ARE WOBEGONGS SOCIAL? SOCIAL NETWORKS OF THE SPOTTED WOBEGONG SHARK (*ORECTOLOBUS MACULATUS*) IN A SMALL MARINE PROTECTED AREA

NICOLETTE C. ARMANSIN

41721764
Marine Predator Research Group
Macquarie University, Sydney 2109
nicolette.armansin@students.mq.edu.au

A thesis submitted in partial fulfilment of the requirements for graduation with

MASTER OF RESEARCH

in the

DEPARTMENT OF BIOLOGICAL SCIENCES
FACULTY OF SCIENCE AND ENGINEERING

10 OCTOBER 2014 (RESUBMITTED 24 DECEMBER 2014)
WORD COUNT: 10 743 (including in-text references)

Supervisor: PROFESSOR ROBERT HARCOURT
Co-supervisor: DR KATHRYN A. LEE

Key Words: sociality, association pattern, social network analysis, acoustic telemetry, VPS, spotted wobbegong, *Orectolobus maculatus*
This thesis is written in the form of a journal article for *Animal Behaviour*.

DECLARATION

I wish to acknowledge the following assistance with the research detailed in this report:

Fieldwork was conducted as part of the PhD requirements of Dr Kathryn Lee. Ethics approval was granted as part of that project. No fieldwork was conducted during the Master of Research component.

Dr Kathryn Lee provided assistance with the R script for kernel density distributions and extending R scripts for utilization distribution overlap indices.

Dr Ian Jonsen assisted with R scripts for data compilation and kernel density analysis.

All other research described in this report is my own original work.

Nicolette C Armansin
10 October 2014
PERSONAL ACKNOWLEDGEMENTS

I wish to thank my supervisors Professor Rob Harcourt and Dr Kate Lee for their bravery in taking me on as a candidate, and for their commitment to the research, gentle (mostly!) guidance and friendship. It has been a pleasure and I hope to work with them both again.

My parents, Philippe and Inge Armansin, have provided extraordinary support over the years, but particularly in these last eight months. I could not have done this without them. I thank my brother, Marc Armansin, for his endless patience in sharing his insight and uncanny ability to produce entertaining and useful analogies. It has helped me wade through some of the more complex analyses in this study.

A big thank you to all my friends for tolerating my regular absences. In particular I would like to thank Isobel Lindley, Sophie Hammond and Amber Colhoun for helping me keep things in perspective and for making me feel like I can achieve anything.

I must acknowledge the expertise and dedication of the Marine Predator Research Group – Dr Ian Jonsen, Gemma Carroll, Vanessa Pirotta, Marcus Salton, Lisa-Marie Harrison, Marine Desprez, Dustin O’Hara, Monique Ladds, Dr Yuna Kim, Dr K-lynn Smith, Paolo Momigliano, Dr Alex Schnell and Dr Ben Pitcher. Their eagerness to share knowledge has been inspiring and I can only hope that I can reciprocate at some point, starting with a round of drinks tonight.

Finally, I could not have done this without the overwhelming encouragement and optimism from my partner, Brett Trollope. Despite the difficulty of being apart for eight months, he always supported my decision to study again. I am eternally grateful for his self-sacrifice and endless patience. I have made it through this year because I know that when I get home, Brett, Pepper and Brad will be there smiling.
“There are some four million different kinds of animals and plants in the world. Four million solutions to the problems of staying alive.”

David Attenborough, Life on Earth (1979)
ABSTRACT

Many shark species form groups, however the drivers of this behaviour are not well understood. Previously it was thought that aggregations may be a function of resource availability or phenological behaviours, but recent studies have suggested that sharks display preferences in their associations with conspecifics and that complex social networks may underpin their movement patterns, demographic distribution and fitness. This study used a network approach to investigate patterns of sociality of a demersal predator, the spotted wobbegong shark, in a small marine reserve. Spatial data obtained from fine-scale passive acoustic telemetry were used to show that some sharks display preferences in their associations, many of which persisted after sharks returned to the reserve from their seasonal migration. These relationships were not exclusive, with some sharks forming associations with multiple individuals. Patterns were evident at the dyadic level, but limited evidence was found of a stable community or network structure. It appears that the species is not primarily gregarious but that benefits may be gained by maintaining a level of familiarity with a limited number of conspecifics. The composition of groups in terms of individual attributes (sex, size and familiarity) suggested that non-social aggregative behaviour was not a strong influence on association patterns. Site fidelity and home range overlap were also found to only marginally influence these associations. This suggests that the observed relationships can be explained, at least in part, by genuine social affiliation and that anthropogenic influences on the population may have more complex impacts than previously thought.
# Table of Contents

1 INTRODUCTION .................................................................................................................. 1

2 METHODS .............................................................................................................................. 6

2.1 OVERVIEW ......................................................................................................................... 6

  2.1.1 Study area ....................................................................................................................... 6

  2.1.2 Data Collection ............................................................................................................... 6

  2.1.3 Ethics ............................................................................................................................... 8

2.2 WHAT ASSOCIATION PATTERNS ARE EVIDENT, IF ANY? ........................................... 9

  2.2.1 Defining Associations ................................................................................................... 9

  2.2.2 Association Calculations ............................................................................................... 12

2.3 ARE THESE PREFERRED ASSOCIATIONS OR RANDOM AGGREGATIONS? .............. 14

  2.3.1 Preferred Associations ................................................................................................ 14

  2.3.2 Assortative Mixing ....................................................................................................... 15

  2.3.3 Ranging Patterns ......................................................................................................... 16

2.4 ARE THESE ASSOCIATIONS PERSISTENT? .................................................................. 17

  2.4.1 Lagged Association Rates ............................................................................................ 17

2.5 HOW CAN THE EMERGING SOCIAL ORGANISATION BE CHARACTERISED? ........... 18

3 RESULTS ............................................................................................................................... 20

  3.1.1 Defining Associations ................................................................................................ 22

  3.1.2 Patterns in Associations .............................................................................................. 23

3.2 ARE THESE PREFERRED ASSOCIATIONS OR RANDOM AGGREGATIONS? ............ 26

  3.2.1 Preferred Associations ................................................................................................ 26

  3.2.2 Assortative Mixing ....................................................................................................... 26

  3.2.3 Space Use Patterns ...................................................................................................... 28

3.3 ARE THESE ASSOCIATIONS PERSISTENT? .................................................................... 31

  3.3.1 Lagged Association Rates ........................................................................................... 31
3.4 HOW CAN THE EMERGENT SOCIAL ORGANISATION BE CHARACTERISED?........ 33

4 DISCUSSION............................................................................................................. 34

5 CONCLUSIONS .................................................................................................... 41

6 SUPPLEMENTARY MATERIAL.............................................................................. 42

6.1 Incorporating positioning error into data screening .......................................... 42

6.2 Home Range Estimates from Kernel Density Analysis....................................... 44

6.3 Animal Behaviour Journal Guide for Authors.................................................. 45

7 REFERENCES .......................................................................................................... 62
List of Figures and Tables

Figure 1: Map of passive acoustic telemetry array in Cabbage Tree Bay Marine Reserve (33°47′57″S, 151°17′44″E) from October 2009 to December 2010 ................................................................. 8

Figure 2: Acoustically tagged Orectolobus maculatus in Cabbage Tree Bay Aquatic Reserve from October 2009 to December 2010 .............................. 21

Figure 3: Sensitivity analysis plot of association strengths (HWI; y-axis) as a function of increasing sampling period time (x-axis), for twelve dyads... 22

Figure 4: Sociogram depicting the network of all associating dyads (HWI >0)......24

Figure 5: Number of associations per individual and the percentage of time spent together (HWI x 100) as a function of time.................................................. 25

Figure 6: Comparison of means of association index (HWI) with spatial overlap index (UDO1) for dyads with HWI >= 0.1................................................. 29

Figure 7: 95% and 50% kernel densities for significantly preferred dyads. .......... 29

Figure 8: Examples of daily plots of locations (projected x, y coordinates, in metres) for W344 (red) and W345 (blue) .............................................................. 30

Figure 9: Standardised lagged association rate.................................................. 32

Table 1: Power analysis across four candidate sampling periods.................... 23

Table 2: Focal dyads (preferred and avoided) from two-sided Monte Carlo permutation tests for dyadic significance......................................................... 27

Table 3: Community Division, by modularity, Q = 0.332................................. 28

Table 4: Mean network measures for all individuals (based on HWIs) and mean measures for 5 000 random networks (permuted within samples). ...... 33
1 INTRODUCTION

Sociality exists on a spectrum. The position of a species along this spectrum reflects an ongoing sequence of tradeoffs that balance the benefits and risks of associating with others (Avilés, 1999, Wallace and Bennett, 1998). Foraging success for example can be enhanced by the formation of groups (Clark and Dukas, 1994) while increasing group size may interfere with foraging efficiency and promote intraspecific competition (Pavlov and Kasumyan, 2000). Likewise, vigilance against predators may be enhanced in large groups, and the risk of predation diluted, but may be amplified as the group becomes more conspicuous (Krause and Ruxton, 2002). Social interactions may provide important information (Conradt and Roper, 2003, Lusseau, 2003) but can increase exposure to parasitism and disease (Leu et al., 2010b, Newman, 2003). Extrinsic influences, such as resource spikes (Johnson et al., 2002), as well as intrinsic biological mechanisms (Krause and Ruxton, 2002) can generate aggregations, often comprised of random members. For some species however mutual benefits are derived from active partner preferences and non-random, social groups form as a result (Croft et al., 2006, Durrell et al., 2004, Gero et al., 2005).

The implications of this are complex. Recurring decisions to cooperate, avoid or antagonise become adaptive over time and feedback loops emerge as individuals influence group dynamics, which in turn impact on the strategies of individuals (J. Krause et al., 2009, Wey et al., 2013). The compromises made can have significant implications for reproductive fitness (Frère et al., 2010, McGuire et al., 2002), demographic and genetic distribution (Lusseau et al., 2006, Storz, 1999) and ultimately the survival of individuals, populations and a species overall. Thus understanding the patterns of these interactions, in the context of a species’ ecological niche, can shed light on the evolution of social behaviour and is critical to predicting the response of animals to the world around them (Ansmann et al., 2012, Dungan et al., 2012).
Aggregation behaviour has been observed in a variety of shark species (Ebert, 1991, Klimley and Nelson, 1984, Scott et al., 1997, Sims et al., 2000, Springer, 1967) however the composition of these groups is not well understood. Both phenotypically assorted and mixed groups have been reported (Mucientes et al., 2009, Wearmouth and Sims, 2008). Many elasmobranch aggregation studies have suggested an underlying social basis for group formation but have relied on anecdotal and descriptive methods to report this (Jacoby et al., 2012c). Recently, research into shark behaviour has incorporated quantitative methods that have identified persistent individual partner preferences and extensive social networks (Guttridge et al., 2009a, Guttridge et al., 2011, Jacoby et al., 2012a, Mourier et al., 2012). The capacity of sharks to be social has been suggested by the presence of complex behaviours, such as dynamic dominance hierarchies (Allee and Dickinson, 1954, Myrberg Jr. and Gruber, 1974, Klimley and Nelson, 1981) and may be supported by a brain-mass to body-mass ratio that is comparable to mammals (Northcutt, 1977). Studies have emerged that highlight the learning capabilities of sharks (Guttridge et al., 2009b, Guttridge et al., 2013) and the presence of personalities (Jacoby et al., 2014). Together these studies suggest that sociality may be an important component of shark behaviour. Given that shark abundance has declined sharply in recent years due to fisheries pressures (Ferretti et al., 2010), investigating the social element of aggregations may refine our understanding of the more subtle impacts of anthropogenic activities on the longevity of shark populations.

The study of sociality is inherently complex, involving relational data and many sources of uncertainty. However, advances in analytical techniques, coupled with developments in movement tracking technologies, have resulted in increasing flexibility and robustness in the exploration of social behaviour of elasmobranchs (reviewed in Wilson et al., 2013). At the core of network theory is the concept that individuals differ in their experience of, and contribution to, the wider population and that indirect connections are important elements of social dynamics (Krause et al., 2007). Social network analysis can capture this level of complexity, at the individual, dyadic, community and network level by using a powerful composite of
tailored quantitative tools (Croft et al., 2008, J. Krause et al., 2009, Kurvers et al., 2014, Lusseau and Newman, 2004, Sih et al., 2009, Wey et al., 2008). The use of network analysis is enhanced by the fine-scale spatio-temporal data available with recent developments in passive acoustic telemetry (Jacoby et al., 2012c). These technologies, however, do not solve the full gamut of challenges faced by researchers (Butts, 2009, Guttridge et al., 2010). Results from analyses are reliant on biologically meaningful inputs and may involve testing the effects of varying parameters to adequately capture the behaviours of selected species (Haddadi et al., 2011).

The spotted wobbegong shark (*Orectolobus maculatus*) is endemic to Australian waters. The species was previously targeted in commercial fisheries that led to conservation concerns in New South Wales (NSW), where they are currently listed as a vulnerable species and several management strategies have been employed to address this. These include the establishment of stringent catch limits and the trial of a captive breeding program to restock local populations (Lee, 2014). Like other demersal sharks (Jacoby et al., 2012a), the spotted wobbegong is relatively sedentary and is primarily active at night when it forages using ambush strategies (Huveneers et al., 2006). Wobbegongs exhibit *K*-selected life history characteristics (Last and Stevens, 2009), including slow growth (Huveneers et al., 2013) and a triennial reproductive cycle (Huveneers et al., 2007) although their precise life span is unknown. Wobbegongs display a high level of short (days) to medium-term (months) site fidelity, and have been observed returning to summer breeding grounds after seasonal migrations (Carraro and Gladstone, 2006, Huveneers et al., 2006; Lee et al., 2014). Although generally seen alone, they are frequently observed in small aggregations (Huveneers et al. 2006), the composition and timing of which have not been investigated in detail. This grouping behaviour, along with their life-history characteristics, may leave them inherently vulnerable to exploitation (Hoenig and Gruber, 1990). In light of their conservation status, and the growing recognition of the fitness implications of sociality (Archie et al., 2014; Kurvers et al., 2014), the interaction patterns of this species is both an interesting and important area for research.
The extent of the current literature points to a pressing need to both understand the influence of sociality in shark populations and apply robust analytical tools that account for the various sources of uncertainty inherent in biological systems. By investigating the social strategies of this poorly known shark, and bringing together contemporary quantitative analytical techniques and advanced tracking techniques, this study aims to address these identified needs. Specifically, this study aims to investigate whether wobbegongs are social by addressing four questions:

1) What association patterns are evident, if any? For most species, interactions between individuals occur at some point in their life history stages (Leu et al., 2010a). The relationships that result from these interactions are a key characteristic of the sociality of a species, as articulated in the conceptual framework developed by Hinde (1976). In the absence of direct observations of the study population, this analysis infers associations based on spatio-temporal proximity as a proxy for interactions (Whitehead and Dufault, 1999).

