

1 **Both environmental conditions and intra- and interspecific interactions**  
2 **influence the movements of a marine predator**

3

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26 **ABSTRACT**

27 Animal movements are typically influenced by multiple environmental factors  
28 simultaneously and individuals vary in their response to this environmental heterogeneity.  
29 Therefore, understanding how environmental aspects, including biotic, abiotic and  
30 anthropogenic factors, influence the movements of wild animals is an important focus of  
31 wildlife research and conservation. We apply exponential random graph models (ERGMs) to  
32 analyse movement networks of a bull shark population in a network of acoustic receivers and  
33 identify the effects of environmental, social or other types of covariates on their movements.  
34 We found that intra- and interspecific factors often had stronger effects on movements than  
35 environmental variables. ERGMs proved to be a potentially useful tool for studying animal  
36 movement network data especially in the context of spatial attribute heterogeneity.

37

38 Keywords: spatial-social interface, acoustic telemetry; *Carcharhinus leucas*; ERGM;  
39 movement networks; Indian Ocean; Reunion Island; shark.

40           Understanding animal movement is not straightforward, as movement decisions result  
41 from a combination of many factors including the internal state of the individual, its intra-  
42 and interspecific neighbourhood, and spatio-temporal variation in abiotic environmental  
43 conditions (Nathan et al., 2008). Additionally, the response of individuals to variation in their  
44 surrounding environment can differ across spatial and temporal scales. Daily activities can be  
45 influenced by environmental factors that vary over a diel cycle (e.g., wind or tidal currents),  
46 while seasonal movement can be governed by changes acting at larger temporal scales (e.g.,  
47 photoperiod, temperature). Quantifying how heterogeneity in an animal's surroundings drives  
48 behaviour, and consequently movement patterns, provides insight into how natural and  
49 anthropogenic changes may impact populations and ecosystems.

50           One potential way to understand the 'causes, mechanisms and spatiotemporal patterns  
51 of movement and their role in various ecological and evolutionary processes' (Nathan et al.  
52 2008) is to link observed movement patterns with spatial and temporal variability in the  
53 underlying environmental conditions (Avgar et al., 2013). Movement patterns result from  
54 interactions between organisms and their environments (Johnson et al., 1992; Morales et al.,  
55 2010; Schick et al., 2008). For example, movement rates are expected to decrease where  
56 resources are rich and decrease where food availability is low (Kuefler et al., 2012; Pyke et  
57 al., 1977). Understanding movement patterns thus requires consideration of the temporally  
58 dynamic nature of these environments (Avgar et al., 2013; Couriot et al., 2018; Mueller et al.,  
59 2011; Riotte-Lambert & Matthiopoulos, 2020; Schick et al., 2008).

60           In addition to interacting with their physical environment (e.g. habitat features  
61 offering essential resources, conditions or shelter), animals also interact with other  
62 individuals of the same or different species. These spatial encounters with conspecific or  
63 heterospecific individuals may be advantageous or unfavourable. For example, aggregations  
64 form to avoid predation or to forage efficiently (Krause & Ruxton, 2002), although the

65 tendency for non-gregarious species to seek or avoid each other is less well known. For all  
66 sexual species, individuals need to encounter conspecifics at least for mating, but avoiding  
67 opposite-sex individuals (sexual segregation) may play a major role in preventing sexual  
68 harassment in some species (Wearmouth & Sims, 2008). Additionally, avoidance strategies  
69 can act at the intra or interspecific level in the context of competition for mates, space or  
70 resources (Giuggioli & Kenkre, 2014), or in the context of predator–prey interactions  
71 (Atwood et al., 2009). Because individuals may select habitats based on exogenous  
72 environmental features (e.g. habitat quality and predation risk), and local population factors  
73 (e.g., mating opportunities, competition or density dependence), we need to quantify the  
74 mechanisms by which dynamic interactions between individuals occur (e.g. movement  
75 towards or away from other individuals).

76         Therefore, social behaviour is intrinsically connected with spatial behaviour and a  
77 burgeoning literature now addresses the link between spatial and social aspects of behaviour  
78 defined as the “spatial-social interface” (Webber et al., 2023). Indeed, while spatial and social  
79 processes have been predominantly considered independently, because movement behaviour  
80 emerges from social and spatial processes, animal movement studies offer an opportunity to  
81 consider and integrate them (Albery et al., 2021; He et al., 2019; Mourier et al., 2019;  
82 Webber et al., 2023).

83         Finally, the human footprint has altered the spatial ecology of many species at  
84 different spatial and temporal scales, for example by decreasing animal movements as a  
85 result of behavioural changes, habitat fragmentation and barrier effects (Tucker et al., 2018),  
86 or by modifying activity-timing (Gilbert et al., 2023). COVID-19 lockdowns provided an  
87 empirical experiment where an abrupt reduction in human activity (so called Anthropause)  
88 led to decreases in animal movement rates and avoidance patterns of human footprint (Tucker  
89 et al., 2023). Human disturbance can also fundamentally alter the way that species interact,

90 such as by causing a spatiotemporal compression of species co-occurrences in disturbed  
91 landscape which can lead to increases in competition, predation and infectious disease  
92 transmission (Gilbert et al., 2022). As such, incorporating human footprint as a potential  
93 factor affecting animal movements at the spatial-social interface is now more relevant than  
94 ever.

95         In this study, we explore the connection between seascape attributes and animal  
96 movement patterns for a population of bull shark (*Carcharhinus leucas*) that inhabit a coastal  
97 zone in Reunion Island (Indian Ocean), which encompasses a variety of environmental  
98 conditions. We evaluate the relative importance of spatiotemporal variables associated with  
99 several main aspects of the seascape (abiotic conditions, social environment, predation risk or  
100 interspecific competition and anthropogenic pressure) as potential drivers of shark movement  
101 patterns. This approach allows us to identify fundamental relationships between local  
102 environmental conditions and animal movement patterns.

