick et al. 2003). Below, we discuss the three distinct ways by which our results demonstrate the interplay between an individual's ecological niche and their long-term social relationships.

Interplay between resource competition and social relationships: a female perspective

Resource competition between females can have important behavioral and fitness consequences including, but not limited to, reproduction (Holand et al. 2004b), physiology (Holand et al. 2004a), and affiliative social behavior and social structure (Wrangham 1980; Sterck et al. 1997; Kappeler and van Schaik 2002). Here, we show that the levels of resource competition females experience covaries with their social avoidances. Specifically, we show that females who experience high resource competition have more social avoidances, perhaps as a way to mitigate conflict. As prey resources are neither shared nor guarded (i.e., are nondefensible) in this population, this strategy may enable certain females to increase foraging success while reducing one major cost of group living (i.e., direct competition/conflict). Other studies show that social avoidance is likely an important social strategy in minimizing/mitigating long-term conflict in animals (Piza-Roca et al. 2018; Strickland et al. 2018; Levengood 2019; Strickland and Frère 2019). Surprisingly, despite decades of research on animal sociality, we understand little about the relative importance of affiliations/associations versus avoidances in shaping animal social organization.
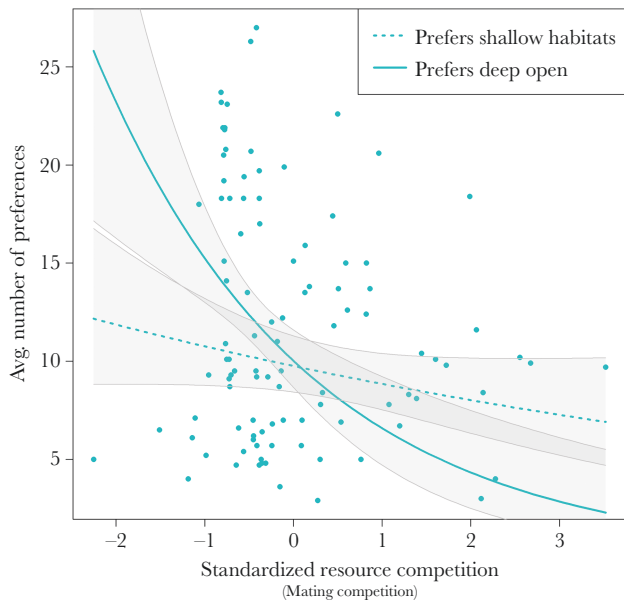
Figure 1

Interactive effect of resource competition and habitat use on the lifetime average of male social preferences among bottlenose dolphins ($n = 101$). Regression lines estimated from Negative Binomial generalized linear models (GLMs) (Table 2). Mating competition is measured as the average number of adult males to adult females in a male's home range. CI of 95% shown with grey bands.

Interplay between habitat preference and social relationships: a female perspective

Habitat has been experimentally shown to influence social structure and organization in a range of animals where structural and composition features dictate conspecific density and thus contact rates (Bennett et al. 2013; Mokross et al. 2014; Leu et al. 2016; He et al. 2019). Here, we show that the habitat females prefer, irrespective of the resource competition they experience, influences their social avoidances. Albeit some caution is warranted with such a small effect size. Nonetheless, females who preferred the deep habitats had more social avoidances than those preferring shallow habitats. This variation across habitats suggests that there are additional habitat-specific and/or ecological drivers beyond competition (for food) that can further influence an individual's social behavior. One explanation is simply that open habitats allow for more space to avoid. Alternatively, ecological drivers such as, competition for space (Murray et al. 2007; Patterson 2012), safety from predators (Cowlishaw 1997; Heithaus and Dill 2002), and/or socioecological drivers, such as male sexual harassment (Connor et al. 1992, 1996; Wallen et al. 2016) may drive these patterns, but further investigation is needed to draw accurate conclusions.

