A framework for the identification of long-term social avoidance in longitudinal datasets

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Animal sociality is of significant interest to evolutionary and behavioural ecologists, with efforts focused on the patterns, causes and fitness outcomes of social preference. However, individual social patterns are the consequence of both attraction to (preference for) and avoidance of conspecifics. Despite this, social avoidance has received far less attention than social preference. Here, we detail the necessary steps to generate a spatially explicit, iterative null model which can be used to identify non-random social avoidance in longitudinal studies of social animals. We specifically identify and detail parameters which will influence the validity of the model. To test the usability of this model, we applied it to two longitudinal studies of social animals (Eastern water dragons (Intelliegama lesueurii) and bottlenose dolphins (Tursiops aduncus)) to identify the presence of social avoidances. Using this model allowed us to identify the presence of social avoidances in both species. We hope that the framework presented here inspires interest in addressing this critical gap in our understanding of animal sociality, in turn allowing for a more holistic understanding of social interactions, relationships and structure.

1. Introduction

Understanding social behaviour is a key component of behavioural and evolutionary ecology. Accordingly, the mechanisms driving social attraction and the adaptive significance of the
Avoidance has previously been measured largely as instances of an individual’s immediate withdrawal from social contact with conspecifics [16–19]. For instance, a subordinate’s immediate avoidance of and withdrawal from contact with approaching or aggressive individuals has been used to determine relative social status in dominance hierarchies [20]. However, as with affiliative social interactions, short-term avoidances may develop into long-term avoidances, where individuals consistently avoid certain conspecifics over time. For instance, we know that, under certain circumstances, short-term affiliative social interactions (e.g. grooming) can, after repeated interactions, develop into stable, social relationships [21–23]. Short-term avoidances such as those described above may, similarly, manifest into long-term avoidances, where individuals, given the spatio-temporal potential for repeated interactions, avoid one another consistently over time. Nevertheless, how, or indeed if, social avoidances are sustained over longer time periods remains unknown.

Avoidance of conspecifics may occur in many social situations, and for a multitude of reasons. For example, Eastern chipmunks (Tamias striatus) with overlapping neighbouring territories avoid each other by adjusting their space use temporally, allowing the chipmunks to use the shared space at different times [24]. Current theory suggests that social animals simultaneously choose to associate with some conspecifics, while avoiding others within their social environment [6–8]. Such avoidances would therefore be expected to occur within the same spatial domain as social associations. In fact, a few studies of social animals have demonstrated that some individuals share much of their space, but do not associate, suggesting that individuals may be avoiding each other (e.g. [25,26]). However, in these studies, the social avoidances were largely identified as a by-product of investigating social preference. Moreover, while many methods that measure pairwise preference also tacitly measure avoidance, the validation of these methods is often with isolating preferences in mind. Consequently, while avoidance of conspecifics has been proposed as an important mechanism in the structuring of social associations [27], the quantitative investigation and identification of non-random social avoidances remains undefined and untested.

Both the presence and absence of social association can occur by chance. For example, animals that share a social environment, and the resources within it, may both encounter each other—or not—solely by chance due to overlapping patterns of space use [28]. Disentangling random processes..
from behavioural choice can be, and often is, done by comparing observed patterns of behaviour with null models [28–31]. Other authors have offered ways to measure social avoidances (e.g. [29,30]), such as by randomizing the membership of groups, or by using pairwise spatial overlap measures as a predictor of associations. However, we propose that the use of a spatially explicit null model is most appropriate. This is because, by accounting for individuals’ observed space use and spatial heterogeneity, this method allows for more robust predictions of random association patterns [28]. In contrast to other methods which also use space, by randomizing individuals’ spatial positions, we are able to better predict patterns of association resulting from space use, thereby isolating instances where individuals would be expected to associate but do not (i.e. avoidance). To identify long-term social avoidances, we provide a general framework using a spatially explicit null association model and demonstrate its application to two species (Indo-Pacific bottlenose dolphins (Tursiops aduncus) and Eastern water dragons (Intellegama lesueurii)) with disparate ecology and social structure.