103         To do so, we used a network-based modelling that account for the non-independence  
104 of the data of movements between location. We applied exponential random graph models  
105 (ERGMs; Lusher, Koskinen, & Robins, 2012; Robins, Pattison, Kalish, & Lusher, 2007) to  
106 monthly individual movement networks of bull sharks between listening stations (i.e.  
107 acoustic receivers) deployed along the west coast of Reunion Island (Mourier et al., 2021;  
108 Soria et al., 2019), using varying covariate attributes at these locations. ERGMs are statistical  
109 models of networks that treat the weight of network edges (i.e. number of movements  
110 between two nodes) as the response variable and network node (i.e. acoustic receivers)  
111 attributes as explanatory variables (Robins, Pattison, et al., 2007; Robins, Snijders, et al.,  
112 2007; Snijders et al., 2006). These models account for the non-independence of the data  
113 expressed as movements between sites acting as sources or sinks (Silk & Fisher, 2017).

114 Bull shark movements are known to be influenced by both biotic and abiotic factors  
115 (Lee et al., 2019; Lubitz et al., 2023; Niella et al., 2022; Werry et al., 2018), and  
116 anthropogenic factors (Hammerschlag et al., 2022; Werry et al., 2012), but less is known  
117 about the importance of con- and heterospecifics in movement decisions. Even if most  
118 studies on the movements of these marine predators have identified environmental factors as  
119 most influential to their movement ecology, we expect that social and competition factors  
120 may be just as important in explaining individual movements. We incorporated swell height,  
121 turbidity and rainfall levels as abiotic predictive variables of movements, turtle densities as a  
122 potential indicator of the presence of sharks as suggested by local people, cumulative number  
123 of sea users as an anthropogenic variable, as well as various intra- and interspecific factors  
124 such as residency times of the opposite sex, abundance of bull sharks and occupancy of tiger  
125 sharks (a larger and likely competitor species). Our analysis was designed to test whether  
126 individual bull sharks move according to the distribution of conspecifics and heterospecifics  
127 in the seascape, and whether these effects were comparable with expected positive effects of  
128 swell height, turbidity and rainfall on shark movements and negative effects of human  
129 densities (with sharks avoiding human presence). While segregation, resource partitioning  
130 and competition processes may all shape bull shark movements, we had no clear directional  
131 predictions of their effect due to the limited previous research on this population on these  
132 aspects.

133

## 134 **METHODS**

### 135 *Study species and local context*

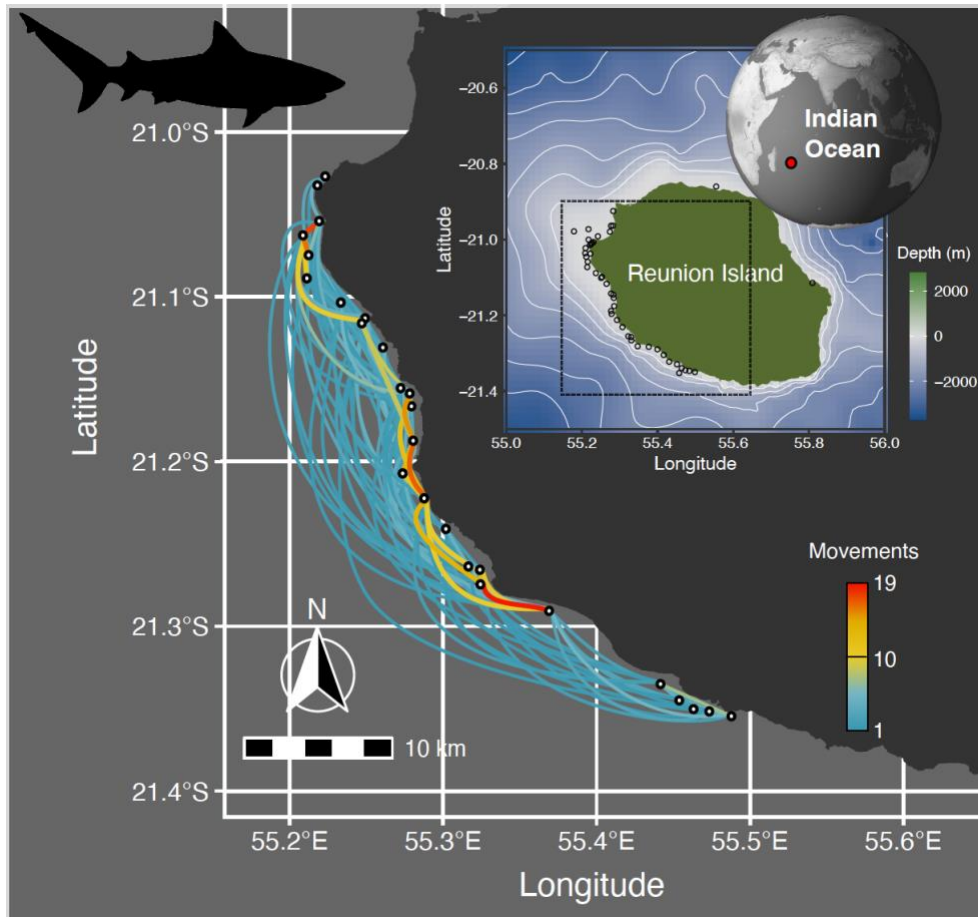
136 The bull shark is a large Carcharhinidae with a wide cosmopolitan distribution along the  
137 continental coasts of all tropical and sub-tropical waters of the world and is known to be  
138 mobile and move across a large range of habitats and environmental conditions

139 (Brunnschweiler et al., 2010; Daly et al., 2014; Espinoza et al., 2016; Heupel et al., 2015; Lee  
140 et al., 2019; Niella et al., 2022). Additionally, it is also an euryhaline elasmobranch that uses  
141 a range of salinities throughout its life-cycle (Niella et al., 2022). Its behaviour varies across  
142 spatial and temporal scales, as well as according to size and sex, with a high individual  
143 variability in the tendency to move (Espinoza et al., 2016; Lee et al., 2019; Mourier, Soria, et  
144 al., 2021). However, much remains unclear about adult bull shark movement decisions.