2) Are these preferred (social) associations or random (non-social) aggregations? Measuring these associations can be confounded by processes that concurrently influence individual grouping behaviour, such as phenological synchrony, ranging preferences and resource availability (Wey et al., 2008). Therefore, determining the extent to which these interactions occur by chance, or are indeed non-random, is key in establishing sociality.

3) Are these patterns temporally persistent? Association patterns are likely to shift in response to ontogenetic and demographic changes (Armitage, 1981, Patriquin et al., 2010, Schiml et al., 1996), fluctuating resources (Carr and Macdonald, 1986, Jarvis et al., 1998) and anthropogenic influences (Banks et al., 2007). As such, accounting for temporal dynamics is essential for an adequately refined understanding of a social system (Hinde, 1976, Hobson et al., 2013).
4) How can the emergent social organisation be characterised? By examining the associations that exist in this wobbegong population, a picture of the social organisation can be abstracted (Hinde, 1976). A deeper understanding of this may assist in effective management of the species as well as shed light on the evolution of sociality.
2 METHODS

2.1 OVERVIEW

2.1.1 Study area
This study was conducted in Cabbage Tree Bay Aquatic Reserve (CTBAR, 33°47’57”S, 151°17’44”E), located in Sydney, Australia. CTBAR is a small (~0.2km²) “no-take” marine reserve that was declared a marine protected area in 2002 in recognition of its high species diversity. The reserve comprises a heterogeneous mosaic of habitats, typical of subtidal inshore rocky reefs of temperate, south-eastern Australia (Underwood et al., 1991). These include barren boulders, areas of dense common kelp (Ecklonia radiata) and rocky reefs with high volumes of macroalgae and sponges. Two distinct reefs are separated by 120 metres of sand. The wobbegong population is estimated at up to 150 sharks during the summer months (Lee et al., 2014) and primarily occupies areas of high crevice volume (per. comms, KA Lee).

2.1.2 Data Collection
The study population was monitored from October 2009 to December 2010. Twenty three wild and captive-bred wobbegongs were tagged with V13-1L acoustic transmitters (nominal interval of 150-250 seconds), which produce a uniquely identifiable transmission at 69 KHz. Wild sharks were randomly captured for tagging by two SCUBA divers using hand-held nets (diameter 1 m; mesh size 3 cm). Anaesthesia was induced aboard the research vessel by placing the sharks in a 200 litre tub containing an oxygen-enriched solution of 30 ppm eugenol (AQUI-S, AQUI-S NZ, Wellington, New Zealand). After full anaesthesia was induced, the V13-1L acoustic transmitter (battery life ~ 1,623 days) was inserted into the coelemic cavity using standard surgery practice (see Lee et al., 2014). A uniquely numbered external identification tag was also placed in the musculature below the first dorsal fin (Lee et al., 2014). Captive-bred sharks were tagged before being released into CTBAR. Individual attributes were recorded for all sharks, including sex, determined by the presence of claspers (Last and Stevens, 2009) and size, which was recorded as total
length and measured using a tape measure. Sharks with a total length of less than 115 cm were classed as juveniles (Huveneers et al., 2007).

Shark locations were gathered using the VR2W Positioning System (VPS), a passive acoustic telemetry system that uses ultrasonic signalling to calculate near-continuous, fine-scale animal locations. This level of spatio-temporal detail allows for behavioural studies such as social analysis. The receiver array was designed to sample a representative proportion of each habitat available within the reserve and to ensure detection coverage in areas with high and low densities of wobbegongs. It comprised eight fixed, autonomous, omni-directional receivers (VR2W-69KHz; Vemco Ltd, Nova Scotia, Canada), positioned in an overlapping arrangement (Figure 1). Receivers were deployed at 6 - 12 m depths, on 1.35 m long steel poles set in concrete filled tyres, in areas with sandy substrate. Local testing was conducted to determine the effective detection range of the receivers (Heupel et al., 2006), which was estimated at a minimum of 200 m in poor conditions (Lee et al., 2014). Additionally, eight V16-4L synchronization tags (nominal transmission interval of 275 seconds) were deployed to correct for clock drift between receivers and to assess the efficacy of the positioning algorithm. The VPS system uses hyperbolic positioning to calculate a location, using the time difference of arrival (TDOA) of transmissions between three or more receivers. The synchronization tags ensure that the difference in clock drift between the receivers can be calculated so that the TDOA can be measured accurately. Downloaded data was post-processed by Vemco using proprietary software. The data returned includes the latitude and longitude of each location, projected Cartesian coordinates derived from these (x,y; in metres) and an estimate of the positional error of each location. This error, known as the Horizontal Position Error (HPE), was used to filter the locations for positional accuracy, the process for which is detailed Section 6.1.

In addition to variation in positional accuracy, overall detectability will vary depending on individual habitat preferences, proximity to receivers and presence in the array, and this may result in an uneven distribution of locations across all sharks. Data truncation based on a detection threshold is common in social studies to
increase accuracy and reduce bias from sampling methods (Baird and Whitehead, 2000, Bejder et al., 1998), with a lower threshold often determined using the average frequency and spread of sightings (Baird and Whitehead, 2000, Chilvers and Corkeron, 2002, Lusseau et al., 2006, Mourier et al., 2012, Wisniewski et al., 2009). In this analysis, sharks with a number of locations below the lower quartile (100 locations over the entire study period) were removed, to strike a balance between maximising precision and preserving data with a low sample size (Wasserman, 1994).

### 2.1.3 Ethics

Data collection protocols involving the handling of live animals were approved by the NSW Fisheries Animal Care and Ethics Committee (ACEC ref: 07/08) and NSW Scientific Collection permit (P08/0039).

![Figure 1: Map of the passive acoustic telemetry array in Cabbage Tree Bay Marine Reserve (33°47′57″S, 151°17′44″E) from October 2009 to December 2010. Yellow dots show the position of eight VR2W receivers and white squares represent synchronisation tags.](image-url)
2.2 WHAT ASSOCIATION PATTERNS ARE EVIDENT, IF ANY?

Unless otherwise indicated, all social analyses were carried out using SOCPROG version 2.5 (uncompiled; Whitehead, 2009) run in a Matlab (version 8.2.0.29) computing environment (The Mathwork Inc., Natick, MS, U.S.A).

2.2.1 Defining Associations

To infer social associations from spatio-temporal proximity with any confidence, three parameters require careful consideration: association distance, association time and sampling periods.

The maximum distance within which a species is likely to associate can vary significantly depending on the behaviour and sensory range of the species in question (Bode et al., 2011, Parsons et al., 2009). There is a clear paucity of research on the behaviour of spotted wobbegongs and so determining a biologically relevant distance was challenging. This study considered a combined value of one body length (defined by the maximum total length of observed sharks in this study group) and the median error rate (HPEm; see Section 6.1) to be within the potential perceptual range of wobbegongs, and therefore enough for a shark to impact on another and potentially share information socially (Bradbury and Vehrencamp, 1998).

A maximum time interval in which an association may occur must also be defined. Average activity bouts were investigated to determine the periods in which wobbegongs can be expected to change position and mix with other conspecifics. To do this, the displacement between consecutive locations per shark was calculated. Any intervals between locations of more than 72 hours were removed, as previous research has shown these may represent excursions out of the array (Huveneers et al., 2006). The median speed of shark movements was derived from the synchronisation tag locations, which therefore represented measurement error from
the acoustic system. This speed was used to delineate “inactive” or “active” states, and unique activity bouts were identified for both states. Inactive bouts were defined as intervals between consecutive locations in which the median speed was less than three metres per hour, and where the speed was greater than or equal to three metres per hour, the bout was categorised as active. The sum of the 90th percentile values for active and inactive bouts was used as the maximum interval in which an association could occur. Movement analyses were run in R Studio version 0.98.1028 (RStudio Inc.) and Excel 2013 Data Analysis extension.

Calculating association indices requires sampling periods to be set. Previous studies have determined these based on the behaviour of the species, natural cycles evident in the dataset or data collection methods and rates (Whitehead, 2008a). An inaccurate sampling period can propagate throughout the analysis and inferences drawn from these analyses can contain significant error. For example, sampling periods set too short can result in little power when testing for preferred associations, and result in false significance being assigned to associations if set too large (Whitehead, 2009).

Due to the near-continuous nature of VPS data, no clear sampling period was evident. Therefore four candidate sampling periods were tested for accuracy and selected as follows:

**Sensitivity Analysis**

A sensitivity analysis was conducted to test the effects of variation in sampling period on resulting associations. Twelve dyads (approximately 10 percent of the total potential dyads from the filtered dataset) that displayed relatively strong associations were selected, based on a 24 hour sampling period. For each of these, an association index was calculated using multiple sampling periods, whilst maintaining all other parameters constant. These were plotted and based on the observed projections a sampling period of 10 days was selected for further testing (see Section 3.1.1 for details on how this was determined).
**Demographic effects**

Consideration was given to a sampling period that may exclude the impacts of demographic effects such as emigration and immigration (Whitehead and Dufault, 1999). Previous acoustic telemetry research has indicated that a sympatric species of wobbegongs, *O. halei*, make excursions out of the array at around three days (Huveneers et al., 2006), and therefore a three day sampling period was tested.

**Diel periodicity**

Previous studies have indicated that wobbegongs show a 24 hour periodicity in their movements (Huveneers et al., 2006). This was considered as a sampling period and is commonly used in analyses involving surveying methods for data collection (Stehfast et al., 2013)

**Nyquist Rate**

Sampling theorem suggests that in order to gain sufficient information about a signal, the minimum rate at which to sample it is twice the highest frequency of that signal (Nyquist, 1924; Platt & Denman, 1975). The 24 hour cycle observed by Huveneers et al. (2006) was calculated using a version of the Fourier transformation and was considered an adequate proxy for an association cycle. A sampling period of 12 hours was therefore also incorporated.

Association matrices were generated for each of the four candidate sampling periods (10 days, three days, 24 hours and 12 hours), using the half-weight association index outlined in Section 2.2.2. These were tested for correlation using Mantel tests (Schnell et al. 1985), to draw out whether large differences were evident. If these differences were notable, it would indicate that the selection of the sampling period required a more detailed analysis. As a final check, the correlation coefficient (*r*) between the true and calculated association indices was calculated for each of the sampling periods. This indicated the power of the analysis to detect the actual social system (values near 1 indicate a good representation) and was determined *post hoc* using the likelihood approximation as outlined by Whitehead (2008a). Based on this result, a sampling period was selected for the subsequent social
analyses and a temporal buffer was coded into the primary dataset to ensure independence between sampling periods (an assumption underlying areas of further analyses).

2.2.2 Association Calculations

Having defined the parameters for an association, the strength of association of pairs of sharks was determined using the Half-Weight Index (HWI; Cairns and Schwager, 1987). The HWI provides a value for each dyad on a scale from 0 (never observed together) to 1 (always observed together; Bejder et al., 1998). The HWI is calculated as:

\[
\text{HWI} = \frac{x}{x + \left(\frac{y_{ab} + y_{a} + y_{b}}{2}\right)}
\]

where \(x\) is the number of sampling periods in which both sharks ‘a’ and ‘b’ were associated, \(y_{ab}\) is the number of sampling periods in which both a and b were detected but not associated, \(y_{a}\) and \(y_{b}\) are the number of sampling periods in which only a and b respectively are identified (Ginsberg and Young, 1992). The HWI is an appropriate measure for this study relative to other indices, as it accounts for some biases in sampling technique (Whitehead, 2008a). It is commonly used in free-ranging marine species studies (Mourier et al., 2012; Foster et al., 2012) and may therefore facilitate comparisons across studies. It may however underestimate the level of association derived from acoustic telemetry locations (Whitehead 2008a). In light of this, association matrices were also generated using a less complex index, the Simple Ratio Index (Cairns and Schwager, 1987; Ginsberg and Young, 1992). The Simple Ratio Index is defined as (using \(x\), \(y_{ab}\), \(y_{a}\) and \(y_{b}\) described above):

\[
\text{SRI} = \frac{x}{x + y_{ab} + y_{a} + y_{b}}
\]
Whitehead (2008a) discusses the importance of index selection for cross-population analysis and states that for within-population studies, such as this, index selection is not critical. To test this, association matrices were generated using both indexes and tested for correlation using Mantel tests in SOCPROG.

The HWI for each dyad were compiled into symmetric, weighted, and undirected matrices of association, which formed the basis of the social analysis. These were derived for the overall study period, and for each month to determine how the dynamics of the associations varied over the study period. Standard errors were calculated using bootstrapping methods in SOCPROG. Mean and maximum association strengths were calculated, as well as the mean number of associations per dyad and individual. Dyads were compiled into a network sociogram in Netdraw (Borgatti et al., 2002) using the spring embedding algorithm. Individual sharks were depicted as nodes and the strength of association (HWI) as the weight of the edges of connected pairs. Reference to two networks is made. The first comprises only those associations with a strength greater than approximately twice the mean association index (HWI \( \geq 0.1 \); Durrell et al., 2004; Gero et al., 2005). This selection of dyads was scrutinized for assortative mixing in Section 2.3.2. The second network consists of all non-zero associations, recognizing that weak links can be potentially important network elements (Granovetter, 1983, James et al., 2009) and these associations were used as the basis for the rest of the analysis.
2.3 ARE THESE PREFERRED ASSOCIATIONS OR RANDOM AGGREGATIONS?

As discussed in Section One, observed associations may be explained by factors other than active social behaviour. Disentangling random aggregations from social affiliations requires consideration of these factors.