2. General framework

The null association model used here produces expected social associations between dyads which result from expected use of space (figure 1). The model does so by randomizing individuals’ spatial positions within their home ranges (the area in which individuals live), using either home range contours or utilization distributions (UDs). Random points are then generated according to individuals’ UD (electronic supplementary material, figure SA1), as well as the probability of being sighted, and random pairwise associations are extracted based on proximity between random spatial positions (see figure 1 and §2.1.4 for how to identify this threshold). Spatial proximity between animals is a well-accepted method of estimating pairwise associations in studies of social species where interactions are infrequent and/or difficult to observe [32,33]. With both the observed and the randomly generated social groupings, the strength of the pairwise associations can then be estimated and compared using an appropriate association index for the study species (e.g. simple ratio index, twice-weight index, social affinity index). Here, we used the half-weight index (HWI) because it is the most suitable index for both systems (see [34]). The HWI is calculated using the following formula:

$$\text{HWI} = \frac{N_{ab}}{N_{ab} + 0.5(N_a + N_b) + Y_{ab}},$$

where $N_{ab}$ is the number of times individuals $a$ and $b$ were seen associated, and $N_a$ and $N_b$ are the number of times each individual was seen and $Y_{ab}$ is the number of times they were seen in the same sampling period but not associated [34]. Applying this model iteratively allows us to generate a random probability distribution against which the observed value can be statistically compared. In other words, a $p$ value for each dyad is calculated as the proportion of times the random association index was smaller (or greater for preferences) than the observed. Avoidances can therefore be defined as instances where 95% (or more) of random HWIs were greater than the observed HWI.

The null association model has been previously described elsewhere [25,35], and integrated in the Digiroo2 package in R [36,37]. Here, we have identified critical parameters essential in the generation of a valid null model for social avoidance. Therefore, in this paper, we expand on the approach described by Carter et al. [25] in order to increase its applicability to other populations, and for its utility in detecting social avoidances.

2.1. Optimizing the null model

A framework is provided below with which to generate the null model, with attention to parameters that vary according to the species’ behavioural ecology, and the observation protocol used during data collection. These are important, as failing to incorporate them may lead to type I and/or type II errors.

2.1.1. Utilization distribution

This spatial model randomizes individuals’ locations according to their home range. Here, we suggest the use of individuals’ UDs because this retains more information about individuals’ variable use of space. More specifically, it accounts for the fact that individuals do not use their space evenly. UDs are home ranges that describe the frequency distribution of an individual’s location data [38], estimating
(1) estimate home range

(2) randomize individual's spatial points

(3) use spatial proximity between random points to assign social groups

(4) calculate pairwise association index (AI)

(5) assign avoidances by comparing random AI with observed AI

<table>
<thead>
<tr>
<th>simulations</th>
<th>example</th>
<th>parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) estimate home range</td>
<td>![individual a] and ![individual b]</td>
<td>ensure home range estimates are accurate (§2.1.1)</td>
</tr>
<tr>
<td>(2) randomize individual's spatial points</td>
<td>![random points]</td>
<td>ensure temporal structure and survey design of observed data are maintained (§§2.1.2 and 2.1.3)</td>
</tr>
<tr>
<td>(3) use spatial proximity between random points to assign social groups</td>
<td>![proximity]</td>
<td>select the appropriate spatial proximity that maintains the sociability of observed data (§2.1.4)</td>
</tr>
<tr>
<td>(4) calculate pairwise association index (AI)</td>
<td>HWI_{ab}^{rand} = 1/0.5(2+2) = 0.5</td>
<td>use association index appropriate for system (e.g. HWI)</td>
</tr>
<tr>
<td>(5) assign avoidances by comparing random AI with observed AI</td>
<td>observed HWI_{ab} = 0 &lt; 0.5 = social avoidance</td>
<td>subset for individuals with enough data to reliably assign relationships (§2.1.5)</td>
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Figure 1. Diagram describing the steps involved with the simulations. The example, based on two individuals, illustrates the steps and the parameters that are important to consider. HWI is calculated as $N_{ab}/(N_{ab} + 0.5(N_a + N_b) + Y_{ab})$ where $N_{ab}$ is the number of times individuals $a$ and $b$ were seen associated, $N_a$ and $N_b$ are the number of times each individual was seen, respectively, and $Y_{ab}$ is the number of times they were seen in the same sampling period but not associated.