145

146 Reunion Island (21°07'S / 55°32'E) is a volcanic island located 700 km east of Madagascar  
147 in the southwest Indian Ocean. The island is 2512 km<sup>2</sup> with 217 km of coastline and  
148 characterized by steep underwater slopes (*ca.* 10-20%) to a depth of 2,000 m. Fringing reefs  
149 stretch over 25 km along the west and south-west coast (Fig. 1) forming a natural coral  
150 barrier that bounds the reef flats and back-reef depressions and lies no further than 500 m  
151 from the beach.

152



153

154 **Figure 1:** Cumulative number of movements across all 44 monthly individual movements  
155 used in the ERGM analyses concentrated on the western part of Reunion Island. Circles  
156 represent acoustic receivers. Inset map represents the location of Reunion Island and the area  
157 where the movements were recorded.

158

### 159 *Acoustic telemetry and movement network*

160 Sharks were captured along the west coast of Reunion Island between September 2012 and  
161 March 2013 (Supplementary material 1 Table S1), using horizontal drifting long-lines 0.2 to  
162 1 km in length and equipped with 20 to 200 baited 16/0 circle hooks (Blaison et al., 2015).  
163 Set times were fixed at a maximum of 3 h to minimize shark and bycatch mortality. Once  
164 captured, a shark was brought alongside the vessel and held still by rubber-encased ropes to  
165 prevent skin lesions and burns and rolled onto its back to induce tonic immobility. The boat



166 moved forward slowly throughout the procedure to allow the shark to breathe. Sanitized  
167 transmitters were implanted into the peritoneal cavity through a midventral incision using a  
168 sterile scalpel. A 1cm incision was made, then enlarged with retractors. The muscle was then  
169 gently torn in the direction of the fibers to allow faster muscle tissue repair. Once the tag was  
170 in place, two stitches were done to close the incision and facilitate healing. A sterile, non-  
171 absorbable synthetic monofilament suture (polyamide) was used. Absorbable sutures  
172 disintegrate too quickly. Braided sutures were more likely to increase the risk of infection  
173 allowing seawater to enter in the tissue. The shark was then freed by cutting the hook at its  
174 base and removing it, untying the lasso, replacing it on its belly and oxygenating it by  
175 moving it back and forth or slowly forward until the first signs of autonomous movement  
176 appear. Sex and total length (TL) were recorded and transmitters (Vemco V16, transmission  
177 interval 40–80 s, estimated battery life 845 days) were implanted into the peritoneal cavity  
178 through a midventral incision.

179

180 An array of 46 Vemco VR2W acoustic receivers was deployed along the coast with receivers  
181 installed an average of approximately 2 km apart at depths of 10–60 m, comprising 33 (71%)  
182 offshore receivers and 13 (29%) inshore receivers placed less than 300 m from shore (Fig. 1).

183

184 For each shark visit at a receiver, we used detection records to calculate a continuous  
185 residency time (CRT) corresponding to the duration within which a tagged shark was  
186 continuously monitored at a specific receiver without one hour-scale (> 1h) absences  
187 (Capello et al., 2015; Ohta & Kakuma, 2005). All detections of the same shark at one  
188 receiver separated by less than a predefined period, called the maximum blanking period  
189 (1 h), were grouped into one CRT and defined as a visit. Each time a tagged shark was

190 detected at a different receiver, a new visit started - ending the visit at the previous receiver -  
191 even if the interval between detections was less than the maximum blanking period.

192

193 We then built monthly movement networks of each shark with each node representing a  
194 receiver along the coast of Reunion Island and each weighted, directed edge represented the  
195 number of movements of the individual (deduced from CRT) from node A to node B (Fig. 1)  
196 within a given month.

197

#### 198 *Ethical Note*

199 All the fieldwork and protocols of handling and tagging of sharks were approved by the  
200 Ethics Committee (n° 114) for the CYROI (Cyclotron Réunion Océan Indien). Procedures  
201 were adapted to minimize stress on animals and avoid mortality. The use of circular hooks  
202 prevented the shark from swallowing them. All sharks swam away in good condition after  
203 being released. The procedure usually lasted less than 30 min. Most sharks were detected and  
204 therefore remained alive during the experiment (mean days of detections  $88.3 \pm 79.4$ ; min =  
205 1, max = 285). Two sharks were caught and removed by local fishermen and two others were  
206 never detected after being released. All operations were carried out or supervised by  
207 scientists with a certificate in animal experimentation and a certificate in experimental  
208 surgery (Oniris, Ecole Nationale Vétérinaire de Nantes).

209

#### 210 *Explanatory variables*

211 We gathered data of different nature (i.e. biological, abiotic, anthropogenic and spatial) that  
212 were accessible in the study area. Although non exhaustive, explanatory variables recorded  
213 included a number of environmental, biological and anthropogenic factors (Table 1; a  
214 detailed description of how they were recorded can be found in Supplementary material 1) as

215 well as the geographical distances between receivers. As all data were not available at the  
 216 same spatial and temporal scale, we chose to standardize all available candidate explanatory  
 217 data at the scale of one month for each receiver. This choice of resolution of the data is a  
 218 compromise to keep a valuable temporal scale of the variability of site conditions and in the  
 219 same time having enough movements to construct individual networks that represent  
 220 biologically meaningful variations. For some environmental variables such as rainfall,  
 221 multiple nearby receivers shared values as data were available for a specific zone including  
 222 several receivers. All explanatory variables were standardized to have a mean of 0 and a  
 223 standard deviation of 1.