2.3.1 Preferred Associations

For association index values to be meaningful indicators of relationships, it is important to assess whether these are more than simply random (Bejder et al., 1998). To determine whether sharks displayed preferred companionships, permutations were conducted testing the null hypothesis that sharks associated with all other individuals with the same probability (Croft et al., 2011, Whitehead, 2008a). A modified version of Monte Carlo randomisation methods were used, originally described by Manly (1997) and Bejder et al. (1998), and further developed by Whitehead et al., (1999) to control for gregariousness, demographic effects and sampling effort. The standard deviation and the coefficient of variation of the association indices of the observed network are measured against the mean of those generated randomly, to determine whether these test statistics could have arisen by chance (Whitehead et al., 1999). A one-tailed test was used to determine whether the actual HWI was greater than 95% of the permuted means, which would indicate that non-random associations exist. As permuted matrices display only marginal variation from the original, the generated datasets are not independent (Whitehead, 2009) and biased p values can be generated with a small numbers of permutations (Whitehead, 2009, Manly, 1995). Therefore, permutations were incrementally increased from 1 000 to 10 000 (with 1 000 trials) at which point the p values stabilized (Bejder et al., 1998). Permutations were run within sampling periods, providing an indication of long-term associations (Whitehead 2008a).
2.3.2 Assortative Mixing

To assess whether wobbegongs associate due to non-social intrinsic factors, such as phenotype, life history stage and familiarity, dyadic and community composition was investigated by attributes of the individual members. For this, sharks were categorised into sex, age class and source (wild or captive-bred sharks from the same release cohort).

_Dyadic Composition_

The attributes of individuals in dyads with HWI \( \geq 0.1 \) (as identified in Section 2.2.2) were assessed. Further, highly significant dyads (those displaying strong preferentiality or avoidance) were identified using the permutation methods described in Section 2.3.1, with two-sided significance level set at 0.05. Dyads with \( p > 0.975 \) were considered to show significant preference in their association, and those with \( p < 0.025 \) were considered to actively avoid each other. The pairs showing highly preferential association were used as focal dyads in the spatial analysis in Section 2.3.3.

_Community Composition_

The presence of communities (substructures comprised of highly associated individuals) was investigated using two techniques, and the communities inspected for patterns in the attributes of members, including sex, age class and release cohort. First, an eigenvector-based modularity method (Newman, 2006) was used, which identifies statistically significant divisions in the network based on the measured HWIs. It provides an estimate of the optimal division modularity value \( (Q) \). Where \( Q \) is greater than 0.3, the generated community division is considered a valid representation of potential subgroups within the population (Newman, 2004).

An ordination of the association indices was then generated using nonmetric multidimensional scaling, which plots highly associated individuals more closely than those less associated. As this method works with iterations of arrangements based on a predetermined start point, rather than computing the optimal arrangement as
part of the process, multiple arrangements were generated with differing starting parameters. The arrangement with the lowest stress is reported here. Stress values below 0.1 are considered to indicate a representative arrangement (Morgan et al., 1976; Whitehead, 2008a).

2.3.3 Ranging Patterns

High associations, inferred from persistent spatial proximity, may be the result of passive habitat preference or site fidelity rather than genuine social affiliations (Lusseau et al., 2006, Wey et al., 2008). Animals that are in close physical proximity may be more likely to socialize and equally those that socialize are likely to have overlapping ranges (Sih et al., 2009). To separate the influence of dyadic range overlap from social associations, a correlation analysis was conducted. To determine individual home ranges, the fixed kernel density method (Worton, 1989) was used, defining the range (95% contour line) and core range (50% contour line) of individual sharks. The utilization distribution overlap index (UDOI; Fieberg and Kochanny, 2005) was calculated to estimate the monthly overlap between the ranges for significant dyads identified in Section 2.3.1. A UDOI value of zero indicates no dyadic overlap and a value of one indicates high overlap, with uniformly distributed ranges. Values greater than one suggest high range overlap with non-uniform space use. Median UDOIs for each dyad were compiled into a matrix, which was compared with the overall association matrix using Mantel Z-tests. UDOI analysis was performed in R Studio using the adehabitatHR package (Calenge, 2006) and the correlation analysis in SOCPROG 2.5 using the Multiple Measures module. Maps of home ranges were generated in ArcGIS version 10.2 (ESRI, California).
2.4 ARE THESE ASSOCIATIONS PERSISTENT?

2.4.1 Lagged Association Rates

Permutation tests indicated possible long-term (between sampling period) relationships. To further assess the stability of these relationships, the population standardised lagged association rates was determined (Whitehead, 1995) for the entire study period. The lagged association rate \( g \) estimates the average probability that previously associated dyads are found to associate after a specified time lag \( \tau \) (Whitehead, 1995). Expressed as a ratio, it is calculated by dividing observed associations repeated \( \tau \) time units apart, by the potential number of these associations, when each individual was identified (Whitehead, 2008a). To account for false absences of associations and variation in identification rates of individuals and dyads (Whitehead, 2008a), the lagged association rate was standardised (SLAR) by incorporating the number of associations recorded for each occasion (Gowans et al., 2001). The SLAR \( g'(\tau) \) was plotted against time lag \( \tau \) based on a sampling period of 10 days. The null SLAR (NSLAR) was also estimated which indicates the lagged association rate that would be expected if only random associations occurred within the population (Whitehead, 1995). A moving average of 4,000 was used to provide some level of smoothing but maintain an acceptable level of precision for both \( g'(\tau) \) (y-axis) and \( \tau \) (x-axis). Standard errors were estimated using jackknifing methods (Whitehead, 2009).

Various candidate mathematical models were fitted to the distribution of \( g'(\tau) \) to characterise the primary relationships in the population and to quantify how relationships changed over time (Whitehead et al. 1991, Whitehead, 1995). The most parsimonious model was considered the best fit, taking into account the lowest quasi-Aikake’s information criterion (QAIC) value (Whitehead, 2008a). All individuals in the filtered dataset were included in the temporal analysis to prevent a positive bias in results (Whitehead, 2008a).
2.5 HOW CAN THE EMERGING SOCIAL ORGANISATION BE CHARACTERISED?

To describe the overall structure of the association patterns identified, several metrics were calculated, including the overall social differentiation of the population and three ego-centric network metrics: strength, eigenvector centrality and clustering coefficient.

Social differentiation (or the variation in sociality within the population) was estimated by the coefficient of variation (CV) of the true association indices, using the likelihood methods as detailed by Whitehead (2008b). Values above 0.5 suggest a highly differentiated society and indicate that the association strength is not evenly distributed across the population (Edenbrow et al., 2011). Standard errors were calculated using 100 bootstrap replications and the resolution of integration for the CV of true associations set at 0.001 to balance precision with computational time.

Individual strength (s) is a network metric that measures the level of connection an individual has to others in the network and indicates general sociability and gregariousness. It is calculated as the sum of an individual’s association indices (Wey et al., 2013). High strengths indicate either strong or many associations and more persistent relationships (Dungan et al., 2012).

Eigenvector centrality values (e) are a measure of how well connected an individual may be, in terms of both number and strength of associations (Whitehead 2008a). Centrality measures provide an idea of the position of an individual in the network and hence their structural importance (Wey et al., 2013, Bonacich, 1987). It is determined from the first eigenvector of the association matrix (Newman, 2004). High values indicate that an individual’s close associates have strong associations with others (Dey et al. 2013, Bonacich, 1987, Newman, 2004).

The clustering coefficient (c) is a measure the cliquishness of an individual, or the density of relationships amongst its associates, and is calculated as the number of
ties that exist between neighbours divided by the maximum possible number of such ties (Barthelemy et al., 2005, Newman, 2003, Wey et al., 2008). Values near zero indicate a low density, near one indicate all associates are equally connected, and are not defined for isolated individuals.

An average of each of the network metrics were calculated to provide a picture of the overall network (mean: Strength = \( S \), Eigenvector Centrality = \( E \), Clustering Coefficient = \( C \)). Standard errors were estimated using bootstrap methods with 5 000 replicates (outlined in Whitehead, 2008a). To test the statistical value of these metrics (James et al., 2009), and set a baseline for comparison of the values, the same metrics were compared to those of randomized networks using the procedure described in Section 2.3.1. This process was run three times, using 5 000 permutations from sampling periods with replacement. The metrics were also calculated per month to provide a deeper insight into the dynamics of the network over the study period.
3 RESULTS

After filtering for positioning error and low numbers of locations, the study group consisted of 15 acoustically tagged sharks, which is approximately 10 per cent of the expected population during periods of peak abundance (Lee et al., 2014). A male-biased sex ratio was evident and detections between classes (sex, age class and source) varied significantly (Figure 2). The number of sharks observed in the array varied by month (range 3-13). At least two-thirds of the group was present in all months, except in the austral autumn (March – May; range: 3-5 sharks) and early winter (June; 5 sharks) of 2010. There were no months in which all 15 sharks were present concurrently.
Figure 2: Acoustically tagged Orectolobus maculatus in Cabbage Tree Bay Aquatic Reserve from October 2009 to December 2010. Sex is indicated by F (female) and M (male). The group consisted of four females (26.6%) and 11 males (73.3%). Age class shows A (adults, total length >=115 cm) and J (juvenile, total length <115 cm). The median total length was 115.9 cm (range: 60 – 148 cm). Ten (66.6%) sharks were classed as adults and five (33.3%) as juveniles. Source refers to W (wild) and C (captive). Release cohort refers to the month in which captive-bred sharks were released into the reserve. A total of seven captive-bred sharks were released in four cohorts. All wild sharks were tagged before the commencement of the study. Sampling effort is shown with the number of months sharks were located in the array, total number of locations per shark and a time series showing the monthly presence (indicated by a black box) in the array for the entire study period.
3.1 WHAT ASSOCIATION PATTERNS ARE EVIDENT, IF ANY?

3.1.1 Defining Associations

The maximum body length observed was 148 cm and the median positioning error was 280 cm (HPEm; see Section 6.1). Shark inactive bouts were approximately 14.69 hours (90th percentile) and active bouts approximately 9.98 hours (90th percentile). An association was therefore considered to occur when two sharks were within a 4 m radius within a 24 hr timeframe.

The sensitivity analysis of sampling period effects showed consistent patterns in dyadic associations, with index strength increasing rapidly between 12 hours and 10 days (Figure 3), after which the values oscillated around the same point. Thus a 10 day sampling period was included in further analysis of sampling period effects.

![Figure 3: Sensitivity analysis plot of association strengths (HWI; y-axis) as a function of increasing sampling period time (x-axis), for twelve dyads. Values increase rapidly between 12 hr and approximately 10 days after which they oscillate around a central value.](image)

All four association matrices generated for each candidate sampling period were strongly and significantly correlated (all Mantel Z-test, range: Z = 0.87995 – 0.98284, all p-values = 1.00e^{-13}, 10 000 permutations). Of these, the value that provided the highest power to represent the true social system was 10 days (Table 1). This was used as the sampling period throughout the rest of the analysis. A buffer of two days was coded into the primary dataset to ensure independence in observations between sampling periods.
Table 1: Power analysis across four candidate sampling periods

Associations defined by spatio-temporal proximity and set at 24 hours, 4 metres. The power of analysis is indicated by r and is calculated as the correlation coefficient between the true and calculated association indices. Values near one indicate a higher strength and the highest power (r value) is shown in bold.

<table>
<thead>
<tr>
<th>Candidate Sampling Period</th>
<th>Number of Sampling Periods</th>
<th>Identifications per Sampling Period</th>
<th>Power of Analysis r (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>12-hours</td>
<td>655</td>
<td>155.55</td>
<td>-0.025 (0.165)</td>
</tr>
<tr>
<td>1-day</td>
<td>354</td>
<td>287.61</td>
<td>0.403(0.021)</td>
</tr>
<tr>
<td>3-days</td>
<td>131</td>
<td>777.2</td>
<td>0.478(0.021)</td>
</tr>
<tr>
<td>10-days</td>
<td>43</td>
<td>2367.74</td>
<td><strong>0.541(0.030)</strong></td>
</tr>
</tbody>
</table>

3.1.2 Patterns in Associations

With a sampling period of 10 (out of 12) days, the number of locations was truncated to 85,129. By incorporating the two day buffer, the number of sampling periods was reduced from 43 (Table 1) to 42. Each sampling period consisted of 2026.9 (mean) identifications, and approximately one third of the sharks (mean = 5) were identified per sampling period. A high correlation was evident between the HWI and SRI association matrices (Mantel Z-test, 0.98931, p = 9.9998e⁻¹³), therefore the results of the HWI analysis only are reported.

The association analysis revealed 35 associating dyads (out of a possible 105) and a complete but sparse network emerged (Figure 4), in which all sharks were associated at least once. Individuals had on average 17.2 associations, and dyads an average of 1.23 associations. The filtered network (with edge weights of HWI >= 0.1) contained 16 edges connecting 10 nodes. The overall mean edge weight (including all dyads with HWI >= 0) was HWI = 0.06 (+/- 0.06) and 0.17 (+/- 0.17) network filtered for HWI >=0.1. The standard errors indicate a high variation in the values across individuals.
Figure 4: Sociogram depicting the network of all associating dyads (HWI > 0). Nodes indicate individual sharks and lines (weighted edges) represent the strength of the association between connected nodes. Adults are shown as inverted triangles and juveniles as circles. Wild sharks are shown in yellow and captive-bred in blue. Sex is shown in label brackets. The relative position of individuals indicates their social proximity, using the spring-embedding algorithm in Netdraw (Borgatti, 2002).
The HWI values, as well as the number of associations, fluctuated significantly depending on the time of year (Figure 5). The mean HWI was above 0.1 for most of the austral spring and summer months (when $N > 5$) and the number of associations (both per individual and dyad) remained relatively stable over the same period. Of the three sharks present in the array from March to May 2010, no associations were evident and all mean values dropped at the end of summer (February) and did not increase until mid winter (June).

Figure 5: Number of associations per individual and the percentage of time spent together (HWI x 100) as a function of time. Mean values are shown for all dyads with HWI > 0. Columns show the number of sharks present and the proportion of total locations per month.
3.2 ARE THESE PREFERRED ASSOCIATIONS OR RANDOM AGGREGATIONS?