an individual’s probability of occurrence within an area across a grid of the study sites’ coordinates. Accurate (i.e. stable) UD estimations depend on sample size, and identifying the minimum number of sightings necessary can be species- or population-specific. The data should include only individuals that meet the required minimum sightings.

2.1.2. Temporal structure of data

When applying the model to longitudinal datasets, it is important for the null model to reflect the temporal structure of the data. This is because demographic events within the study population such as birth, death, immigration and emigration will affect the extent to which pairs of individuals overlap temporally in the observed data. This can be achieved, for instance, by restricting data in analyses to time periods in which there were few demographic changes (e.g. births/deaths). If restricting data is neither
possible nor desirable, the model can be set up so that individuals are included in random sampling periods (e.g. 1 day) only if they overlap temporally. This may be especially important for difficult-to-observe species in which the observation period required to achieve accurate home range estimates extends over an amount of time in which demographic changes are unavoidable.

2.1.3. Survey design

Null models must consider how the surveys (animal sighting records) were collected. During the simulations, individuals sighted within random sampling periods are randomly selected from the population; however, the survey design of some studies does not cover the entire study site in each sampling period. This would result in uneven sampling coverage which must be accounted for within the model.

2.1.4. Reflecting population sociability

The null model must incorporate the amount of time individuals in the population spend together (e.g. sociability of the population), while randomizing the membership of groups or pairs formed. The sociability of populations can be estimated in several ways (e.g. average association index, average number of groups or average group size), and obtaining comparable levels of sociability in the null can also be done in several ways. Retaining group size and number of groups, as per the Manly–Bejder permutation method [39], may be applicable for group-living species (e.g. dolphins); however, a more general measure is needed when applying this method to species which do not live in clearly defined groups (e.g. water dragons). Therefore, due to the general applicability of the average association index (e.g. HWI), we suggest this measure as the most appropriate.

Animals do not move randomly. As such, when simulations move animals randomly within their home range (as in the null model), the number of social associations will be greatly reduced. As a result, to optimize the null model to retain the sociability of the population, we must manipulate certain parameters of the observed data. This can be done in a number of ways, but we focused on two major options: increasing the distance proxy used for social associations, or increasing the number of individuals sighted per random sampling period. However, increasing the sample size per sampling period would result in inflating the likelihood of dyads being sighted within the same sampling period. Because association indices such as the HWI are calculated based on pairwise sample size, any difference in dyads being sighted within the same sampling period would result in random pairwise HWIs which are no longer comparable to the observed HWI. Therefore, we suggest that to achieve comparable HWIs, the distance within which individuals are grouped together (gprox) should be adjusted. This will, in most instances, result in a larger gprox than is used in the observed data because, in most instances, using the same distance will result in underestimating the sociability of the population. This is also the most flexible approach, as it may be that a large proportion of the population were sighted within each sampling period, thus making increasing the number of individuals per random sampling period difficult.