Environmental heterogeneity, in both structure and composition, not only shapes the spatial distribution and availability of resources across the landscape but also influences a suite of important life-history traits in animals (e.g., movement (Barraquand and Benhamou 2008), foraging (Sargeant et al. 2007), reproduction (Trevail et al. 2019), and cooperation (Kun and Dieckmann 2013; He et al. 2019)). Here, we show that the magnitude and
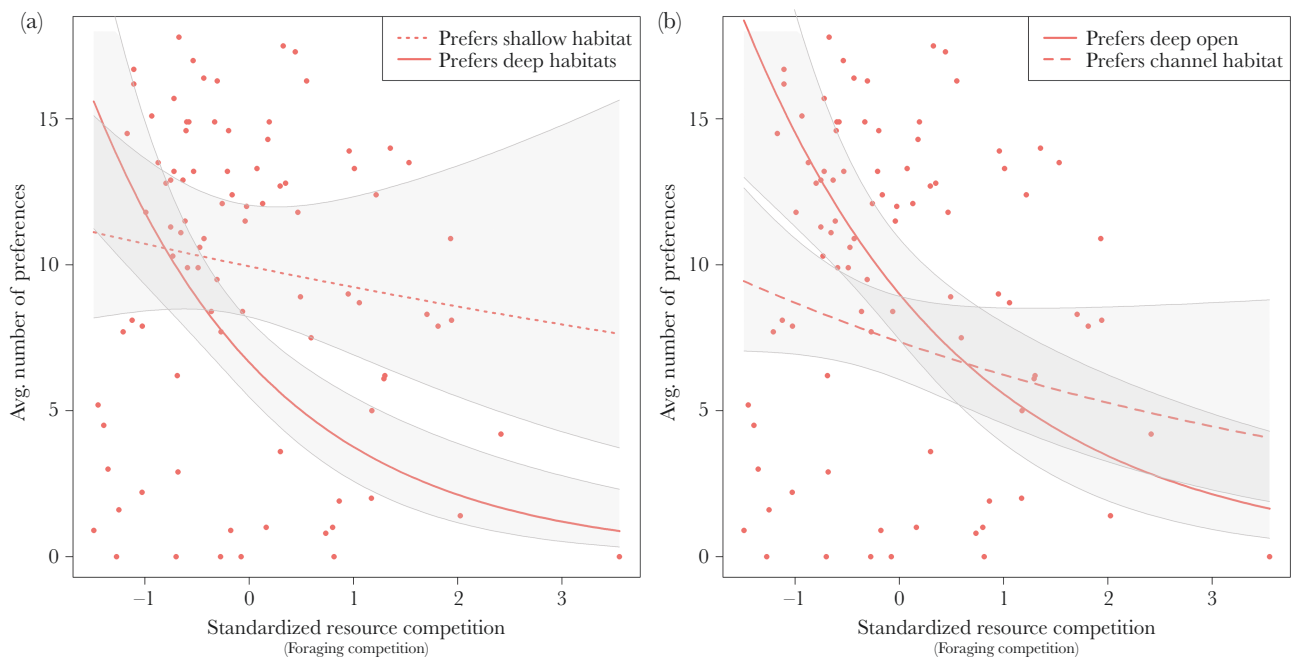