3.2.1 Preferred Associations

Monte Carlo permutations found both the standard deviation (one-tailed, 0.12818, mean of random = 0.11552, p = 0.00000) and the coefficient of variation (one-tailed, 2.24160, mean of random = 2.02915, p = 0.0001) of the association indices of the observed network were both significantly higher than random. This test detects companionships over multiple sampling periods (not only within a sampling period) and these results indicate that some dyads maintain preferences that persist for more than a 10 day period. The proportion of non-zero elements was significantly lower than random (one-tailed, p = 0.0099) suggesting that some individuals actively avoid others.

3.2.2 Assortative Mixing

*Dyadic Composition*

No clear pattern was evident in the individual attributes of dyads. Of the 16 dyads identified with HWI >= 0.1, the majority consisted of either all-male (9) or male-female mixes (7). No all-female pairs were observed. Almost two thirds (10) of the dyads were adult pairs, with only one juvenile pair evident (a 62 cm male and 60 cm female, the smallest of each in the study group). The remaining were adult-juvenile pairs (5), although three of these involved one juvenile female associating with three different males, and two pairs were male adults with male juveniles. Fifty percent of dyads (8) were comprised of all wild sharks, two with all captive and six wild-captive mixes.

Dyadic significance tests identified three pairs with significantly high association preferences and two dyads with low preferences, indicating avoidance (Table 2). The largest shark in the study group (W262) was identified in two preferred dyads (with W263, a wild adult female and with W737, a captive male and the smallest male in the study group). Both W262 and W737 were found to avoid another wild
male adult (W345). Dyad membership was not exclusive but no clear pattern in partner choice based on identified attributes was observed.

Table 2: Focal dyads (highly significantly preferred and avoided) from two-sided Monte Carlo permutation tests for dyadic significance.

<table>
<thead>
<tr>
<th>Dyads</th>
<th>Status</th>
<th>P</th>
<th>Index</th>
<th>Composition</th>
</tr>
</thead>
<tbody>
<tr>
<td>W263 - W262</td>
<td>Preferred</td>
<td>0.9956</td>
<td>0.32</td>
<td>Wild adult female</td>
</tr>
<tr>
<td>W737 - W262</td>
<td>Preferred</td>
<td>0.9784</td>
<td>0.17</td>
<td>Wild adult male (148 cm – largest male) Captive juvenile male (62 cm – smallest male)</td>
</tr>
<tr>
<td>W345 - W344</td>
<td>Preferred</td>
<td>0.9831</td>
<td>0.80</td>
<td>Wild adult males</td>
</tr>
<tr>
<td>W345 - W262</td>
<td>Avoided</td>
<td>0.0018</td>
<td>0.09</td>
<td>Wild adult male</td>
</tr>
<tr>
<td>W737 - W345</td>
<td>Avoided</td>
<td>0.0074</td>
<td>0.00</td>
<td>Wild adult male (148 cm – largest male) Captive juvenile male (62 cm – smallest male)</td>
</tr>
</tbody>
</table>

(P > 0.975 indicate highly preferred associations; P<0.025 indicate avoidance). Status is estimated by SOCPROG.

Group Composition

Three heterogeneous clusters were evident from the community division analysis (Table 3). The overall modularity was 0.332 (Q, Modularity 1: from gregariousness), which suggests that this is a valid analysis in detecting divisions in the population, however the composition of the clusters was highly varied, with no clear pattern of attributes amongst the sharks. Several of the individuals had values near 0, indicating uncertainty in their assignment to that cluster. Furthermore, plotting associations using non-metric multidimensional scaling (random start; 2 dimensions; stress: 0.063227) showed ambiguous, sparsely distributed groups except for one dyad (W344-W345). This, along with the results of the community division by modularity, suggests that grouping is not explained by individual shark attributes.
### Table 3: Community division by modularity, $Q = 0.332$

| Community (N) | Sex Ratio | Age Class Ratio | Source Ratio (Release cohort) | Shark Identification (Assignment certainty***)
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (5 sharks)</td>
<td>M:F 5:0</td>
<td>A:J 3:2</td>
<td>W:C 3:2 (2 cohorts)</td>
<td>W265 (-0.5946) W273 (-0.103) W344 (-0.0513) W345 (-0.0096) W346 (-0.3918)</td>
</tr>
<tr>
<td>2 (7 sharks)</td>
<td>3:4</td>
<td>5:3</td>
<td>5:2 (2 cohorts)</td>
<td>W257 (0.0871) W260 (0.0492) W262 (0.5079) W263 (0.4114) W264 (0.293) W732 (0.0132)</td>
</tr>
<tr>
<td>3 (3 sharks)</td>
<td>1:2</td>
<td>2:1</td>
<td>0:3 (2 cohorts)</td>
<td>W731 (0.2232) W734 (0.4634) W736 (0.4638)</td>
</tr>
</tbody>
</table>


*** Level of certainty of the assignment of a shark to a community is determined from the eigenvector corresponding to the final bifurcation of the association matrix. Values near 0 indicate low certainty.

#### 3.2.3 Space Use Patterns

Home and core ranges were calculated for all sharks (see Section 6.2) to show individual positions in the array. The dyadic overlap indices (UDOI) were determined for the 16 dyads with HWI > 0.1. The overall means for the HWI and UDOI per dyad (with HWI >= 0.1) are shown in Figure 6. The spatial distribution of sharks was not highly correlated with association strength (Mantel z-test, 10 000 permutations: $z = 0.25124$, $p = 1.0003e^{13}$), however a high level of variation is evident. Some dyads, such as W345 – W344, show a high association and relatively low spatial overlap, indicating that shared space use does not entirely explain the level of association. Similarly, W263-W264 show a low association and relatively high range overlap, suggesting that their social behaviour is not highly influenced by their spatial proximity or that the sharks may in fact avoid one another. Furthermore, the significant dyads were found to be associating despite shifts in their home ranges when they returned to the array (Figure 7). Some dyads showed associations across different locations over a period of days (Figure 8), suggesting that site fidelity does not necessarily explain HWI values.
Figure 6: Comparison of means of association index (HWI) with spatial overlap index (UDOI) for dyads with HWI $\geq 0.1$.

Figure 7: 95% and 50% kernel densities for significantly preferred dyads.

A: W344 – W345 in October 2009  
B: W344 – W345 in October 2010  
C: W262 – W263 in October 2009  
D: W262 – W263 and W262 – W737 in October 2010  
(W737 was not released into the array until May 2010).

Maps generated in ArcGIS version 10.2.
Figure 8: Examples of daily plots of locations (projected x, y coordinates, in metres) for W344 (red) and W345 (blue). Plots show an overlap in space use in differing locations over days in November 2009.
3.3 ARE THESE ASSOCIATIONS PERSISTENT?

3.3.1 Lagged Association Rates

Plotting the standardised lagged association rates (Figure 9) showed a rapid decline in association rates from time zero (October 2009) to approximately 240 days into the study period (June 2010). This increased for around 50 days (to August 2010) and then declined slowly in the latter quarter of the study. The values remained significantly above the null association rates throughout the study, further indicating the existence of preferred (non-random) associations.

The most parsimonious model to describe these temporal relationships was that of preferred companionship and casual acquaintances (PC + CA). Of the four models, PC + CA displayed the lowest QAIC (4920.7944; preferred companions ΔQAIC = 61.5353; casual acquaintances ΔQAIC = 4.5279; two levels of casual acquaintances ΔQAIC = 0.8848). The model was structured as \( g'(\tau) = a + c \times e^{-b \tau} \) where a is the proportion of preferred companionships (0.15906), c is the proportion of casual companionships (0.15546), b is the disassociation factor (-0.10624). This suggests that at any one time, approximately 16 percent of a shark’s associations were long-term, consistent companions, and about 16 percent of associations are short-term acquaintances that decayed after about 100 days.
Figure 9: Standardised lagged association rate

The SLAR (solid line) shows the probability that previously associated dyads are associating after the indicated time lag (x-axis; 10 day sampling periods). Dashed line shows the null standardised lagged association rate (NSLAR), or the probability expected if sharks were associating randomly. Dotted line shows the best fitted model to describe relationships (preferred companionships and casual acquaintances). Bootstrapped standard errors shown by vertical lines.
3.4 HOW CAN THE EMERGENT SOCIAL ORGANISATION BE CHARACTERISED?

The estimated coefficient of variation of the true association indices, using the likelihood method, was 1.176 (SE +/- 0.038) indicating a highly differentiated society. For all network measures (strength, eigenvector centrality and coefficient of variation), the mean value of observed data was equal to or less than the mean of the randomly generated network measures (Table 4). This indicates that these values are less than those that would be expected in the absence of preferential associations. Variation was evident in network metrics across individuals, as demonstrated by the high values of the standard deviation in relation to the mean metric values, although this may be the result of detection variability between individuals. Network measures were highest in the austral spring and summer months. A rapid decrease was evident from February to June 2010, where strength values were near zero and the clustering coefficient could not be calculated. This may indicate that sharks maintained only limited or weak contacts, or be reflective of the absence of the tagged sharks during the autumn and early winter months. In the first and last month of the study period, the clustering coefficient was zero.

Table 4: Mean network measures for all individuals (based on HWIs) and mean measures for 5 000 random networks (permuted within samples).

<table>
<thead>
<tr>
<th></th>
<th>Strength S (sd)</th>
<th>Eigenvector centrality E(sd)</th>
<th>Clustering coefficient C (sd)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean of observed data</td>
<td>0.80 (0.80)</td>
<td>0.18 (0.19)</td>
<td>0.37 (0.26)</td>
</tr>
<tr>
<td></td>
<td>[SE = 0.08]</td>
<td>[SE=0.01]</td>
<td>[SE = 0.17]</td>
</tr>
<tr>
<td>Mean of random data</td>
<td>0.80 (0.82)</td>
<td>0.19 (0.18)</td>
<td>0.44 (0.25)</td>
</tr>
<tr>
<td>P</td>
<td>0.82 (0.01)</td>
<td>0.00 (1.00)</td>
<td>0.08 (0.53)</td>
</tr>
</tbody>
</table>

Standard deviation in round parentheses, bootstrapped standard errors (5 000 permutations) in square parentheses. P is the proportion of permuted values that are less than the observed.
4 DISCUSSION

Social network theory has become a useful tool in studying the social structure and behaviour of wild animals. Passive monitoring, when able to provide high resolution spatio-temporal data on the movement of animals, may aid in assessing the social behaviour of free-ranging marine animals, such as the spotted wobbegong shark, where long-term direct observation is otherwise difficult. The application of these techniques in this study showed that some spotted wobbegongs do form preferred associations with particular conspecifics and that these can be either long-term or casual associations. A complete network was evident, within which all sharks associated at least once. However associations were sparse, with only one third of the potential pairings being filled. Although associations were non-exclusive, the low number of associates per shark suggests that this population is not gregarious.

At the dyadic level some patterns of association emerged between certain individuals, however structure at the community and network level was ambiguous. This may suggest that wobbegongs have a loose social system, in which some individuals are social, or may be reflective of methodological constraints detailed further below.

This study investigated the composition of dyads and communities to disentangle non-social aggregation behaviour from the patterns of associations observed. Despite the presence of phenotypically similar dyads, many mixed pairs were evident and thus assortative mixing was not an apparently characteristic feature of associations. This suggests that typical aggregation behaviours may not strictly be driving association levels. Half of the dyads in this study (with HWI >= 0.1) consisted of same-sex pairs and half were of mixed sex. Sexual segregation is common in elasmobranchs (Carrier et al., 1994, Sims, 2000, Springer, 1976) and is thought to provide protection from male harassment during breeding (Wearmouth and Sims, 2008) or reflect habitat preferences to enhance gestation (Hight and Lowe, 2007). On the other hand, mixed-sex groups have been observed in a demersal shark species, the bull huss (Scyliorhinus stellaris; Scott et al., 1997), where a captive population showed a preference for proximity to other conspecifics but maintained
fluid groups. In a free-ranging, mid-water shark Mourier et al. (2012) found stable mixed-sex communities, although at the dyadic level some same-sex preferences were noted. The authors suggest that although sexual segregation was not a dominant feature of the social organisation, preferential associations between individuals of the same sex may reflect mating strategies, and dominance hierarchies, as well as level of familiarity.

It is important to note that the observed composition may be indicative of the male-biased sex ratio observed in this study. The absence of female-only dyads may suggest that localised behavioural segregation (Backus et al., 1956) may not be occurring or that females are simply not being detected. This may be due to behavioural differences that influence the detectability of the sexes (Croft et al., 2006, Sano, 1993) or can indicate a level of wider geographical segregation (Wearmouth and Sims, 2008). The breeding season of the spotted wobbegong is thought to occur from December to January and parturition from September to October (Huveneers et al. 2007b), and as wobbegongs are ovoviviparous, the low number of detected females (as well as neonates) may suggest that areas outside of reserve may be used as birthing and nursery grounds. Huveneers et al. (2007b) also observed that gravid females were generally not located as far south as Sydney. The presence of some adult females, however, may reflect the triennial oestrus cycle. To determine the extent to which the observed sociality is reflective of mating and reproductive strategies, a study period that incorporates the triennial reproductive cycle of the females would be beneficial.

Age segregation was also not clearly established. Despite the majority of pairs being comprised of either adults or juveniles only, at least one third contained mixed age classes. Of the significant dyads identified, the largest male had regular associations with the smallest male. These results are surprising, as juvenile aggregations are a common strategy amongst shark species to gain protection from predators (Heupel and Simpfendorfer, 2005) and this behaviour would be likely in wobbegong species as they exhibit intraspecific predation (Huveneers et al., 2007a). On the other hand, juveniles can benefit from associating with adults through guided learning, in which
inexperienced individuals shadow older conspecifics to gain experience and information on, for example, migration routes (reviewed in Brown and Laland, 2003). Although this has been less commonly observed in sharks, Guttridge et al. (2011) found that in groups of lemon sharks (*N.brevirostris*), leading individuals were usually larger than other group members. In this wobbegong population, ontogenetic changes may underlie some of the observations of age mixing, as sharks tagged before the commencement of the study period may have shifted age classes over this time. Additionally, age class definitions may have imposed an unnecessary constraint. Total length did not vary significantly around the value used to determine age class (115 cm). Although age class was determined by sexual maturity observed from wobbegongs along the NSW coast, size at sexual maturity is acknowledged to be geographically dependent (Huveneers et al., 2007b) and therefore these classes may be misleading within the local context. This can have a significant influence on the expected behaviours of the age classes (Gero et al., 2005).