2.1.5. Post hoc selection of individuals

Estimates of social associations are influenced by the number of sightings each individual has. Moreover, the variance in sample size between individuals will affect the accuracy of the classification of that relationship [34]. Often this is accounted for, first by using appropriate association indices and, second, by only using individuals with sufficient sightings to accurately measure the population’s sociability. When building the null model, we first used a subset of the data to include only individuals that had enough sightings to accurately estimate their UD (see §2.1.1). However, in most cases, to obtain reliable assignment of relationships (e.g. avoid—random—prefer), more sightings will be needed than that which is needed to gain accurate home range estimations. Therefore, for post hoc analysis we selected only individuals which had the minimum number of sightings required to classify pairwise relationships (e.g. avoidance—random/neutral—preference) accurately. We selected individuals for identification of avoidance (and preference) post hoc because, in the null model, it is important to retain as many individuals as possible in order to optimize the null accurately (i.e. to match observed sociability). Nonetheless, selecting individuals with enough social data post simulations results in confident identification of pairwise relationships.
2.2. Identifying avoidances and preferences

Avoidances are identified by randomizing groups according to individuals’ UD, and then generating a distribution of random HWIs for each pair. Following this, a $p$ value for each dyad is calculated as follows:

$$P = \sum_{j=1}^{B} \frac{Y_j \leq X}{B},$$

where $B$ is the number of replicates, $Y$ is the random HWI and $X$ is the observed HWI [40]. Thus, the $p$ value represents the proportion of times the random association index was smaller than the observed. Here, we classify pairwise avoidances as those that are seen together significantly less than would be expected if they moved randomly (with a 95% CI). Therefore, these avoidances can be instances of both HWI = 0, but also of HWI > 0. Preferences can also be identified by calculating a $p$ value as the proportion of times the observed HWI is greater than in the null model (with a 95% CI).

The strength of pairwise avoidances may be assessed by using a measure of pairwise home range overlap. For example, a pair of individuals that avoid each other and share 100% of their home ranges could be seen to be a stronger social avoidance than in instances where a pair share 30% of their home ranges.

3. Case study: dragons and dolphins

We used longitudinal data from two social vertebrates (Eastern water dragons and bottlenose dolphins) to illustrate and test the framework’s utility in identifying long-term social avoidances. The framework was applied using individuals’ 100% UD, and then repeated using only data that fell within each animal’s 50% UD to examine behaviour in the ‘core’ home range.

Eastern water dragons are a gregarious reptile, whose social dynamics resemble fission–fusion systems [41]. Males are plastic in their mating tactics (territoriality or satellite) [42] and, importantly, there are instances where pairs of individuals share large proportions of their home range but are never seen together [41]. To quantify social associations, a 1.85 m distance proxy is used [41]. This distance is used for three reasons. First, it was identified statistically by taking the upper first percentile of all pairwise geographical proximities [41]. Second, affiliative interactions require time within close proximity of one another [28,43–45]. Third, our observations have shown that individuals which do not tolerate each other will react aggressively to one another within this distance. Data are, however, filtered to remove those instances where aggressiveness is observed to ensure that close social proximity reflects social tolerance.

We used data collected as part of an ongoing behavioural study (2010–present) of a population of dragons at Roma St Parklands, Brisbane, Australia [46]. The population has an estimated size of 336 individuals (estimated using Jolly–Seber mark-recapture methods in SOCPROG v. 2.6 [30]). Behavioural surveys were conducted along the same transect of the Parklands, which covers approximately 85% of the population. Surveys were carried out twice a day (AM and PM), on average three times a week. This time period represents the time in which they are most active (i.e. not hibernating). For each individual sighted, we collected head profile photograph (using Canon EOS 600 digital camera), GPS coordinates (using GARMIN eTrex10 handheld device, accurate to 3 m), sex and observations of aggressive behaviour typical of agamid lizards (e.g. head bob, tail slap, arm wave, push-ups). Sex was assigned based on sexual dichromatism and sexual dimorphism present in the species [47]. Profile photographs were used to identify individuals using the I3SManta software package [48] using unique scale patterns and coloration [46].

Bottlenose dolphins (Tursiops aduncus) live in open communities, exhibiting fission–fusion social organization, characterized by changing group membership through space and time [49–53]. In Shark Bay, Western Australia, males form stable long-term alliances [54–57], while females are more socially flexible, forming relatively loose, kin-based associations [26,49,58]. In Shark Bay, dolphins are bisexually philopatric and have large, overlapping temporally stable home ranges [59].