Figure 2

Interactive effects of resource competition and habitat use between shallow and deep habitats (A) and between the deep open and channel (B) on the lifetime average of female social preferences ($n = 90$ dolphins). Regression lines estimated from Negative Binomial generalized linear models (GLMs) (Table 2). Foraging competition is measured by the average number of females in a female's foraging home range per year divided by habitat area of that foraging home range, where the seagrass area is multiplied by 5 (an average prey biomass factor). CI of 95% shown with grey bands.
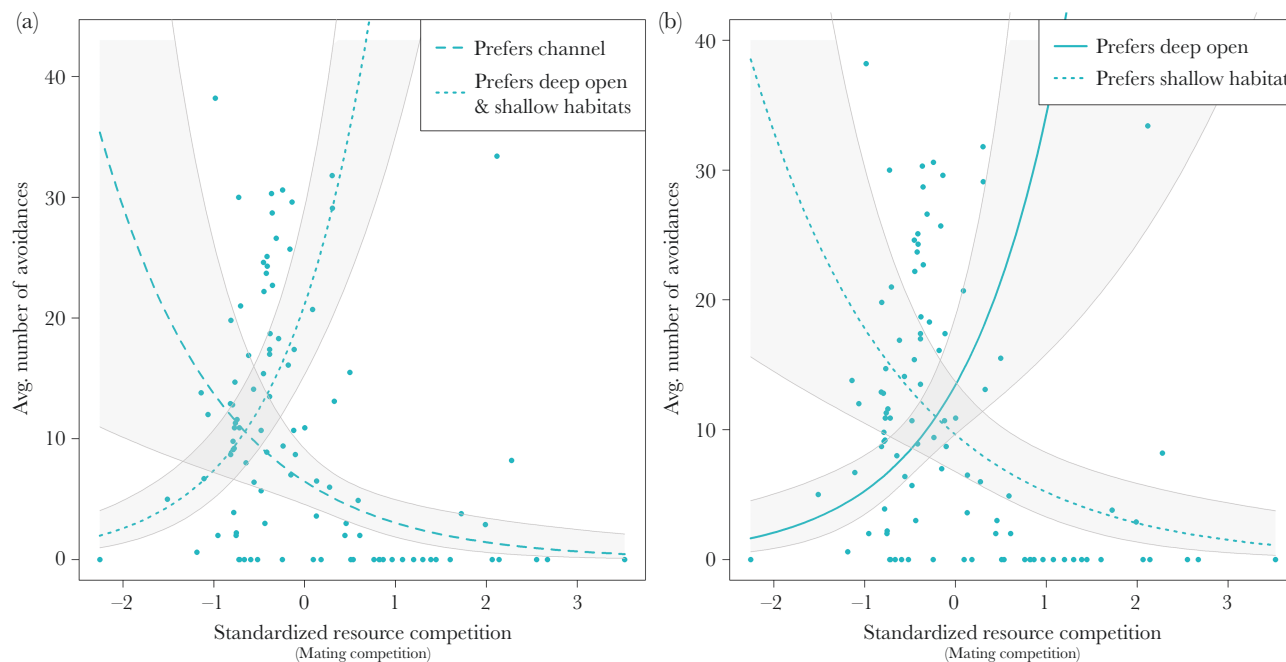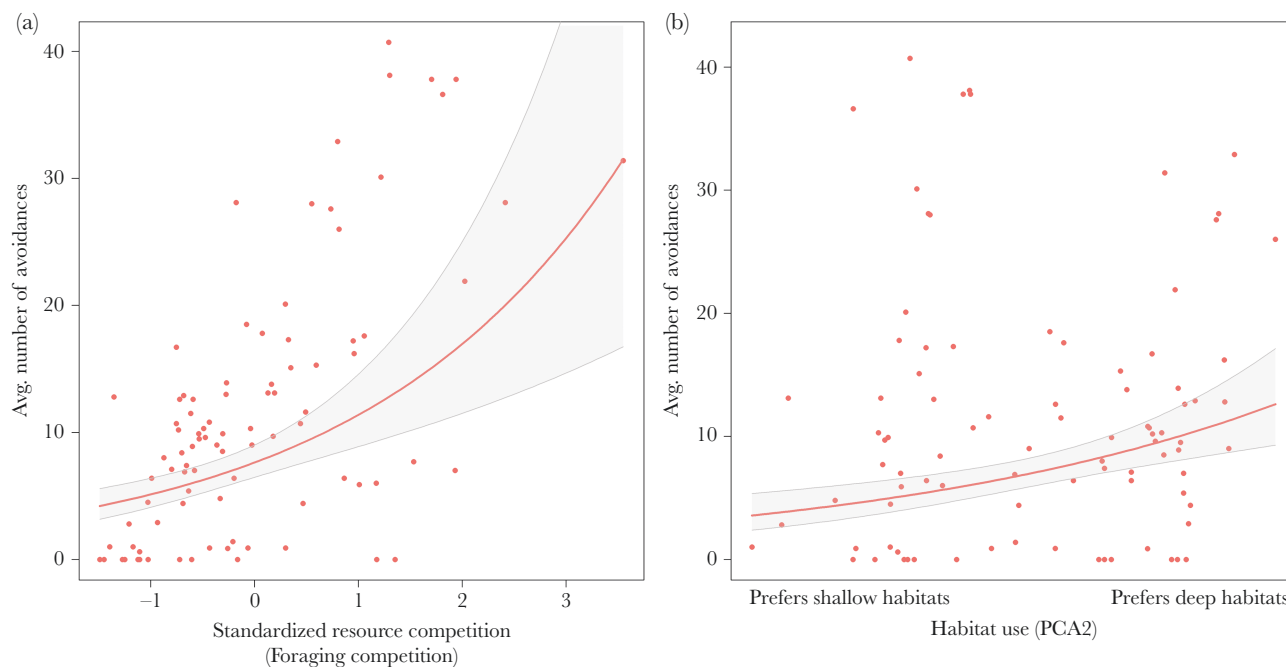
Figure 3

Interactive effects of resource competition and habitat use between the channel versus the deep open and shallow habitats (A) and then within the deep open and the shallow habitats (B) on the lifetime average of male social avoidances ($n = 101$ dolphins). Regression lines estimated from Negative Binomial generalized linear models (GLMs) (Table 2). Mating competition is measure as the average number of adult males to adult females in a male's home range. CI of 95% shown with grey bands.