Familiarity has also been identified as a driver of associative behaviours in some sharks (Jacoby et al., 2012a) and teleost fishes (Stehfast et al., 2013). However, in this study captive-bred sharks from the same release cohorts (raised in the same facility) were only found in two of the main dyads. The reasons for this could be similar to those of juvenile-adult mixing, in that several of the captive-bred sharks were new to the location during the period of this study. These sharks in particular may benefit from associating with unfamiliar sharks.

A sympatric species of wobbegong shows short-term site fidelity (*O. halei*, Carraro and Gladstone, 2006) and the potential for this to underlie association levels must be considered. The results of the Mantel tests however suggest that only a weak connection exists between shared space use (UDOI) and associations (HWI). Some correlation would be expected, as associating individuals are inherently sharing space. However, some dyads formed preferentially despite a limited overlap in range. Others appeared to limit their association despite a low overlap index. This may be the result of temporally asynchronous use of the overlapping space or
alternatively, it may be explained by active avoidance behaviour, which is indicative of social preferences, as observed by Mourier et al. (2012) in a reef shark. The use of home range analysis however, does not entirely disentangle passive space use from active social preferences. Inferring associations from location data may be confounded by site preferences of individuals. It is therefore a significant indication of a level of sociality if the same pairs are found to be associating in multiple locations within the array, particularly in a small marine reserve, as was found with some dyads in this study. Although a level of philopatry was evident, as the sharks returned to similar locations across seasons, fine-scale site fidelity does not appear to be the primary underlying mechanism for high association levels.

Lee et al. (2014) used acoustic telemetry and underwater visual surveys to estimate abundance of this population over the same study period. The decline in the number of associations from March – May 2010 is consistent with low abundance and high emigration rates during this period. The overall decline in HWIs and network measures may, therefore, be partially explained by animals leaving the array. Sharks associating prior to this period were found to be associating again in late winter when the probability of emigration was lowest (Lee et al., 2014). Of the sharks remaining in the array over autumn and early winter, limited associations were evident. These sharks were predominantly captive-bred that were recently released into the reserve (January 2010 and May 2010 cohorts) and had, therefore, possibly not established home ranges and migratory paths. During the period of lowest abundance (shark abundance = 13-29, July 2010; Lee et al., 2014) the mean association (HWI = 0.15, N = 7) was higher than the overall mean (0.05, N=15). Also, the month with highest estimated abundance (shark abundance = 96-112, October 2010; Lee et al., 2014), showed dyads maintained associations, despite the presence of many other (untagged) sharks. This provides some confirmation of the seasonal persistence of many of the associations, and potentially shows that habitat saturation does not necessarily drive associations.

The social model that was found to best fit the lagged association rate describes the structure of associations as a combination of long-term preferred companionships
and casual acquaintances. The existence of long-term associations has been observed previously in elasmobranch populations and is thought to be a common strategy for long-lived species (Mourier et al., 2012). In studying the social organisation of sleepy lizards, Leu et al. (2010) suggested that maintaining pair bonds during inactive periods may be less costly than re-establishing them. Maintaining long-term associations may also facilitate communication in relation to migration and resource availability (Lusseau, 2003, Whitehead and Weilgart, 2000) and a breakdown in this can have important consequences for the viability of the population by reducing knowledge of intra-seasonal habitat and resource hotspots (Lusseau, 2003).

Social fidelity amongst individuals, rather than large groups, is evident in this study group. Although some clear dyads emerged, sharks did not form exclusive pairs. The community divisions were ambiguous, both in form and composition. This contrasts with other recent quantitative studies that have found strong stable communities in sharks (Mourier et al., 2012, Guttridge et al., 2011). The network values were consistently less than those randomly generated. A low strength value suggests that the population is not gregarious, although some variation between individuals was observed. The low centrality may reflect a strategy for maintaining the population within a variable environment. Networks that consist of several highly centralised individuals contain less redundancy than more distributed systems, and may be more vulnerable to perturbations (Lusseau et al., 2004). These measures, coupled with high social differentiation, suggest a diversely connected but weak network. Interestingly, however, despite an overall clustering coefficient value that was less than the random, wobbegongs appeared to be more cliquish in spring and summer months, suggesting that that social cohesion may be relatively high in the pre-breeding and breeding seasons. Further analysis into triadic motifs (Croft et al., 2008, Pinter-Wollman et al., 2013) may shed light on more complex underlying patterns in association that are not explained by dyadic or community level analysis.

The organisation of semi-solitary species has been studied in various contexts, and is not uncommon in predators (Bekoff et al., 1984). Lurs and Kappeler (2013) describe
facultative male sociality of fossa (*Cryptoprocta ferox*), in which some males remained solitary while others formed stable partnerships with varying levels of cohesion. Croft et al. (2006) reported that persistent associations between pairs of guppies indicate a level of cooperation in dealing with predators. A level of familiarity can also result in decreased aggression among neighbours (Mourier et al., 2012) and may enhance the flow of information about resource availability within the area and during migration periods.

Maintaining few associations may also be reflective of the crypsis strategies of the species. Wobbegong sharks are ambush predators and group living may therefore disrupt foraging, as observed in other solitary ambush predators (McDonald, 1983). Some other benthic sharks are regularly observed in large groups and this may be explained by the differences in their foraging strategies. For example, *S. canicula* is an opportunistic forager, and prey mostly upon crabs and molluscs (Jacoby et al., 2012a). Maintaining small group sizes may also aid in avoiding predators, or may suggest that predation is not a primary concern the species in the study area. Overall, the social structure of the observed wobbegong population may be the results of both social affinity (cooperation and information sharing) and aversion (avoidance of aggression; Wearmouth and Sims, 2008) strategies and this may allow for many sharks to coexist in the small reserve.

Despite some patterns of sociality emerging from this study, the methodological context of these results is worth consideration. Inferring social relationships, and the structure of entire networks, from spatial proximity comes with a great deal of uncertainty (Castles et al., 2014). The use of passive acoustic telemetry such as VPS, allows for relatively precise, fine-scale information on animal locations (Espinoza et al., 2011) however, as the probability of getting a VPS location depends on a number of variables (detailed in Section 2.1.2), there is a high degree of variation in the number of locations across sharks. This can have a number of implications on focal measures that are commonly used in social network analyses, such as means and standard deviations. The analysis here controlled for this in several ways, including the use of an association index that accounts for temporal autocorrelation resulting
from this variation and by excluding individuals with an excessively low number of locations. However, the use of arbitrary thresholds may enhance other biases (James et al., 2009) through for example, a reduced sample size. The sampled sharks represented approximately 10 percent of the estimated population in periods of peak abundance, however the relatively low sample size (N = 15; Whitehead, 2008a) was nevertheless addressed by a post hoc power analysis (revealing adequate representation of the true social system) and through the use of contemporary iterations of permutation methods (James et al., 2009, Whitehead et al., 2005).

Another area of uncertainty is the selection of biologically meaningful parameters to define an association. With near-continuous locations, and limited reference to behavioural literature of the species, selecting association criteria and sampling periods was challenging. Although the combined average movement cycles were calculated at 24 hours, which concurs with the diel periodicity observed by Huveneers et al. (2006), the frequency of association cycles are unknown and established theories such as the Nyquist rate therefore have troublesome application. There are no clear universal guidelines for determining a biologically appropriate spatio-temporal scale. Other studies of shark sociality have used varied approaches to setting these parameters. For example, Mourier et al. (2012) set a sampling period of 15 days to account for data collection rates, and many have simply not reported it. In this context, association indexes may be better interpreted as a relative measure useful for highlighting patterns, rather than an actual measure of the time a dyad spends together. Other studies have incorporated parameter testing (Haddadi et al., 2011, Stehfast et al., 2013; Whitehead, 1991) and this study attempted to quantitatively assess association parameters in a similar vein.
5 CONCLUSIONS

This study aimed to provide a comprehensive and replicable example of how statistically robust social network analysis, combined with fine-scale spatio-temporal data, can be used to investigate social behaviours of a demersal predator. But is this enough to conclude sociality? Following Hinde’s (1976) conceptual framework, this study addresses some of the fundamental building blocks of social organisation. Clear patterns emerged, with some sharks displaying preferred, yet non-exclusive, associations with conspecifics of different sex, size and origin, many of which persisted over space and time. No doubt there is a complex interplay of factors beneath the surface of these observations, shaping the patterns of association. Further research should address these possible explanatory variables, such as how the timing and nature of breeding patterns and resources shifts influence social behaviours. Given their vulnerability to fishing, shedding further light on the nature and composition of wobbegong social structures will not only enhance our understanding of the evolution of sociality across diverse phyla, but may help in ensuring a sustained wobbegong population into the future.
6 SUPPLEMENTARY MATERIAL

6.1 Incorporating positioning error into data screening

The VPS system assumes ideal propagation of signals from transmitters, however interference is generally encountered from signal collisions, position of animals within (or distance from) the array, and attenuation from habitat preference and environmental influences (Espinoza et al., 2011). Accordingly the system provides an estimate of positioning error for each location known as Horizontal Positioning Error (HPE). Animals within the core area of the array have higher precision (lower HPE) than those in areas of poorer coverage and this can lead to significant variation in detectability. Large areas of preferred habitat, as observed during underwater surveys within the area (Lee et al., 2014) and from anecdotal evidence from local divers, were located around the edges of the array. Thus, selecting an HPE cutoff that was too low would decrease the sampling area and may result in the loss of important information. Such spatial biases can result in significant over or underestimation of social associations and therefore incorporating positional error into the analysis at an early stage of the analysis is important.

The HPE provided for animal tags is a unit-less, relative measure of the precision of a location and can only be used as a quality audit for all locations. However, since the fixed location of sync-tags is known, an HPE and a measured error estimate in metres (HPEm) were estimated for each sync-tag location. No correlation was found between the HPE and HPEm (Spearman’s Rank, $S = 3.09$, $p = 2.2\times10^{-16}$, rho $0.650404291$), therefore the HPE values provided for the animal tags (in which fixed positions are not known) could not reliably be used in direct calculations. The HPE value that would preserve 90 percent of the data was therefore calculated (HPE = 13.4). This was used as a threshold above which locations were excluded. To gain a general idea of the meter value of the relative error, HPE values of the sync-tags were binned and corresponding HPEm values for the median, 90th and 95th percentiles for the sync-tags (Coates et al., 2013) were determined. The median of the filtered dataset (HPE = 4.6) was calculated and the associated HPEm equated to
approximately 2.8 m (CI = 0.07, range 0-13.1), which was deemed an acceptable range for this analysis. As the sync-tags are stationery and well-positioned within the array, locations may not be subject to the same positioning error as tags on animals, however the error was calculated by Vemco in similar way for both stationery and moving tags, and therefore may contain similar accuracy (Coates et al., 2013). This filtering process aimed to both maximize positional precision while maintaining sufficient data and the resulting filtered locations were used in subsequent analyses.
6.2 Home Range Estimates from Kernel Density Analysis
6.3 Animal Behaviour Journal Guide for Authors

TABLE OF CONTENTS

- Description p.1
- Audience p.1
- Impact Factor p.1
- Abstracting and Indexing p.1
- Editorial Board p.2
- Guide for Authors p.3

DESCRIPTION

First published in 1953, Animal Behaviour is a leading international publication and has wide appeal, containing critical reviews, original papers, and research articles on all aspects of animal behaviour. Book Reviews and Books Received sections are also included.

Growing interest in behavioural biology and the international reputation of Animal Behaviour prompted an expansion to monthly publication in 1989. Animal Behaviour continues to be the Journal of choice for biologists, ethologists, psychologists, physiologists, and veterinarians with an interest in the subject.

Research Areas include:
- Behavioural ecology
- Evolution of behaviour
- Sociobiology
- Ethology
- Behavioural psychology
- Behavioural physiology
- Population biology
- Sensory behaviour
- Navigation and migration

AUDIENCE

Behaviourists, behavioural ecologists, behavioural neuroscientists, ethologists, evolutionary ecologists

IMPACT FACTOR

2013: 3.068 © Thomson Reuters Journal Citation Reports 2014

ABSTRACTING AND INDEXING

Scopus
EMBiology
GUIDE FOR AUTHORS

Your Paper Your Way
ypyw-gfa-banner.gifyour paper your way

INTRODUCTION

Types of article

Research papers

Animal Behaviour publishes original papers relating to all aspects of the behaviour of animals, including humans. Papers may be field, laboratory or theoretical studies. Preference is given to studies that are likely to be of interest to the broad readership of the Journal and that test explicit hypotheses rather than being purely descriptive.

Reviews

These should address fundamental issues relating to behaviour and provide new insights into the subject(s) they cover. Original interdisciplinary syntheses are especially welcome. Reviews should be no longer than 6000 words (excluding references) and should include an abstract of up to 300 words. In the first instance, a preliminary outline of up to 600 words should be submitted online (see Contact details for submission below). The decision as to whether to proceed to a full review then rests with the Executive Editors or invited advisers. Contributions submitted on this basis will be subjected to the same refereeing process as normal manuscripts.

Essays

These should address fundamental issues relating to behaviour and provide new insights into the subject(s) they cover. In contrast to Reviews, Essays provide an opportunity for authors to express opinions, consider the subject area in a historical context and speculate on its future development. Essays should be no longer than 6000 words (excluding references) and should include an abstract of up to 300 words. In the first instance, a preliminary outline of up to 600 words should be submitted online (see Contact details for submission below). The decision as to whether to proceed to a full essay then rests with the Executive Editors or invited advisers. Contributions submitted on this basis will be subjected to the same refereeing process as normal manuscripts.

Commentaries

The Commentaries section of the Journal provides an opportunity to raise issues of general importance to the study of behaviour, including statistical analysis, theory, methodology and ethics. Unless there are clearly broader implications for the study of behaviour as a whole, critiques of particular papers or issues of more local interest should be reserved for the Forum section (see below). Decisions as to whether borderline submissions are more appropriate to the Commentaries or Forum section rest with the Executive Editors. Contributions should be brief, normally not more than six printed pages, and should not contain an abstract. Methodological contributions may be longer, and may contain an abstract, subject to the discretion of the Executive Editors. The initial decision as to prima facie merit rests with the Executive Editors or invited advisers. Contributions with prima facie merit are subjected to the same refereeing process as normal manuscripts, but responses or complementary articles may be solicited by the Executive Editors at their discretion. Other contributions are returned unrefereed to the author(s).