We used data from an ongoing, long-term (approx. 30 year) study of over 1600 bottlenose dolphins resident to the eastern gulf of Shark Bay, Western Australia. The main study site is approximately 300 km$^2$ and is highly environmentally heterogeneous [60]. Data were collected using boat-based opportunistic surveys, where scan sampling [61,62] was used for the first five minutes to determine group composition. Individuals were identified using standard dorsal fin identification techniques [63]. Sex was determined either by the presence of a dependent calf, views of the genital area [49] and, where available, genetic
sex determination [64]. Age was assigned by physical and behavioural characteristics [65,66]. Group membership was determined using a 10 m chain rule, where all individuals within 10 m of each other were considered to be associating [49]. Ecological data (e.g. GPS location, water depth, sea state and seafloor substrate) were recorded during each survey.

3.1. Optimizing the null model

We optimized the null model for both the full dataset, and a dataset restricted to the core home range (50% UD) in order to investigate differences in the presence of avoidance at different spatial scales.

3.1.1. Utilization distribution

UDs were estimated using GPS relocations for each individual and an optimized smoothing parameter. Pairwise home range overlap was calculated using 95% and 50% volume of intersection (VI) [38]. VI is a commonly used index of pairwise home range overlap. It measures the amount of overlap between two UDs and calculates a value between 0 (no overlap) and 1 (complete overlap). All home range analyses were conducted using the adehabitatHR package within the R statistical environment [37,67].

To determine the minimum number of sightings required to gain accurate estimates of individuals’ UD, we estimated home range size for the same individuals multiple times, randomly selecting sequentially increasing numbers of sightings (dragons from 5 to 40 sightings; dolphins from 20 to 70 sightings). We further measured pairwise VI with each set of randomly selected sightings and assessed correlations between these and VI estimated from the full data. In both dolphins and dragons, VI was very stable across sightings (see electronic supplementary material, table SA1). However, in order to be confident that we have measured home ranges accurately, we identified the minimum number of sightings required at which the size of the home range area stabilizes (i.e. stops increasing) (figure 2).

3.1.1.1. Dragons

For dragons, a previously optimized smoothing parameter of seven metres [46] was used and a minimum number of 25 sightings was required for stable home range estimates (figure 2a). Although estimates at 20 and 25 sightings were comparable, we selected 25 sightings as a conservative estimate in order to increase the accuracy of home range measurements.

3.1.1.2. Dolphins

For dolphins, UDs were estimated using an individual-specific reference bandwidth smoothing parameter [68], accounting for a land boundary (simplified from the coastline of the Peron peninsula) [69], as implemented in adehabitatHR [67]. Because our simplified boundary could not completely account for the tortuosity of the coastline, any remaining land area was removed from all final UDs and probability densities were re-standardized to 1. A minimum number of 45 sightings were required to gain stable home range estimates (figure 2b).
3.1.2. Temporal structure of data

3.1.2.1. Dragons

We used data collected between September 2015 and April 2016. This was because during this field season, we reliably captured enough sightings per individual. The data used in this study constituted 142 surveys (i.e. sampling periods), during which an average of 54 unique individuals (± 12 individuals) and 17 pairs (± 12 pairs) were sighted per survey.

3.1.2.2. Dolphins

For this study, we used data collected during a period of 15 years (2001–2015). We used only survey data from May to September to reduce the influence of range shifts due to the breeding season [70,71]. All dependent calves, as well as any individual under 4 years old (average weaning age [72]) were omitted from analysis. 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 [59].

Because we used a 15-year dataset, we designed our model to account for demographic turnover caused by the entrance/exit of individuals within the population. This is important because failing to account for the temporal opportunity for pairs to interact can mask real social processes and structure [73]. Demographic turnover was accounted for in two ways. First, observed patterns of temporal overlap were incorporated within the null model by allowing only individuals who were available simultaneously to be included within the same random sampling period. Second, we only calculated HWIs over the period in which both animals were available to associate. We used conservative measures (i.e. last sighting date) to restrict animal associations in the absence of precise death dates.