224

225 Table 1: Predictor parameters included in the ERGMs.

Variables	Category	Description	Range	Source
Occupancy Tiger sharks	Biological	Frequency of days at least a tiger shark was detected at the receiver for each month (%)	[0-0.409]	Current acoustic telemetry data
Same sex CRT	Biological	Total CRT of bull sharks of the same sex for each month (hour)	[0.033-118.425]	Current acoustic telemetry data
Opposite sex CRT	Biological	Total CRT of bull sharks of the opposite sex for each month (hour)	[0.033-118.425]	Current acoustic telemetry data
Bull Shark abundance	Biological	Number of bull sharks present at the listening station divided by the number of bull shark with an active tag for each month	[0-1.24]	Current acoustic telemetry data
Turtle density	Biological	Mean density of turtles in the area of the receiver from aerial survey (nb/km <sup>2</sup> )	[0-15.873]	Aerial surveys
Turbidity	Environmental	Average monthly reflectance for each zone over the multiple images (%)	[4.101-8.886]	Satellite SPOT 4 & 5
Rain	Environmental	Mean rain fall for each watershed for each month (mm)	[0.008-25.460]	METEO-France
Swell	Environmental	Height of the swell near the listening station for each month (m)	[0.557-2.636]	AVISO portal, CANDHIS & METEOLAMER platform
Human activities	Anthropogenic	Cumulated number of human activities (boats, swimmers, nautical activities) for each month	[0-1276.5]	Aerial surveys
Geodist	Spatial	Distance between stations (km)	[0.9-120]	Current acoustic telemetry data

226

227

## 228 *Exponential Random Graph Models*

229 As care is required when conducting statistical analysis of network data because of issues  
 230 related to potential non-independence among neighbouring nodes and edges (Croft et al.,  
 231 2011), we used Exponential Random Graph Models (ERGMs). ERGMs are statistical models  
 232 of networks that treat the weight of network edges as the response variable and network node

233 and edge attributes as explanatory variables (Robins, Pattison, et al., 2007; Robins, Snijders,  
234 et al., 2007; Snijders et al., 2006). Such models are analogical to Generalized Linear Models  
235 (GLMs) except that they enable hypothesis testing about the processes driving network  
236 structure and link formation. These models have been mostly applied in social science, but  
237 their properties also make them useful for answering questions related to how and why  
238 animals move between locations in the context of movement networks (Fletcher et al., 2011;  
239 Jacoby & Freeman, 2016; López-Calderón et al., 2023). Effectively the movement network  
240 becomes the response in a regression model, where the predictors are the propensity for  
241 nodes (i.e. locations) of similar or dissimilar attributes to be linked by movements.

242

243 The general form for an ERGM can be written as:

244 
$$P(Y = y; \theta, x) = \frac{\exp(\theta^T g(y, x))}{\kappa(\theta, x)} \quad (1)$$

245 where:

- 246 •  $Y$  is the random variable for the state of the network (with realization  $y$ ),
- 247 •  $g(y, x)$  is a vector of model statistics for network  $y$ ,
- 248 •  $\theta$  is the vector of coefficients for those statistics, and
- 249 •  $\kappa(\theta)$  is a normalizing term which ensures that equation (1) is a proper probability  
250 distribution. It represents the quantity in the numerator summed over all possible  
251 networks (typically constrained to be all networks with the same node set as  $y$ ).

252 The numerator represents a formula that is linear in the log form:

253 
$$\log(\exp(\theta' g(y))) = \theta_1 g_1(y) + \theta_2 g_2(y) + \dots + \theta_p g_p(y)$$

254 where  $p$  is the number of terms in the model. From this one can more easily observe the  
255 analogy to a traditional statistical model. The functions  $g(y)$  are counts of configurations in  
256 the network  $y$  and the parameters  $\theta$  weight the relative importance of the respective  
257 configurations, effectively the size and direction of the effects of the covariates. Parameter

258 estimation in most specifications of ERGMs uses maximum pseudo-likelihood, an  
259 approximation of maximum likelihood based on Monte Carlo estimation.

260 All ERGMs were fitted using R packages *ergm* and *ergm.count* (Hunter et al., 2008).

261

### 262 *Model-fitting process*

263 Node attributes were varying at the month scale so we built a model for each monthly-  
264 individual network. To ensure that it was possible to fit ERGMs to monthly networks and  
265 improve model convergence, we first removed from monthly movement networks all  
266 receivers that were deployed less than 20 days during the month, as well as all individuals  
267 that did not present an active tag for at least 20 days during a month. This empirical choice  
268 was made as a compromise between data loss and data representativity. We also retained only  
269 monthly individual networks containing at least 10 different directed movements between  
270 receivers, as networks including low numbers of movements caused problems with model  
271 convergence and parameter estimation. We also excluded two monthly networks that were  
272 binary (i.e. only contained at most single movements along any particular edge). This left us  
273 with 42 monthly networks of 13 individuals (9 females: 4 males; mean/median/range of  
274 monthly networks per individual = 3.1/3/1-6).

275

276 For each monthly network for each shark, we then fitted two alternative versions of the full  
277 model that each modelled different effects of the environmental variables being studied  
278 (Table 1). The effect estimated for each factor represents the difference from the intercept as  
279 with classical GLMs. All models included the term “non-zero” to control for zero-inflation  
280 generated by the weighted movement networks being sparse and the term “sum”,  
281 corresponding to the sum of all link values, was included as the equivalent to the intercept in  
282 a linear model (Dey & Quinn, 2014).

283

284 The two model sets differed as follows:

- 285 • Model set 1: we tested the association between the current state of the environment at  
286 each receiver location and number of movements towards and away from it (i.e. effect  
287 of an attribute on out- and in-degree). These models used the *nodecov* term in the  
288 fitted ERGMs.
- 289 • Model set 2: we tested the association between the absolute difference in current state  
290 of the environment at dyads (pairs) of receiver locations and number of movements  
291 between them. These models used the *absdiff* term in the fitted ERGMs.

292

293 We used a *nodecov* model rather than separate *nodeicov* and *nodeocov* models (movements  
294 towards and away from receivers respectively) as simulations indicated the results were  
295 qualitatively identical (see Supplementary material 2).

296 We fitted the *nodecov* and *absdiff* models separately to facilitate model parsimony and  
297 convergence and test the robustness of the movement patterns discovered while controlling  
298 for the full suite of environmental variables. Indeed, incorporating all variables and models  
299 sets combinations would prevent convergence of models and render interpretation of output  
300 complex. To account for the effect of the spatial distribution of nodes in our models, we  
301 included as a covariate the matrix of distances between nodes.