Forum

The Forum section is published on ScienceDirect with contributions listed in the contents of the relevant hardcopy issue and cited as indicated in References below. The section accepts critiques of published papers relevant to the areas of interest of the Journal, and provides an opportunity for constructive exchanges on issues surrounding particular fields of study. Submission, review and acceptance procedures are as for Commentaries (see above), but there is no word limit. In the case of Forum critiques of published papers, the author(s) of the target article must be contacted and trivial points of difference or misunderstanding resolved; this correspondence must be submitted in a cover letter accompanying the Forum article with the knowledge of the author(s) of the target article. More general correspondence on matters relating to behavioural research is published, unrefereed, in the newsletters of ASAB and ABS. Such correspondence should be sent to the newsletter editors: Dr. Lisa M. Collins, Queen’s University Belfast, Department of Biological Sciences, Medical Biology Centre, 97 Lisburn Road, Belfast, UK, e-mail: asabnewslettereditor@gmail.com for ASAB; Susan M. Bertram, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada, e-mail: Sue_Bertram@carleton.ca for ABS.
Single and double blind peer review
Animal Behaviour has instituted a double blind peer review process (i.e., where neither the authors' nor the reviewers' identities are known to each other). Reciprocal anonymity is suggested to provide a more objective and potentially less biased assessment of manuscripts, and help ensure that the process is fair to both junior and well-established scientists. The switch to double blind review requires some changes to editorial procedures, and we ask potential authors to pay close attention to our revised submission guidelines. Our policy with respect to reviewers is to allow them to waive anonymity if they wish, and in accord with this, authors may also choose to submit their papers without being blinded, giving both authors and reviewers maximum flexibility in how they wish their work and comments to be assessed. Animal Behaviour is one of the foremost journals in its field, and the implementation of double blind review aims at ensuring our reputation for integrity, fairness and openness to new ideas.

Contact details for submission
Authors should submit manuscripts online to http://ees.elsevier.com/anbeh. When submitting online, authors are requested to select the article type (Research paper, Review, Essay, Review/Essay Proposal, Commentary, Forum). Each category of article is further divided into US and UK articles (e.g. US Research paper, UK Research paper, etc.) depending on whether the US or UK Editorial Office is responsible for processing the manuscript. Authors whose current address is in the Americas, or neighbouring islands, or who are members of the Animal Behavior Society should select the US article types and authors in other geographical areas or who are members of the Association for the Study of Animal Behaviour should select the UK article types. Hard copies are not required in addition to copies submitted online. Authors who are submitting a manuscript online for the first time should read the Author Tutorial on the submission site. For enquiries relating to submissions via EES, please contact the Journal Manager at Elsevier via e-mail (yanbe@elsevier.com).

For other general correspondence:
The address of the UK office is: Dr A.K. Turner, Managing Editor, Animal Behaviour Editorial Office, School of Life Sciences, University of Nottingham, University Park, Nottingham NG7 2RD, U.K. (fax: (0) 115 9 513 249, e-mail: angela.turner@nottingham.ac.uk).
The address of the US office is: Kris Bruner, Managing Editor, Animal Behavior Society Central Office, Indiana University, 402 N. Park Avenue, Bloomington, IN 47408-3828, U.S.A. (fax: 812 856 5542; e-mail: kbruner@indiana.edu).
Correspondence about book reviews handled through the North American office should be sent to:
Dr P. Loesche, Department of Psychology, Box 351525, University of Washington, Seattle, WA 98195, U.S.A. (e-mail: loes@uw.edu).
Resubmitted manuscripts should also include a detailed explanation of how the author has dealt with each of the reviewers' and Editor's comments. These comments should be uploaded as 'Revision Comments' on EES.

BEFORE YOU BEGIN
Ethics in publishing
Animal Behaviour publishes papers by scientists conducting research at locations around the globe. Publication is, therefore, based upon mutual trust between publisher and authors. Professional integrity in the conduct and reporting of research is an absolute requirement of publication in the journal, as is a willingness to share information with other members of the scientific community. Consequently, as a condition of publication in Animal Behaviour, authors must agree both to honour any reasonable request for materials or methods needed to verify or replicate experiments reported in the journal and to make available, upon request, any data sets upon which published studies are based. Anyone who encounters a persistent refusal to comply with these guidelines, or has reason to suspect some other departure from acceptable standards of scientific conduct, should contact the appropriate Executive Editor (European or American) of the journal. The Executive Editors will act in accordance with the guidelines of the Committee for Publication Ethics (http://www.publicationethics.org) and may inform an author's institution of a purported infraction. Statements on scientific integrity by the Association for the Study of Animal Behaviour and Animal Behavior Society can be found at, respectively, http://www.asab.org and http://animalbehaviorsociety.org.
Originality and plagiarism
As noted in Elsevier’s publishing and ethical guidelines, authors should ensure that they have written entirely original works. If authors have used the work, data, or words of others or their own earlier publications, please ensure that this has been appropriately cited or quoted. Please also declare such overlaps in the cover letter on submission. Plagiarism takes many forms, from ‘passing off’ another’s paper as the author’s own paper, to copying or paraphrasing substantial parts of another’s paper or indeed one’s own earlier paper (without attribution), to claiming results from research conducted by others. Plagiarism in all its forms constitutes unethical publishing behaviour and is unacceptable. All manuscripts are automatically put through a plagiarism check program and flagged results are evaluated individually.

For further information on Ethics in Publishing and Ethical guidelines for journal publication, see also http://www.elsevier.com/publishingethics and http://www.elsevier.com/ethicalguidelines.

Animal welfare
The research should adhere to the ASAB/ABS Guidelines for the Use of Animals in Research (updated in each January issue of the Journal and on the Journal Web site: http://www.elsevier.com/framework_products/promis_misc/ASAB2006.pdf), the legal requirements of the country in which the work was carried out, and all institutional guidelines. The Guide to Ethical Information Required for Animal Behaviour Papers (http://www.elsevier.com/framework_products/promis_misc/ethanbe.doc) should be consulted and its requirements met. ASAB and ABS endorse the ARRIVE guidelines for reporting experiments using live animals (http://www.nc3rs.org.uk/downloaddoc.asp?id=1206&page=1357&skin=0). Animal Behaviour has exceptionally high standards for animal care for both vertebrates and invertebrates. In addition to the usual requests for permit and agency approval numbers, we would frequently like more information to address concerns that the animals were treated as well as possible given the constraints of the experimental design.

Conflict of interest
All authors are requested to disclose any actual or potential conflict of interest including any financial, personal or other relationships with other people or organizations within three years of beginning the submitted work that could inappropriately influence, or be perceived to influence, their work. See also http://www.elsevier.com/conflictsOfInterest. Further information and an example of a Conflict of Interest form can be found at: http://help.elsevier.com/app/answers/detail/a_id/286/p/7923.

Animal Behaviour will not consider submissions that have been published elsewhere, nor will it republish data found in other publications, unless the data are re-evaluated to provide new information not found in the original. Abstracts that both appear in published conference proceedings with ISBNs or ISSN, such as special editions of journals, and provide explicit quantitative summaries of the key results, are considered as prior publication. Overlap between submitted manuscripts and published abstracts containing qualitative descriptions of the manuscript will be allowed, provided that such abstracts are not verbatim reproductions of the abstract contained within the submitted manuscript. Include details of all abstracts and other published materials in a cover letter accompanying the submitted manuscript on EES.

Submission declaration and verification
Submission of an article implies that the work described has not been published previously (except in the form of an abstract or as part of a published lecture or academic thesis or as an electronic preprint, see http://www.elsevier.com/postingpolicy), that it is not under consideration for publication elsewhere, that its publication is approved by all authors and tacitly or explicitly by the responsible authorities where the work was carried out, and that, if accepted, it will not be published elsewhere in the same form, in English or in any other language, including electronically without the written consent of the copyright-holder. To verify originality, your article may be checked by the originality detection service CrossCheck http://www.elsevier.com/editors/plagdetect.

Changes to authorship
This policy concerns the addition, deletion, or rearrangement of author names in the authorship of accepted manuscripts:
Before the accepted manuscript is published in an online issue: Requests to add or remove an author, or to rearrange the author names, must be sent to the Journal Manager from the corresponding author of the accepted manuscript and must include: (a) the reason the name should be added or removed, or the author names rearranged and (b) written confirmation (e-mail, fax, letter) from all authors that they agree with the addition, removal or rearrangement. In the case of addition or removal of authors,
this includes confirmation from the author being added or removed. Requests that are not sent by
the corresponding author will be forwarded by the Journal Manager to the corresponding author, who
must follow the procedure as described above. Note that: (1) Journal Managers will inform the Journal
Editors of any such requests and (2) publication of the accepted manuscript in an online issue is
suspended until authorship has been agreed.

After the accepted manuscript is published in an online issue: Any requests to add, delete, or rearrange
author names in an article published in an online issue will follow the same policies as noted above
and result in a corrigendum.

Article transfer service
This journal is part of our Article Transfer Service. This means that if the Editor feels your
article is more suitable in one of our other participating journals, then you may be asked to
consider transferring the article to one of those. If you agree, your article will be transferred
automatically on your behalf with no need to reformat. More information about this can be found
here: http://www.elsevier.com/authors/article-transfer-service.

Copyright
This journal offers authors a choice in publishing their research: Open access and Subscription.

For subscription articles
Upon acceptance of an article, authors will be asked to complete a ‘Journal Publishing Agreement’ (for
more information on this and copyright, see http://www.elsevier.com/copyright). An e-mail will be
sent to the corresponding author confirming receipt of the manuscript together with a ‘Journal
Publishing Agreement’ form or a link to the online version of this agreement.

Subscribers may reproduce tables of contents or prepare lists of articles including abstracts for internal
circulation within their institutions. Permission of the Publisher is required for resale or distribution
outside the institution and for all other derivative works, including compilations and translations
(please consult http://www.elsevier.com/permissions). If excerpts from other copyrighted works are
included, the author(s) must obtain written permission from the copyright owners and credit the
source(s) in the article. Elsevier has preprinted forms for use by authors in these cases: please consult

For open access articles
Upon acceptance of an article, authors will be asked to complete an ‘Exclusive License Agreement’ (for more information see http://www.elsevier.com/OAauthoragreement). Permitted
reuse of open access articles is determined by the author’s choice of user license (see

Retained author rights
As an author you (or your employer or institution) retain certain rights. For more information on
author rights for:
Subscription articles please see http://www.elsevier.com/journal-authors/author-rights-and-responsibilities.
Open access articles please see http://www.elsevier.com/OAauthoragreement.

Role of the funding source
You are requested to identify who provided financial support for the conduct of the research and/or
preparation of the article in the Acknowledgments section of the manuscript.

Funding body agreements and policies
Elsevier has established agreements and developed policies to allow authors whose articles appear in
journals published by Elsevier, to comply with potential manuscript archiving requirements as specified
as conditions of their grant awards. To learn more about existing agreements and policies please visit

Open access
This journal offers authors a choice in publishing their research:

Open access
• Articles are freely available to both subscribers and the wider public with permitted reuse
• An open access publication fee is payable by authors or their research funder

Subscription
• Articles are made available to subscribers as well as developing countries and patient groups through our access programs (http://www.elsevier.com/access)
• No open access publication fee

All articles published open access will be immediately and permanently free for everyone to read and download. Permitted reuse is defined by your choice of one of the following Creative Commons user licenses:

Creative Commons Attribution (CC BY): lets others distribute and copy the article, to create extracts, abstracts, and other revised versions, adaptations or derivative works of or from an article (such as a translation), to include in a collective work (such as an anthology), to text or data mine the article, even for commercial purposes, as long as they credit the author(s), do not represent the author as endorsing their adaptation of the article, and do not modify the article in such a way as to damage the author’s honor or reputation.

Creative Commons Attribution-NonCommercial-ShareAlike (CC BY-NC-SA): for non-commercial purposes, lets others distribute and copy the article, to create extracts, abstracts and other revised versions, adaptations or derivative works of or from an article (such as a translation), to include in a collective work (such as an anthology), to text and data mine the article, as long as they credit the author(s), do not represent the author as endorsing their adaptation of the article, do not modify the article in such a way as to damage the author’s honor or reputation, and license their new adaptations or creations under identical terms (CC BY-NC-SA).

Creative Commons Attribution-NonCommercial-NoDerivs (CC BY-NC-ND): for non-commercial purposes, lets others distribute and copy the article, and to include in a collective work (such as an anthology), as long as they credit the author(s) and provided they do not alter or modify the article.

To provide open access, this Journal has a publication fee which needs to be met by the authors or their research funders for each article published open access. Your publication choice will have no effect on the peer review process or acceptance of submitted articles.

The publication fee for Open Access in this journal is $2,200, excluding taxes. Learn more about Elsevier’s pricing policy: http://www.elsevier.com/openaccesspricing.

Language and language services
Manuscripts should be written in British English. Authors who are unsure of correct English usage should have their manuscript checked by someone proficient in the language. Manuscripts in which the English is difficult to understand may be returned to the author for revision before scientific review. Papers that are accepted but incorrectly prepared or whose English is poor, may also be subject to delays in the press. After acceptance, the Editorial Offices will edit papers in accordance with the house style and will help authors to communicate effectively.

Authors who require information about language editing and copyediting services pre- and post-submission please visit http://www.elsevier.com/languagepolishing or our customer support site at http://epsupport.elsevier.com for more information. Please note Elsevier neither endorses nor takes responsibility for any products, goods or services offered by outside vendors through our services or in any advertising. For more information please refer to our Terms & Conditions: http://www.elsevier.com/termsandconditions

Submission
Submission to this journal proceeds totally online and you will be guided stepwise through the creation and uploading of your files. The system automatically converts source files to a single PDF file of the article, which is used in the peer-review process. Please note that even though manuscript source files are converted to PDF files at submission for the review process, these source files are needed for further processing after acceptance. All correspondence, including notification of the Editor’s decision and requests for revision, takes place by e-mail removing the need for a paper trail.

Before submitting online, make sure you have the following details: all authors’ names and addresses and their permission to proceed with submission, the details of any licences/permits/institutional approval you had for the study, suggestions for referees and any opposed referees. You will need to upload a cover letter, title page, acknowledgments and manuscript.