3.1.3. Survey design

3.1.3.1. Dragons

Surveys conducted at Roma St Parklands cover the full transect during each sampling period. Therefore, we did not need to account for the spatial structure of the surveys within the null model.

3.1.3.2. Dolphins

Owing to the size of the study site, the opportunistic surveying method and the necessity to begin all survey effort from the same launch point, our study site was unequally sampled. To account for this, we incorporated our spatial survey structure into our simulated data. This was done by creating daily minimum convex hulls with a 1 km buffer around each day’s survey locations and the launch point (see electronic supplementary material, appendix figure SA2). Dolphin sightings were then randomly simulated within their UD according to the probability that each animal would be sighted within each daily area. The number of individual sightings in each sampling period was determined using a standard population density for the study site (0.45 dolphins km$^{-2}$), and ranged from 2 to 40 animals per day (mean 9 ± 6).

3.1.4. Reflecting population sociability

The null model for both dragons and dolphins was optimized by changing the pairwise geographical proximity threshold ($g_{prox}$). We tested a series of distances in sequential increments equal to our grid cell size used in calculation of UD. It is important to ensure that the $g_{prox}$ value accurately groups individuals from appropriate social environments (e.g. within a biologically meaningful distance). Therefore, we ensured that the $g_{prox}$ distances that were tested were contained within the smallest observed centroid to contour distance. This ensures that the null’s $g_{prox}$ value, though greater than the proximity used in the real data, is still biologically possible. The $g_{prox}$ value which produced a null model that best matched the observed average HWI was then selected for use in the final null model.

3.1.4.1. Dragons

One hundred and eleven individuals (of 330) had at least 25 sightings and were therefore included in analyses. The null model randomized positions for 64 individuals in each of the 114 random sampling periods. This maintained the observed average number of individuals sighted per sampling period, and
The number of sampling periods in the data. The optimal null model for dragons used a \( g_{prox} \) value of five metres for the full home range, and four metres for the core home range (table 1).

3.1.4.2. Dolphins

Seventy-six individuals (of 738) had at least 45 sightings and were therefore included in analyses. We simulated positions for individuals in each of the 809 sampling period days accounting for both temporal availability and survey effort. The optimal null model for the dolphins used a \( g_{prox} \) value of 1000 m for the full home range and 1100 m for the core home range (table 1).

3.1.5. Post hoc selection of individuals

To ensure that we accurately measured the sociality of pairs, we investigated how sighting frequency affected the stability of classifications (i.e. preference—random—avoidance). To do this, we repeated analyses with increased increments of randomly selected sightings per individual. Using these restricted datasets, we generated 100 simulations per increment and estimated pairwise \( p \) values for each pair. We then compared correlations of classifications generated from these different numbers of sightings with the full dataset to determine the minimum number of sightings needed to obtain reliable pairwise classifications (table 2).

3.1.5.1. Dragons

Correlations of classifications generated with different numbers of sightings reached 0.9 at 20 sightings (table 2). However, the rate of type I errors (e.g. false avoidances) dropped at 30 sightings, indicating that at 30 sightings, we have reliably estimated pairwise sociality while also reducing any error rate (table 3).

3.1.5.2. Dolphins

Correlations of classification reached 0.89 at 70 sightings, and correlations did not increase significantly with more than 70 sightings (table 2). Interestingly, error rates were not sightings dependent for dolphins (table 3). This indicated that using 70 sightings produced reliable estimates of pairwise sociality.

Having optimized the null model for each species (table 1), we generated 1000 optimized random datasets for both the full dataset, and a dataset restricted to the core home range (50% UD). We
resulting in 4703 dyads. We found four cases of pairwise avoidance when using data from the full dataset. A total of 99 individuals had at least 30 sightings and were therefore included in the final analyses, then compared our random pairwise association values to those calculated from the observed data. Relationships were classified as ‘avoidance’ if they fell below the 95% distribution of random values, and ‘preference’ if they fell above it.