302 For each model set, we then wrote a model formula including all potential predictors as  
303 follows:

304  $graph\sim nonzero + sum + term(Variable\ 1) + term(Variable\ 2) + \dots + term(Variable\ n) +$   
305  $edgecov(Geodist, 'Geodist')$

306 where *term* can be replaced by *nodecov* and *absdiff* in model sets 1 and 2 respectively. An  
307 *edgecov* term was added to control for the distance between locations. Models were fitted

308 with a Poisson reference distribution for edge weights creating the familiar log-linear effect.  
309 The final coefficient estimates indicate log-linear increase in the weight variable  
310 (movements). MCMLE.Hummel.maxit was set to 1000 and MPLE.type was set to  
311 “penalized” so that the maximum penalized likelihood estimate was calculated using a bias-  
312 reduced method.  
313 For each model set for each individual monthly network, we used Akaike Information  
314 Criterion (AIC) to compare the AIC of 49 candidate models nested within the full model and  
315 keep only the model that most parsimoniously explained the movements of the individual  
316 during the month considered. Any models with convergence issues were discarded.  
317 We then re-fitted all selected ERGMs for each combination of both model sets (*nodcov* and  
318 *absdiff*) and individual monthly networks. From these final models we extracted model  
319 estimates and their standard errors, and also MCMC diagnostics (Gewecke’s convergence  
320 diagnostic and  $\hat{R}$ ) to ensure convergence.  
321 To summarize the results incorporating each selected models, we extracted parameter  
322 estimates and associated standard errors from selected variables from each selected models,  
323 and followed a meta-analysis procedure in which each sample (monthly-individual  
324 movement network) was treated as a single ‘Study’. Effect sizes were calculated using and  
325 inverse-variance weighting meta-analysis for each sample and grouped by variables using a  
326 sub-grouping analysis. This allows to test if differences in effect sizes exist only due to  
327 sampling error, or because of true differences in the effect sizes. This procedure was made for  
328 the overall samples as well as separating by sex and by season. The meta-analysis was  
329 conducted using the package ‘meta’ in R (Schwarzer, 2007).  
330

331 *Simulation methods*

332 To ensure the correct interpretation of our model results and check for potential limitations of  
333 the ERGM methods applied to our dataset we used a simulation approach. In short, we  
334 simulated a series of individual movement trajectories that matched our empirically collected  
335 data. We then fitted ERGMs in the same way we did for the empirical data.  
336 We generated sets of 25 receiver locations (equivalent to the empirical data) positioned in 2D  
337 space and generated three environmental properties for each receiver location termed  
338 factorA, factorB and factorC. We then generated 21 simulation input parameter sets that  
339 varied the effect of factorA on the probability of movements between locations while keeping  
340 factorB and factorC fixed as having no effects on movement (Supplementary material 2  
341 Table S2). We considered scenarios where movements were conducted according to a  
342 gradient in factorA or occurred between similarly high or low factorA locations. For each  
343 simulation input parameter set we simulated the movements of 10 sharks. The number of  
344 movements for each shark was drawn from a Poisson distribution with a mean of 23  
345 (equivalent to the empirical dataset). Detailed methods are in Supplementary materials 2.