Submit your article
Please submit your article via http://ees.elsevier.com/anbeh.

AUTHOR INFORMATION PACK 9 Oct 2014 www.elsevier.com/locate/anbehav
Referees
Please submit, with the manuscript, the names and e-mail addresses of 4 potential referees. In case of double blind peer review, please make sure that all text that may reveal your identity is excluded from the source files.

PREPARATION

NEW SUBMISSIONS
Submission to this journal proceeds totally online and you will be guided stepwise through the creation and uploading of your files. The system automatically converts your files to a single PDF file, which is used in the peer-review process.

As part of the Your Paper Your Way service, you may choose to submit your manuscript as a single file to be used in the refereeing process. This can be a PDF file or a Word document, in any format or layout that can be used by referees to evaluate your manuscript. It should contain high enough quality figures for refereeing. If you prefer to do so, you may still provide all or some of the source files at the initial submission. Please note that individual figure files larger than 10 MB must be uploaded separately.

References
There are no strict requirements on reference formatting at submission. References can be in any style or format as long as the style is consistent. Where applicable, author(s) name(s), journal title/book title, chapter title/article title, year of publication, volume number/book chapter and the pagination must be present. Use of DOI is highly encouraged. The reference style used by the journal will be applied to the accepted article by Elsevier at the proof stage. Note that missing data will be highlighted at proof stage for the author to correct.

Formatting requirements
There are no strict formatting requirements but all manuscripts must contain the essential elements needed to convey your manuscript, for example Title page, Abstract, Keywords, Introduction, Methods, Results, Discussion, References, Tables, Figure Legends, Figures, and bulleted Highlights summarizing your article. If your article includes any Videos and/or other Supplementary material, this should be included in your initial submission for peer review purposes. Divide the article into clearly defined sections.

Line numbering and double spacing text
Please ensure the text of your paper is double-spaced and has consecutive line numbering – this is an essential peer review requirement.

Figures and tables embedded in text
Please ensure the figures and the tables included in the single file are placed next to the relevant text in the manuscript, rather than at the bottom or the top of the file.

REVISED SUBMISSIONS

Language
Please write your text in good English (British usage only is accepted). Use decimal points (not decimal commas); use a space for thousands (10 000 and above).

Use of word processing software
Regardless of the file format of the original submission, at revision you must provide us with an editable file of the entire article. Keep the layout of the text as simple as possible. Most formatting codes will be removed and replaced on processing the article. The electronic text should be prepared in a way very similar to that of conventional manuscripts (see also the Guide to Publishing with Elsevier: http://www.elsevier.com/guidepublication). See also the section on Electronic artwork.

To avoid unnecessary errors you are strongly advised to use the ‘spell-check’ and ‘grammar-check’ functions of your word processor.

Article structure

Subdivision - unnumbered sections
Divide your article into clearly defined sections. Each subsection is given a brief heading. Each heading should appear on its own separate line. Subsections should be used as much as possible when cross-referencing text: refer to the subsection by heading as opposed to simply “the text”.

The usual main headings for Research papers are: Methods, Results, Discussion, Acknowledgments and References (no heading is used for the Abstract or Introduction). Papers should not be forced to fit into this pattern of headings, however, if they do not naturally do so. Type main headings in
capitalsonaseparatelinenontheleftofthepage.Typesubheadingsinitalicsatthetalineofthepageon
aseparate word with a capital letter. Type the main words with a capital letter. Type subheadings on a
new line, aligned full left. Start the text on a new line after subheadings and sub-subheadings. When
presenting multiple experiments, authors may use main headings for the titles of each experiment,
with the Methods and Results of each experiment listed as subheadings. Try to keep subheadings
short enough to fit within a single column.

Introduction
State the objectives of the work and provide an adequate background, avoiding a detailed literature
survey or a summary of the results. The Introduction should be brief, not normally exceeding two manuscript pages. Keep references to
a minimum by citing reviews rather than primary research papers where appropriate.

Methods
Provide sufficient detail to allow the work to be reproduced. Methods already published should be
indicated by a reference: only relevant modifications should be described.
Give the names and addresses of companies providing trademarked products. Always state sample
sizes (the number of animals used in the study) and the age, sex, breed/strain and source of animals.
Full details of testing or observational regimes should be given. If captive animals were used, include
details of housing conditions relevant to the study (e.g. cage size and type, bedding, group size and
composition, lighting, temperature, ambient noise conditions, maintenance diets) both during the
study and during any period before the study that might bear on the results. The Methods section
may also contain a description of the kinds of statistics used and the activities that were recorded.

Ethical note. Where ethical considerations arise from the study, these should be addressed in the
Methods, either in the main Methods section itself (where the additional discussion is relatively minor),
or in a separate subsection of the Methods headed Ethical note. Any ethical implications of the
experimental design and procedures should be identified, and any licences acquired to carry out the
work specified. Procedures that were taken to minimize the welfare impact on subjects, including
colony size, use of pilot tests and predetermined rules for inter-vivo testing and predeterminated rules for
Any steps taken to enhance the welfare of subjects (e.g. through ‘environmental enrichment’) should
also be indicated. If the study involved keeping wild animals in captivity, state for how long the animals
were captive and whether, where and how they were returned to the wild at the end of the study.

Results
Results should be clear and concise. This section should include only results that are relevant to the
hypotheses outlined in the Introduction and considered in the Discussion. The text should complement
material given in Tables or Figures but should not directly repeat it. Give full details of statistical
analysis either in the text or in Tables or Figure legends. Include the type of test, the precise data to
which the test was applied, the value of the relevant statistic, the sample size and/or degrees of freedom,
and the probability level. Number Tables and Figures in the order to which they are referred in the text.
Means and standard errors/standard deviations (and medians and interquartile ranges/confidence
limits), with their associated sample sizes, are given in the format X +SE = 10.20±1.01 g, N = 15,
not X = 10.20, SE = 1.01, N = 15.
For significance tests, give the name of the test followed by a colon, the test statistic and its value,
the degrees of freedom or sample size (whichever is the convention for the test) and the P value
(note that P values have two degrees of freedom). The different parts of the statistical quotation are
separated by a comma. Note use of italics for F, P, N and other variables.
If the test statistic is conventionally quoted with degrees of freedom, these are presented as a
subscript to the test statistic. For example:

ANOVA: F1,11 = 7.89, P = 0.017
Kruskal-Wallis test: H11 = 287.8, P = 0.001
Chi-square test: X22 = 0.19, P = 0.91
Paired t test: t12 = 1.99, P = 0.07

If the test is conventionally quoted with the sample size, this should follow the test statistic value.
For example:

Spearman rank correlation: rs = 0.80, N = 11, P < 0.01
Wilcoxon signed-ranks test: T = 6, N = 14, P < 0.01
Mann-Whitney U test: U = 74, N1 = N 2 = 17, P < 0.02

AUTHOR INFORMATION PACK 9 Oct 2014 www.elsevier.com/locate/anbehav
Are Wobbegongs Social?

\[ P \text{ values for significant outcomes can be quoted as below a threshold significance value (e.g. } P < 0.05, 0.01, 0.001) \text{, but wherever possible should be quoted as an exact probability value. Departure from a significance threshold of 0.05 should be stated and justified in the Methods. Marginally nonsignificant outcomes can be indicated as exact probability values or as } P < 0.1. \text{ Nonsignificant outcomes should be indicated with an exact probability value whenever possible, or as } N S \text{ or } P > 0.05, \text{ as appropriate for the test.}

State whether a test is one tailed or two tailed (or specific or nonspecific in the case of Meddis’ nonparametric ANOVAs). One-tailed (or specific) tests should be used with caution. Their use is justified only when there are strong a priori reasons for predicting the direction of a difference or trend and results in the opposite direction can reasonably be regarded as equivalent to no difference or trend at all. Authors are referred to Kimmel (1957, Psychological Bulletin, 54, 315-353).

Do not quote decimals with naked points, for example quote 0.01, not .01, or normally to more than three decimal places (the exception being \( P \) values for significance tests, which may be quoted to four decimal places where appropriate, e.g. 0.0001).

\textit{Regression and analyses of variance.} The significance of regressions should be tested with } F \text{ or } t \text{ but not the correlation coefficient } r. R^2 \text{ should be quoted with both regressions and parametric analyses of variance.}

\textit{Multiple range tests.} Unplanned multiple range tests following ANOVA should be avoided unless their appropriateness for the comparisons in question is verified explicitly. Authors are referred to the review by Day and Quinn (1989, Ecological Monographs, 59, 433-463).

\textit{Power tests.} Where a significance test based on a small sample size yields a nonsignificant result, explicit consideration should be given to the power of the data for accepting the null hypothesis. Authors are referred to Thomas and Janes (1996, Animal Behaviour, 52, 856-859) and Colegrave and Ruxton (2003, Behavioural Ecology, 14, 446-447) for guidance on the appropriate use of power tests. Providing a value for power based on a priori tests is preferred. Values of observed power are not appropriate. Authors should consider effect sizes and their confidence intervals in drawing conclusions regarding the null hypothesis.

\textit{Transformations.} Where data have been transformed for parametric significance tests, the nature of the transformation and the reason for its selection (e.g. log } x, x^2, \text{ arcsine) should be stated.

\textit{Discussion} It is often helpful to begin the Discussion with a summary of the main results. The main purpose of the Discussion, however, is to comment on the significance of the results and set them in the context of previous work. The Discussion should be concise and not excessively speculative, and references should be kept to a minimum by citing review articles as much as possible.

\textit{Conclusions} The main conclusions of the study may be presented in a short Conclusions section, as a subsection of a Discussion or Results and Discussion section.

\textit{Appendices} If there is more than one appendix, they should be identified as 1, 2, etc. Formulae and equations in appendices should be given separate numbering: equation (A1), equation (A2), etc.

\textit{Essential title page information} Title. This should be brief and informative, and should not exceed 120 characters. Avoid abbreviations, as well as part numbers unless the papers are to be published consecutively in the same issue of the Journal.

Author names and affiliations. Where the family name may be ambiguous (e.g. a double name), please indicate this clearly. Present the authors’ affiliation addresses (where the actual work was done) below the names. Indicate all affiliations with a lower-case superscript letter immediately after the author’s name and in front of the appropriate address. Affiliations should not include street, box number, postal (zip) code, country (when that is obvious) or city, state, province, etc., when that is redundant with the University name.
Corresponding author. Clearly indicate who is willing to handle correspondence at all stages of refereeing and publication, also post-publication. Ensure that telephone and fax numbers (with country and area code) are provided in addition to the e-mail address and the complete postal address.

Correspondence. At the bottom of the page, give the full postal address and e-mail address (if desired) of the corresponding author and the present addresses of any co-authors if different from their affiliations; e-mail addresses of co-authors may also be given.

Word count. Include a word count for the text.

Reviews. These should address fundamental issues relating to behaviour and provide new insights into the subject(s) they cover. Original interdisciplinary syntheses are especially welcome. Reviews should be no longer than 6000 words (excluding references) and should include an abstract of up to 300 words. In the first instance, a preliminary outline of up to 600 words should be submitted online (as a Review proposal). The decision as to whether to proceed to a full review then rests with the Executive Editors of invited advisers. Contributions submitted on this basis will be subjected to the same refereeing process as normal manuscripts.

Essays. These should address fundamental issues relating to behaviour and provide new insights into the subject(s) they cover. In contrast to Reviews, Essays provide an opportunity for authors to express opinions, consider the subject area in a historical context and speculate on its future development. Essays should be no longer than 6000 words (excluding references) and should include an abstract of up to 300 words. In the first instance, a preliminary outline of up to 600 words should be submitted online (as an Essay proposal). The decision as to whether to proceed to a full essay then rests with the Executive Editor or invited advisers. Contributions submitted on this basis will be subjected to the same refereeing process as normal manuscripts.

Title document
The title document should contain the title of the article, all affiliations of the corresponding author and co-authors and the corresponding author's address. In case of double blind peer review, this information should not appear in any other file, in order not to yield the authors identity to the reviewer.

Abstract
The Abstract should describe the purpose of the study, outline the major findings and state the main conclusions. It should be concise, informative, explicit and intelligible without reference to the text. Abstracts should usually be limited to 300 words. Use both common and scientific names of animals at first mention in the Abstract unless they are given in the title. Avoid using references; if used, give the journal name, volume and page numbers, or the book title and publisher.

Highlights
Highlights are mandatory for this journal for research articles, essays, reviews, commentaries and forum articles. They consist of a short collection of bullet points that convey the core findings of the article and should be submitted in a separate file in the online submission system. Please use "Highlights" in the file name and include 3 to 5 bullet points (maximum 85 characters including spaces and each bullet point should be on a separate line). See http://www.elsevier.com/highlights for examples.

Keywords
Immediately after the abstract, provide up to 10 keywords, using British spelling and avoiding general and plural terms and multiple concepts (avoid, for example, "and", "of"). Be sparing with abbreviations: only abbreviations firmly established in the field may be eligible.

Abbreviations
Define abbreviations that are not standard in this field at their first mention in the abstract and the main text. Ensure consistency of abbreviations throughout the article.

Acknowledgements
Collate acknowledgements in a separate section at the end of the article before the references and do not, therefore, include them on the title page, as a footnote to the title or otherwise. List here those individuals who provided help during the research (e.g., providing language help, writing assistance or proof reading the article, etc.).
**Nomenclature and units**
Follow internationally accepted rules and conventions: use the international system of units (SI). If other quantities are mentioned, give their equivalent in SI.

**Database linking**
Elsevier encourages authors to connect articles with external databases, giving their readers one-click access to relevant databases that help to build a better understanding of the described research. Please refer to relevant database identifiers using the following format in your article: Database: xxxx (e.g., TAIR: AT1G01020; CCDC: 734053; PDB: 1XFN). See http://www.elsevier.com/da
dabase linking for more information and a full list of supported databases.

**Math formulae**
Present simple formulae in the line of normal text where possible. Single-letter variables should be italics. Number consecutively any equations that have to be displayed separately from the text.

**Footnotes**
Use footnotes only to add information below the body of a Table (using superscript letters or numbers), for probability values in Figures and Tables (using multiple asterisks) and, on the title page, for authors' affiliations (using an asterisk for the corresponding author and superscript letters for authors' affiliations). Superscript numbers may be used for coauthors' e-mail addresses and/or changes of address, and other information such as a deceased author.