4. Results

4.1. Dragons

A total of 99 individuals had at least 30 sightings and were therefore included in the final analyses, resulting in 4703 dyads. We found four cases of pairwise avoidance when using data from the full dataset.
Of these, three were male–female and the remaining were male–male pairs. When restricting analyses to the 50% core home range, we found 34 cases of pairwise avoidance. Of these, 47% (n = 16) were male–female, 23% (n = 7) were male–male and 30% (n = 11) were female–female pairs. In both cases, more preferences were found than avoidances (full = 199, core = 76). Similar to avoidances, the majority of preferences were male–female pairs at both the full and at the core home range.

### 4.2. Dolphins

A total of 48 individuals had at least 70 sightings and were included in the analyses, resulting in a total of 1073 pairs. We found 332 cases of pairwise avoidance in the full dolphin dataset. Of these, 61% (n = 202) were male–female, 13% (n = 45) were male–male and 26% (n = 85) were female–female dyads. When data were restricted to the core home range, we found 247 cases of pairwise avoidance. Similarly to the full range, the majority were male–female dyads (male–female: 63%, n = 156; male–male: 17%, n = 41; female–female: 20%, n = 50). In both cases, there were fewer preferences than avoidances: full = 216, core = 181.

For both dolphins and dragons, preferences and avoidances were found to occur within similar levels of shared space (figure 3). However, the levels of home range overlap that individuals that avoided each other shared were in the ranges of 10–90% (dolphins) and 5–50% (dragons) (figure 3). This indicates that some pairwise avoidances may be stronger than others.

### 5. Discussion

Despite being an integral part of an animal’s social behaviour [6–8], long-term social avoidance has received little empirical attention. In this paper, we build on the framework initially presented by Carter et al. [25], addressing and implementing critical features of the data into the analysis of animals’ social behaviour. The results, using data from two longitudinal studies, illustrate the utility of simulation-based methods, such as the method presented here, for isolating social avoidances.

The framework implemented in our model aims to predict associations assuming that animals move randomly within their home range. This has the advantage of accounting for the effect that space use has on pairwise associations [26,44]. Other methods for analysing social structure have also begun to suggest ways of accounting for the effect of space use. For example, Whitehead & James [29] suggested using pairwise spatial overlap measures (e.g. VI) as a predictor of associations when creating generalized affiliation indices (GAs). Avoidances can then be isolated as instances where the GAI is in the lower fifth percentile (e.g. lower than expected given degree of spatial overlap). However, the advantage of our null model is that the spatial information used is of higher resolution, resulting in more robust predictions of random spatial associations and therefore providing greater precision in...
identifying pairwise avoidances. More specifically, when assigning avoidances based on the GAI, pairs of individuals with identical VI overlap and an HWI of zero would both be assigned as an avoidance. We, however, found that when identifying avoidances using the simulation model, dyads with similar VI and an HWI of, for example, zero were not all considered as avoidances. This is because the size of the shared area is taken into account, and, as such, pairs with the same VI and an HWI of zero may not both be assigned as avoidances.

In agreement with Best et al. [35], we found that the most reliable way to optimize the null model was to alter the grouping distance proxy used within the model to ensure the null model matched the observed level of sociability. In dolphins, this distance was slightly larger at the core range than at the full range. This may be because there are fewer social associations within dolphins’ core ranges in comparison to their full range; thus, to obtain comparable levels of associations in the null model, the distance must be increased. Alternatively, it may be that there is less overlap between dolphins’ core home ranges. This would also result in a greater distance proxy required to group individuals in the null model. In both species, however, altering this proxy resulted in a grouping distance larger than is used in the observed data. This indicates that, as expected, individuals do not move randomly. For example, the distribution of resources influences how individuals move within their home range. Similarly, an individual’s movement may also be influenced by the distribution of conspecifics; in particular, individuals’ spatial distribution may not only influence social interactions, but may also, in part, be determined by them. Disentangling whether the formation of social relationships is caused by overlapping spatial distributions, or overlapping distributions are caused by social relationships would be extremely challenging. Some might argue that social relationships should therefore be assessed without controlling for spatial activity (e.g. using the Manly–Bejder permutations implemented in the SOCPROG software [30,39]). However, in dolphins, for instance, social preferences have been shown to exist despite very little spatial overlap [59,60]. Moreover, the confounded effects of spatial distribution and social relationships would not affect the identification of social avoidances, given that these are identified as pairs of individuals which do not associate despite sharing significant portions of their home range.