346

347

348 **RESULTS**

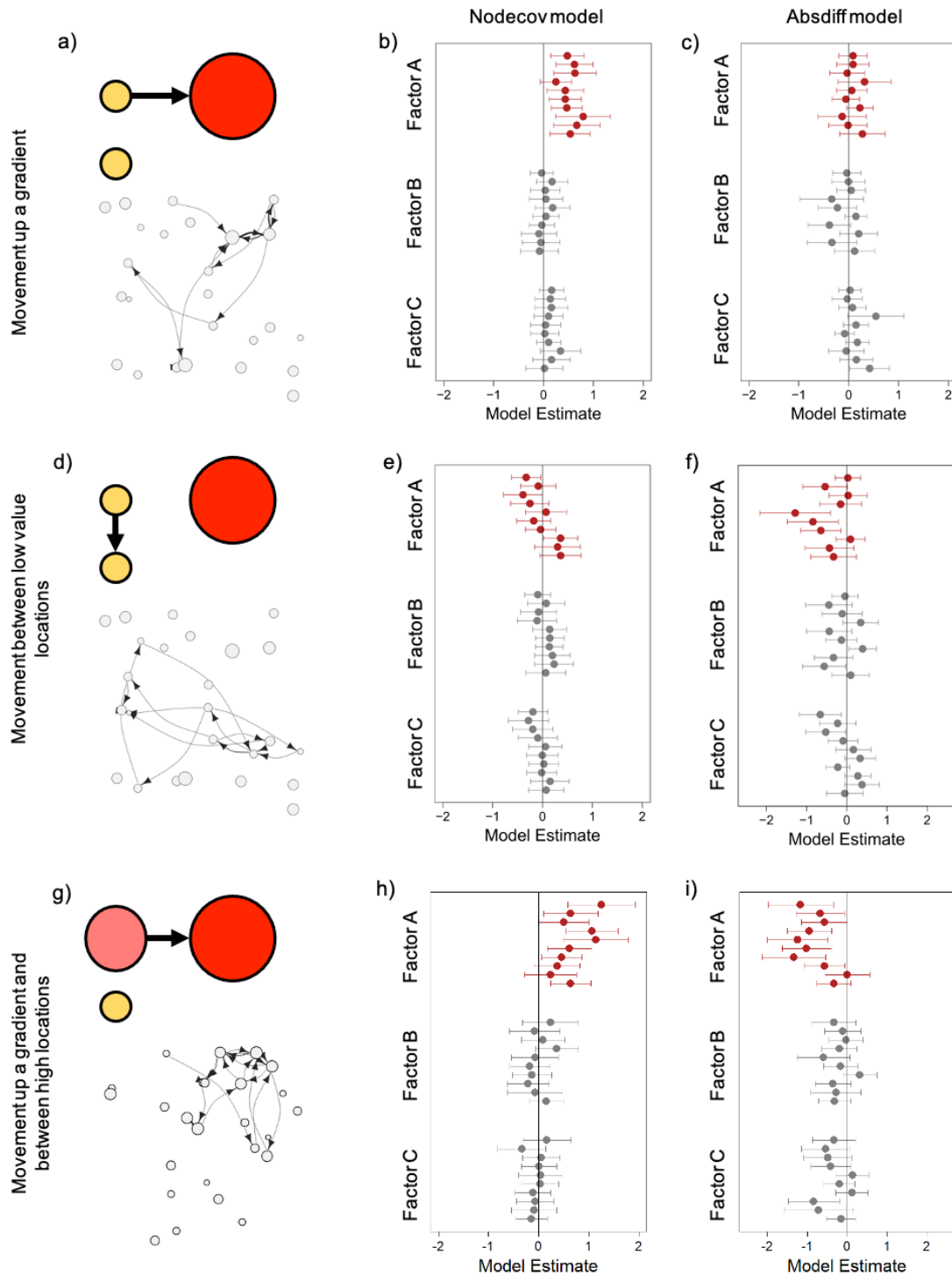
349

350 *Interpretations of model outputs from simulations*

351 Our simulation study revealed ERGMs performed as expected when analysing movement  
352 networks of a similar size and structure to our empirically-measured networks (see  
353 Supplementary Materials 2). Model estimates for the *nodecov* and *absdiff* models typically  
354 accurately represented the presence of movements up a gradient or between similar locations  
355 respectively (Fig. 2). The statistical power to detect true effects was limited for individual



356 networks, and there were slightly elevated false positive rates for the *absdiff* models.  
357 However, effect size estimates were largely unbiased (both with and without true simulated  
358 effects), with the only exceptions being that *absdiff* models underestimated the tendency to  
359 move between similar locations when there was also a gradient effect, and that *absdiff* models  
360 overestimated the tendency to move between similar locations when sharks tended to start  
361 moving from high value locations and had a strong tendency to move up a gradient (although  
362 the latter would be expected if this resulted in sharks moving only between high value  
363 locations). Collectively these results indicate that collating estimates from multiple models  
364 (as we do in our main analysis) will provide the most informative results. Simulations also  
365 indicated that *nodeicov* and *nodeocov* models provided closely correlated results leading to us  
366 using a single *nodecov* model in our empirical analysis (see above).



367

368 Figure 2: Interpretation of the model output for each scenario based on simulations: (a, b, c)

369 movements up a gradient of Factor A (e.g. swell height), (d, e, f) movements between

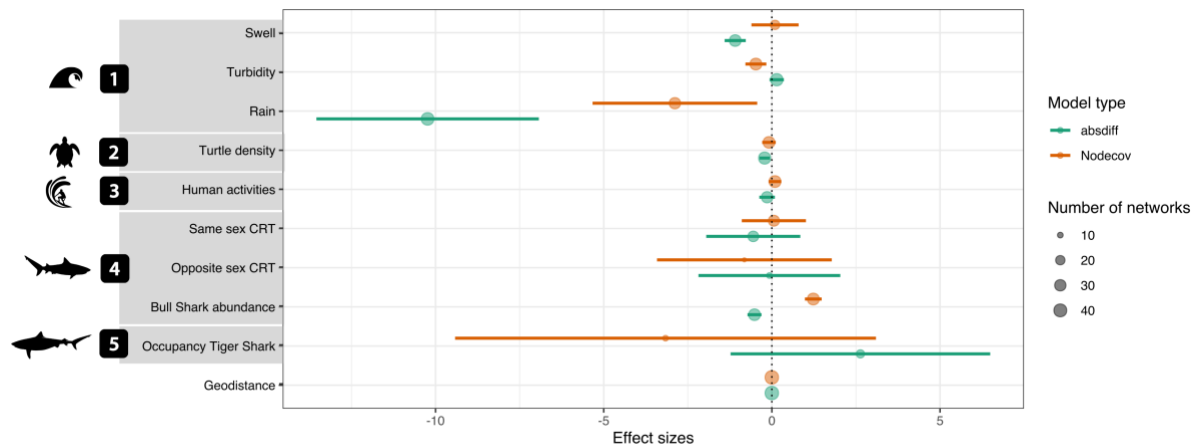
370 locations of low Factor A and (g, h, i) movement up a gradient and between locations of high

371 Factor A. (a, d, g) Toy examples on the left and movement network for the first shark. (b, e,

372 h) model estimates for *nodecov* and (c, f, i) model estimates for *absdiff*. The model estimates  
373 are for the three effects (highlighting the one where there is a true effect in red) and then for  
374 each of the 10 sharks simulated.

375

### 376 *Effects of abiotic conditions*



377

378 Figure 3: Summary of the outputs from the ERGM models from the 42 selected individual  
379 monthly movement networks. Effect sizes and their 95% confidence intervals pooled over  
380 variables are reported for the parameter estimate of terms *nodecov* and *absdiff*. Variables  
381 were grouped in several categories: (1) environmental factors, (2) turtle density, (3)  
382 anthropogenic factors, (4) social or intraspecific interactions, and (5) competitive or  
383 interspecific interactions. The variable “Geodistance” controls for the distance between  
384 receivers. Circle size is proportional to the number of models in which the coefficient of the  
385 term was significant and therefore selected.

386

387 Our models were designed to test whether sharks were moving between locations with  
388 similar values (tested by the *absdiff* term) and/or towards locations with higher/lower values  
389 (tested by the *nodecov* term) of an abiotic condition, specifically swell height, degree of  
390 turbidity and level of rainfall. Model results indicated the environmental variables that were

391 associated with movement network structure (Fig. 3). While high swell at a location was not  
392 significantly associated with more movements, movements between locations that differed  
393 considerably in swell height were much less frequent than movements between locations with  
394 similar swells as demonstrated by negative values of the *absdiff* model. Together, these  
395 outputs indicate that sharks move between locations characterized by similar swell and not  
396 across a gradient of swell heights. The *nodecov* model revealed a statistically negative effect  
397 of turbidity on movements, indicating that more movements occurred through low turbidity  
398 locations. Further, the *absdiff* model revealed that sharks were also more likely to move  
399 between receiver locations that differed from each other in their turbidity. Collectively these  
400 results suggest that sharks moved down turbidity gradients and then more frequently among  
401 locations with lower turbidity. Sharks also tended to move between receiver locations with  
402 similar and low rainfall levels.