**Artwork**
**Image manipulation**
While it is accepted that authors sometimes need to manipulate images for clarity, manipulation for purposes of deception or fraud will be seen as scientific ethical abuse and will be dealt with accordingly. For graphical images, this journal is applying the following policy: no specific feature within an image may be enhanced, obscured, moved, removed, or introduced. Adjustments of brightness, contrast, or colour balance are acceptable if and as long as they do not obscure or eliminate any information present in the original. Nonlinear adjustments (e.g. changes to gamma settings) must be disclosed in the figure legend.

**Electronic artwork**
**General points**
- Make sure you use uniform lettering and sizing of your original artwork.
- Preferred fonts: Arial (or Helvetica), Times New Roman (or Times), Symbol, Courier.
- Number the illustrations according to their sequence in the text.
- Use a logical naming convention for your artwork files.
- Indicate per figure if it is a single, 1.5 or 2-column fitting image.
- For Word submissions only, you may still provide figures and their captions, and tables within a single file at the revision stage.
- Please note that individual figure files larger than 10 MB must be provided in separate source files.

A detailed guide on electronic artwork is available on our website: http://www.elsevier.com/artworkinstructions.

**You are urged to visit this site; some excerpts from the detailed information are given here.**

**Formats**
Regardless of the application used, when your electronic artwork is finalized, please ‘save as’ or convert the images to one of the following formats (note the resolution requirements for line drawings, halftones, and line/halftone combinations given below):
- EPS (or PDF): Vector drawings. Embed the font or save the text as ‘graphics’.
- TIFF (or JPEG): Colour or greyscale photographs (halftones): always use a minimum of 300 dpi.
- TIFF (or JPEG): Bitmapped line drawings: use a minimum of 1000 dpi.
- TIFF (or JPEG): Combinations bitmapped line/halftone (colour or greyscale): a minimum of 500 dpi is required.

**Please do not:**
- Supply files that are optimized for screen use (e.g., GIF, BMP, PICT, WPG); the resolution is too low.
- Supply files that are too low in resolution.
- Submit graphics that are disproportionately large for the content.

**Colour artwork**
If, together with your accepted article, you submit usable colour figures, then Elsevier will ensure, at no additional charge, that these figures will appear in colour on the Web (e.g. ScienceDirect and other sites) regardless of whether these illustrations are reproduced in colour in the printed...
version. For colour reproduction in print, you will receive information regarding the costs from Elsevier's art department after receipt of your accepted article. Please indicate your preference for colour in print or on the Web only. For further information on the preparation of electronic artwork, please see http://www.elsevier.com/artworkinstructions.

Please note: Because of technical complications that can arise by converting colour figures to "greyscale" (for the printed version should you not opt for colour in print) please submit in addition usable black and white versions of all the colour illustrations.

Figure captions
Ensure that each illustration has a caption. A caption should comprise a brief title (not on the figure itself) and a description of the illustration. Keep text in the illustrations themselves to a minimum but explain all symbols and abbreviations used.

Tables
Number tables consecutively, with Arabic numerals, in accordance with their appearance in the text. Place footnotes to tables below the table body and indicate them with superscript symbols. Be sparing in the use of tables and ensure that the data presented in tables do not duplicate results described elsewhere in the article. Do not divide tables into two or more parts. Tables should not contain vertical rules, and the main body of the table should not contain horizontal rules. Large tables should be narrow (across the page) and long (down the page) rather than wide and short, so that they can be fitted into the column width of the Journal.

References

Citations in the text
Check that all references in the text are in the reference list and vice versa, that their dates and spellings match, and that complete bibliographical details are given, including page numbers, names of editors, names and full place of publication if the article is published and full place of publ. References cited in the Abstract must be given in full. Unpublished results are not recommended in the reference list. If these references are included in the reference list, they should follow the standard reference style of the Journal. Check foreign language references particularly carefully for accuracy of diacritical marks such as accents and umlauts. For papers in the course of publication, use 'in press' to replace the date and give the journal name in the references.

Web references
Because of the ephemeral nature of many Web sites, other Web citations will be reviewed by the Editors to ensure they are appropriate to an archival Journal. As a minimum, the full URL should be given. Any further information, if known (DOI, author names, dates, reference to a source publication, etc.), should also be given.

References in a special issue
Please ensure that the words 'this issue' are added to any references in the list (and any citations in the text) to other articles in the same Special Issue.

Reference management software
This journal has standard templates available in key reference management packages EndNote (http://www.endnote.com/support/enstyles.asp) and Reference Manager (http://refman.com/support/rmstyles.asp). Using plug-ins to wordprocessing packages, authors only need to select the appropriate journal template when preparing their article and the list of references and citations to these will be formatted according to the Journal style which is described below.

Reference formatting
There are no strict requirements on reference formatting at submission. References can be in any style or format as long as the style is consistent. Where applicable, author(s) name(s), journal title/book title, chapter title/article title, year of publication, volume number/book chapter and the pagination must be present. Use of DOI is highly encouraged. The reference style used by the Journal will be applied to the accepted article by Elsevier at the proof stage. Note that missing data will be highlighted at proof stage for the author to correct. If you do wish to format the references yourself they should be arranged according to the following examples:
Reference style


For text citations with:
(a) One or two authors: give each author's surname and the year of publication.
(b) Three to five authors: give each author's surname and the year of publication at first mention; at subsequent mention, give the first author's surname followed by "et al." and the year of publication.
(exception: when two or more sources shorten to the same form (i.e. they have the same primary author but different multiple coauthors), list as many of the coauthors' surnames as needed to distinguish between the sources, followed by a comma and 'et al.:' Zuur, Ieno, et al., 2009; Zuur, Walker, et al., 2009).
(c) Six or more authors: give the first author's surname followed by "et al." and the year of publication (but see exception above).

Note that 'et al.' is not in italics. Use a comma to separate the author from the date. Use lower-case letters to distinguish between two papers by the same authors in the same year (e.g. Packer, 1979a, 1979b). When two or more primary authors have the same surname, include the primary author's initials in all text citations (A. T. Smith & Ivins, 1987; F. V. Smith & Bird, 1964). List multiple citations in alphabetical, then chronological, order (e.g. Arnold, 1981a, 1981b; Halliday, 1978; Nussey et al., 2011; Sih, in press-a, in press-b; Zuur, Ieno, Walker, Savelev, & Smith, 2009), using a semicolon to separate each reference. In running text, use 'and' instead of ' & ' before the final name in a multiple-author citation: 'as described in Smith and Jones (2013)'.

Reference List:

References should be arranged first alphabetically and then further sorted chronologically if necessary. For sources with more than six authors, include the surnames and initials of the first six authors, followed by 'et al.'. More than one reference from the same author(s) in the same year must be identified as "(in press-a)", "(in press-b)", etc.

Examples:

Reference to a periodical:


Reference to a book:


Reference to an article in an edited book:


Reference to a thesis:

AUTHOR INFORMATION PACK 9 Oct 2014 www.elsevier.com/locate/anbehav


Note that journal titles in the reference list should be written in full.

For publications in any Latin script language other than English, give the original title and, in brackets, the English translation. Titles of publications in non-Latin scripts should be transliterated. Work accepted for publication but not yet published should be referred to as “in press”. Cite “personal communications” in the text only. Provide the initials and surname(s) for personal communications and give the date of the personal communication (as exact as possible), separated by a comma (A. Smith, personal communication, 9 September 2013).

**Video data**

Elsevier accepts video material and animation sequences to support and enhance your scientific research. Authors who have video or animation files that they wish to submit with their article are strongly encouraged to include links to these within the body of the article. This can be done in the same way as a figure or table by referring to the video or animation content and noting in the body text where it should be placed. All submitted files should be properly labeled so that they directly relate to the video file's content. In order to ensure that your video or animation material is directly usable, please provide the files in one of our recommended file formats with a preferred maximum size of 50 MB. Video and animation files supplied will be published online in the electronic version of your article in Elsevier Web products, including ScienceDirect: http://www.sciencedirect.com. Please supply 'stills' with your files: you can choose any frame from the video or animation or make a separate image. These will be used instead of standard icons and will personalize the link to your video data. For more detailed instructions please visit our video instruction pages at http://www.elsevier.com/artworkinstructions. Note: since video and animation cannot be embedded in the print version of the journal, please provide text for both the electronic and the print version for the portions of the article that refer to this content.

**AudioSlides**

The journal encourages authors to create an AudioSlides presentation with their published article. AudioSlides are brief, webinar-style presentations that are shown next to the online article on ScienceDirect. This gives authors the opportunity to summarize their research in their own words and to help readers understand what the paper is about. More information and examples are available at http://www.elsevier.com/audioslides. Authors of this journal will automatically receive an invitation e-mail to create an AudioSlides presentation after acceptance of their paper.

**Supplementary data**

Elsevier accepts electronic supplementary material to support and enhance your scientific research. Supplementary files offer the author additional possibilities to publish supporting applications, high-resolution images, background datasets, sound clips and more. Supplementary files supplied will be published online alongside the electronic version of your article in Elsevier Web products, including ScienceDirect: http://www.sciencedirect.com. In order to ensure that your submitted material is directly usable, please provide the data in one of our recommended file formats. Authors should submit the material in electronic format together with the article and supply a concise and descriptive caption for each file. For more detailed instructions please visit our artwork instruction pages at http://www.elsevier.com/artworkinstructions.

**Google Maps and KML files**

KML (Keyhole Markup Language) files (optional): You can enrich your online articles by providing KML or KMZ files which will be visualized using Google maps. The KML or KMZ files can be uploaded in our online submission system. KML is an XML schema for expressing geographic annotation and visualization within Internet-based Earth browsers. Elsevier will generate Google Maps from the submitted KML files and include these in the article when published online. Submitted KML files will also be available for downloading from your online article on ScienceDirect. For more information see http://www.elsevier.com/gooliemaps.
**Submission checklist**

The following list will be useful during the final checking of an article prior to sending it to the journal for review. Please consult this Guide for Authors for further details of any item.

**Ensure that the following items are present:**

One author has been designated as the corresponding author with contact details:

- E-mail address
- Full postal address
- Telephone

All necessary files have been uploaded, and contain:

- Keywords
- All figure captions
- All tables (including title, description, footnotes)

Further considerations:

- Manuscript has been 'spell-checked' and 'grammar-checked'
- Manuscript should have continuous line numbers and double spacing
- All references mentioned in the Reference list are cited in the text, and vice versa
- Permission has been obtained for use of copyrighted material from other sources (including the Web)
- Color figures are clearly marked as being intended for color reproduction on the Web (free of charge)
- and in print, or to be reproduced in color on the Web (free of charge) and in black-and-white in print
- If only color on the Web is required, black-and-white versions of the figures are also supplied for printing purposes

For any further information please visit our customer support site at [http://support.elsevier.com](http://support.elsevier.com).

**AFTER ACCEPTANCE**

**Use of the Digital Object Identifier**

The Digital Object Identifier (DOI) may be used to cite and link to electronic documents. The DOI consists of a unique alpha-numeric character string which is assigned to a document by the publisher upon the initial electronic publication. The assigned DOI never changes. Therefore, it is an ideal medium for citing a document, particularly ‘Articles in press’ because they have not yet received their full bibliographic information. Example of a correctly given DOI (in URL format; here an article in the journal *Physics Letters B*):

[http://dx.doi.org/10.1016/j.physletb.2010.09.059](http://dx.doi.org/10.1016/j.physletb.2010.09.059)

When you use a DOI to create links to documents on the web, the DOIs are guaranteed never to change.

**Proofs**

One set of page proofs in PDF format will be sent by e-mail to the corresponding author. Elsevier now sends PDF proofs which can be annotated; for this you will need to download Adobe Reader® version 7 (or higher) available free from [http://www.adobe.com/products/acrobat/readstep2.html](http://www.adobe.com/products/acrobat/readstep2.html). Instructions on how to annotate PDF files will accompany the proofs. The exact system requirements are given at the Adobe site: [http://www.adobe.com/products/reader/systemreqs](http://www.adobe.com/products/reader/systemreqs). If you do not wish to use the PDF annotations function, you may list the corrections (including replies to the Query Form) in an e-mail. Please list your corrections quoting line number. If, for any reason, this is not possible, then mark the corrections and any other comments (including replies to the Query Form) on a printout of your proof and return by fax, or scan the pages and e-mail, or by post. Please use this proof only for checking the typesetting, editing, completeness and correctness of the text, tables and figures. Significant changes to the article as accepted for publication will only be considered at this stage with permission from the Editor. We will do everything possible to get your article published quickly and accurately. Therefore, it is important to ensure that all of your corrections are sent back to us in one communication: please check carefully before replying, as inclusion of any subsequent corrections cannot be guaranteed. Proofreading is solely your responsibility. Note that Elsevier may proceed with the publication of your article if no response is received.

**Author’s discount**

Contributors to Elsevier journals are entitled to a 30% discount on most Elsevier books, if ordered directly from Elsevier.

**Offprints**

The corresponding author, at no cost, will be provided with 25 free paper offprints, or, alternatively, a personalized link providing 50 days free access to the final published version of the article on [ScienceDirect](http://www.sciencedirect.com). This link can also be used for sharing via
email and social networks. For an extra charge, more paper offprints can be ordered
via the offprint order form which is sent once the article is accepted for publication.
Both corresponding and co-authors may order offprints at any time via Elsevier’s WebShop
(http://webshop.elsevier.com/myarticleservices/offprints). Authors requiring printed copies of
multiple articles may use Elsevier WebShop’s 'Create Your Own Book' service to collate multiple articles
within a single cover (http://webshop.elsevier.com/myarticleservices/booklets).

AUTHOR INQUIRIES
You can track your submitted article at http://help.elsevier.com/app/answers/detail/a_id/89/p/8045/.
You can track your accepted article at http://www.elsevier.com/trackarticle. You are also welcome to

© Copyright 2014 Elsevier | http://www.elsevier.com
7 REFERENCES


IVKOVICH, T., FILATOVA, O. A., BURDIN, A. M., SATO, H. & HOYT, E. 2010. The social organization of resident-type killer whales (Orcinus orca) in Avacha Gulf,