In addition to considerations suggested by Best et al. [35], we identified other key parameters, not previously detailed by these authors, paramount to the correct use of the model. These included, for instance, maintaining the sample size within each sampling period, which is an integral feature of the Manly–Bejder [39] well-established permutation technique. Another key parameter identified was accounting for temporal overlap of individuals, which has also been discussed conceptually elsewhere [29], but not yet fully implemented (but see [52]). Accounting for each of the parameters detailed within this framework is important because slight violations will result in spurious results. Therefore, the strength of the framework we present here lies in both the unification, and extension of, principles independently used within established methodologies.

Here, we show that, as theory suggests (e.g. [5,7]), individuals of both species avoid and preferentially associate within the same space. This indicates that, similar to Eastern chipmunks [24], non-random social avoidances occur in both space and time (i.e. they share space but not at the same time). Interestingly, we found that avoidances in dragons primarily existed within their core home range. Dragons are territorial animals [42,47], and so it may be that the core home range may better represent the individuals’ territories, and therefore their primary social environment. Further investigation is needed to explore such ideas. In contrast, bottlenose dolphins live in an open social network (where affiliative interactions extend beyond the individuals’ social group to members of other groups) [70] with high levels of home range overlap, suggesting that avoidances will occur throughout individuals’ full home ranges.

We present the first evidence, to our knowledge, for the presence of long-term social avoidances measured across multiple species using the same framework. The causality of the social avoidances identified here is probably diverse. For instance, it may be that some avoidances are caused by the need to avoid conflict (e.g. avoidance of large or aggressive individuals). Alternatively, some avoidances may be driven by groups of individuals (e.g. ages of sexes) using space and/or resources at different times. Even so, the study of avoidance has hitherto been unexplored, and in using this framework to identify social avoidances, future research can focus on exploring the biology, and causality, of the avoidances found here. In addition, studying avoidance behaviour means to approach the study of social behaviour holistically, inclusive of both components of an individual’s sociality (e.g. attraction/avoidance). A few methodologies (e.g. [30]) have suggested such an approach, yet this is rarely implemented in full, often without consideration of space use, which results in a somewhat skewed view of animal social...
behaviour. While at this stage we cannot elucidate either the directionality (i.e. who avoids whom) or the biological significance of the social avoidances we have identified, the framework provided can be used in addressing this critical gap in our understanding of animal social behaviour. We hope that this paper stimulates interest in a shift in the approach to studying social behaviour through inclusion of both avoidance and affiliative social associations.

Ethics. Both projects were carried out with approval from the University of the Sunshine Coast’s animal ethics committee (dragons: AN/ A/14/87; dolphins: AN/S/15/35). The dolphin project was also carried out with ethics approval from Georgetown University (IACUC-13-069, 07-041, 10-023), and permission from Department of Parks and Wildlife, Western Australia (SF-009876, SF-010347, SF-008076, SF009311, SF007457).

Data accessibility. Data and R code are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.tn36j [74]. Data and R code for the dolphin project can also be found at https://github.com/vjf2/digidolph.

Authors’ contributions. K.S. and C.H.F. conceived and coordinated the study. All authors contributed to data collection. K.S., A.L. and V.F. analysed data and created the framework, with input from C.H.F. and J.M. K.S. wrote the manuscript with input from all authors. All authors gave their final approval for publication.

Competing interests. We declare we have no competing interests.

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