403

#### 404 *Effect of turtle densities*

405 Our models could also test whether sharks were moving toward high or low densities of  
406 turtles (tested by the *nodecov* term) and/or were remaining in habitats with similar densities  
407 (tested by the *absdiff* term). Model outputs indicated that movements were more likely  
408 between receiver locations with more similar turtle densities (negative estimate from *absdiff*  
409 model). However, parameter estimates were small indicating that the biological importance  
410 of turtle distribution densities may be limited.

411

#### 412 *Effect of anthropogenic factors*

413 Our models were also set up to test whether sharks were avoiding (tested by the *nodecov* term  
414 with an expected negative coefficient) and/or remaining in areas of similar human activity  
415 (tested by the *absdiff* term with an expected negative coefficient). Models indicated that there

416 were more movements among locations with high human activities (positive *nodecov* effect  
417 and negative *absdiff* effect). However, parameter estimates from the models were close to  
418 zero suggesting that the biological importance of anthropogenic factors such as human  
419 activities on bull shark movements in the monitored area were relatively limited.

420

#### 421 *Influence of conspecifics*

422 Our models were also used to test whether sharks moved towards or avoided conspecifics  
423 (tested by the *nodecov* term) and/or remained within areas with similar populations of  
424 conspecifics (tested by the *absdiff* term). Receiver locations in which bull sharks were present  
425 or more abundant were more strongly connected in the movement network. Outputs from  
426 *absdiff* model also indicated that movements tended to occur between locations with similar  
427 bull shark abundance, suggesting individuals were predominantly moving among a subset of  
428 preferred locations. While controlling for the abundance effect, there was (overall) some  
429 evidence for a negative effect of the residency time of sharks of the opposite sex, suggesting  
430 some spatial segregation between the sexes, but this effect varied seasonally (see below).

431

#### 432 *Effect of inter-specific competition*

433 We also used our models to test whether the presence of larger tiger sharks was influencing  
434 bull shark movements by moving to/away from areas used by tiger sharks (tested by the  
435 *nodecov* term) and/or moving between sites with similar numbers of tiger sharks (tested by  
436 the *absdiff* term). There was weak evidence (due to wide confidence intervals and the small  
437 number of times this parameter was selected in the top model) for the presence of tiger sharks  
438 affecting bull shark movement network structure. Positive effects in *absdiff* model indicated  
439 individuals tended to move across gradients of tiger shark occupancy, perhaps indicating

440 active avoidance of tiger sharks, with some additional weak evidence of reduced movements  
441 through locations with higher occupancy of tiger sharks.

442

#### 443 *Sex differences in movement network structure*

444 Analysing movement network structure for the two sexes independently revealed similar

445 broad trends as the overall movement network, except in the case of social factors and the

446 tiger shark occupancy (Fig. 4). While females tended to move toward locations with high

447 residency times for other females, males showed a general pattern of avoiding locations with

448 high residency times of either sex (while controlling for overall bull shark abundance). The

449 weak overall evidence for reduced movements through locations with high tiger shark

450 occupancy was driven by divergent effects between females and males. Female movements

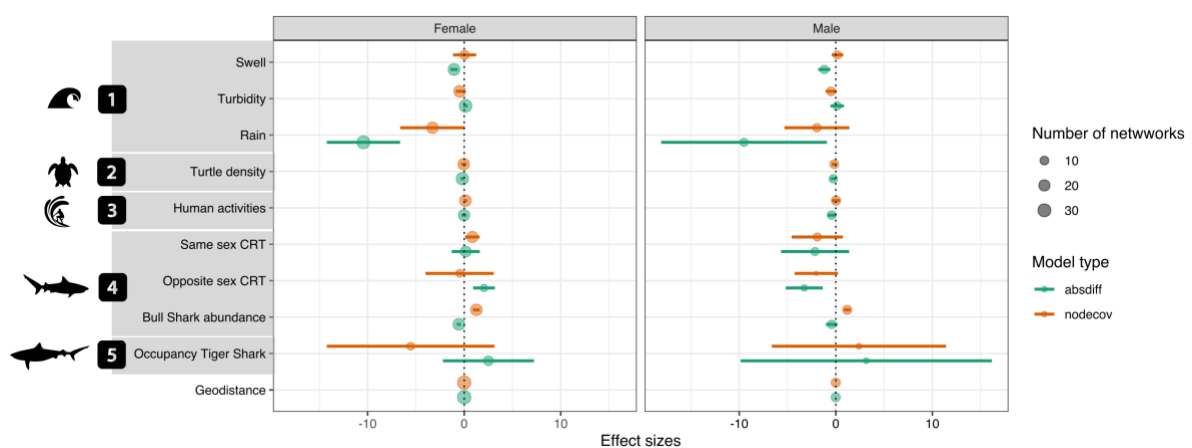
451 were directed towards locations with low tiger shark occupancy while male movements were

452 directed towards locations with high tiger shark occupancy, indicating sex differences in how

453 competitors influenced movement through receiver locations, although these effects have

454 high uncertainty around them.