Figure 4

Relationship between the degree of resource competition (A) and individual habitat use (PCA2) (B) to the lifetime average of female social avoidances ($n = 90$ dolphins). Regression lines estimated from Negative Binomial generalized linear models (GLMs) (Table 2). Foraging competition is measured by the average number of females in a female's foraging home range per year divided by habitat area of that foraging home range, where the seagrass area is multiplied by 5 (an average prey biomass factor). PCA 2 is a habitat PCA output that groups females that choose the deep habitats (channel and deep open) over the shallow habitats (sand and seagrass). The x-axis (PCA 2) operates along a continuum. CI of 95% shown with grey bands.

directionality of the relationship between the mean level of re-
source competition individuals experience and the average number
and type of social relationships they foster can be habitat-use de-
pendent. Both males and females, reduce their social preferences
with increased resource competition, but the magnitude in reduc-
tion is habitat dependent. For social avoidances, however, we found
that habitat use influences both the magnitude and the direction-
ality of the relationship between resource competition and avoid-
ances. Indeed, males who preferentially use channel and shallow
habitats reduce their social avoidances as resource competition in-
creases, while males who preferentially use deep open habitats do
the opposite: they increase their social avoidances as resource com-
petition increases.

Interestingly, Shark Bay dolphins live in a highly heterogeneous
environment, which is spatially diverse in both structure (e.g., depth,
substrate, and/or physical space) (Patterson 2012) and resource avail-
ability (Heithaus and Dill 2002; Heithaus 2004). For example, one of
the substrates of the shallow habitat (i.e., seagrasses) promotes greater
prey abundance and biomass (Heithaus 2004), yet the shallow habitat
is smaller in area and provides less three-dimensional space compared
to the deep habitats (Patterson 2012). These physical structural prop-
erties may affect both foraging and mating competition by influencing
the ability for individuals to congregate. Furthermore, the deep open
waters have vast omnidirectional space (Patterson 2012) which may
allow individuals to detect, identify, and eavesdrop on their competi-
tion (Janik 2000; Jensen et al. 2012), while also providing ample space
to avoid conspecifics undetected. Our results suggest that the males
in our study may be leveraging this habitat property in order to avoid
"rival" males or male alliances when competition for females is at its
highest. Finally, the channel habitat, although deep, is narrow, bisected
by shallow habitats, and covers a much smaller area (Patterson 2012).
Since space is more limited in the channel this may affect mating
competition by hindering male's abilities to easily avoid one another,
or at least tolerance between male alliances in channel habitats might
protect them from larger alliances in the deep open (Connor et al.
2017; O'Brien et al. 2020).

In conclusion, as the individual is the target for natural selection,
identifying factors that contribute to variation in the social relation-
ships that individuals foster is critical to theories of social evolution
(Bolnick et al. 2003; Webber and Vander Wal 2018). Our work em-
pirically demonstrates that variation in a dolphin's long-term so-
cial relationships is tightly linked to its socioecological environment,
strengthening the argument that social behavior is ultimately the
expression of an individual's relationship with its social and phys-
ical environment (Muller et al. 2018; Strickland et al. 2018; Webber
and Vander Wal 2018). Though we did not investigate the mechan-
isms by which this variation may occur, it is important to acknowl-
edge that personality/social niche specialization (Bergmüller and
Taborsky 2010; Dall et al. 2012; Evans et al. 2021) and/or social
plasticity (Schradin et al. 2012; Taborsky and Oliveira 2012) may be
the underlying processes that allow for variation in the social rela-
tionships that individuals foster. Furthermore, our investigation into
long-term social relationships was measured by lifetime averages, but
future work could take a more fine-scale approach examining the
plastic element across both competition and social behavior. Finally,
by studying multiple types of social relationship, we show the impor-
tance of studying both affiliative and avoidance behavior given their
likely co-contribution to shaping animal social organization.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at Behavioral Ecology online.

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