455



456

457 Figure 4: Summary of the outputs from the ERGM models presented separately for females

458 and males. Effect sizes and their 95% confidence intervals pooled over variables are reported

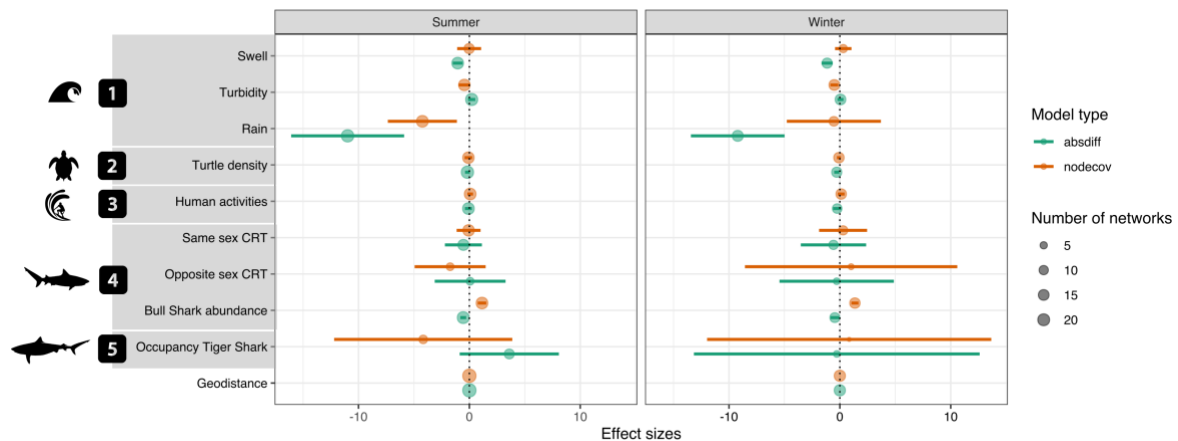
459 for the coefficient of terms *nodecov* and *absdiff*. The variable “Geodistance” controls for the  
460 distance between receivers. Circles represent the number of models in which the coefficient  
461 of the term was significant and therefore selected.

462

### 463 *Seasonal differences in movement network structure*

464 The factors that explained movement network structure remained similar between winter and  
465 summer, with only competition and rainfall changing qualitatively (Fig. 5). While rainfall  
466 levels had effects on movements in both seasons, the pattern was less clear during winter,  
467 which is expected as rainfall is a seasonally-driven factor. It appears there is a shift in  
468 behaviour related to the presence of tiger sharks. While there was no apparent movement  
469 pattern related to tiger shark occupancy during winter, there was a pattern of movements  
470 towards locations with low occupancy of tiger shark in summer as demonstrated by positive  
471 *absdiff* coefficients and negatives coefficient of *nodecov*.

472



473

474 Figure 5: Summary of the outputs from the ERGM models presented separately for summer  
475 and winter. Effect sizes and their 95% confidence intervals pooled over variables are reported  
476 for the coefficient of terms *nodecov* and *absdiff*. The variable “Geodistance” controls for the

477 distance between receivers. Circles represent the number of models in which the coefficient  
478 of the term was significant and therefore selected.

479

480

## 481 **DISCUSSION**

482

483 We predicted that bull sharks would respond specifically to certain environmental factors,  
484 being attracted to high levels of turbidity, rainfall and swell. We also expected that bull shark  
485 movements would be influenced by the distribution of conspecifics and heterospecifics in the  
486 seascape, although we could not predict the direction of these effects. We were thus  
487 interested whether these con- and heterospecific effects were as important as abiotic variables  
488 in explaining movement patterns. Using Exponential random graph models (ERGMs), we  
489 found evidence that abiotic factors, turtle density, anthropogenic factors, intraspecific  
490 interactions, and competitive or interspecific interactions all contribute to bull shark  
491 movement network structure, albeit with varying importance. As we hypothesized, our  
492 models revealed that social factors were at least as important as abiotic parameters.  
493 Additionally, the direction of response to abiotic variables were not always as predicted,  
494 indicating that the role of physical variables in shaping movement network structure may be  
495 context dependent or vary across spatial and temporal scales.

496

### 497 *Effects of abiotic factors on movements*

498 Our results indicate that environmental factors impact the movements of bull sharks,  
499 however, while we expected to find positive effects of swell height, turbidity and rainfall on  
500 shark movements as suggested by previous studies, we found opposite patterns. Bull sharks  
501 were found to be mostly moving through areas with lower rainfall. While bull sharks are



502 known to respond to rainfall and freshwater runoff and are able to transit between freshwater  
503 and marine habitats within hours or remain in low salinity areas for days (Niella et al., 2022;  
504 Werry et al., 2018), selection of lower rainfall levels could be due to the spatial and temporal  
505 resolution at which they react to such rapid environmental changes. In addition, bull sharks  
506 may prefer to predominantly remain (at our scale of observation) in the same conditions of  
507 rain, turbidity and salinity as rain levels are often strong and fast in tropical areas. Werry et  
508 al. (2018) suggested that bull sharks are attracted to estuarine and associated nearshore areas  
509 following high rainfall events in part due to increased prey availability while Niella et al.  
510 (2022) suggested a more complex pattern with differences in response between the sexes.  
511 Matich et al., (2020) also highlighted that during exceptional events bull sharks can avoid  
512 high rainfall and high turbidity, moving away from sites with fast and strong perturbations.  
513 The rainfall data entered in our models represent distinct watershed values that can  
514 potentially incorporate multiple receivers, and can potentially explain why our models found  
515 disproportionately strong effect of movements between (nearby) locations with similar levels  
516 of rainfall. In addition, Werry et al. (2018) found a one-week lag in the response of sharks to  
517 rainfall which could reflect changes in food availability and foraging effectiveness with  
518 changes in salinity, a pattern that would be difficult to reveal with our models. Previous  
519 studies that found strong behavioural response of bull sharks to rainfall were conducted in  
520 large estuarine system where rainfall levels and consequences (e.g. induced turbidity) could  
521 contrast with the coral reef coast of Reunion Island. Finally, movements in response to  
522 attractive effects of environmental factors (swell, turbidity and rainfall) that are ephemeral  
523 and irregular may occur over shorter timescales and be difficult to detect with monthly data.  
524 While we expected to find stronger seasonal differences because the variations in these  
525 parameters are more important and persistent in summer than during winter, the lack of such  
526 behavioural differences could be due to bull sharks being resident for less lengthy periods

527 during summer (Blaison et al., 2015). It is important to note that other potential factors that  
528 we did not measure could also contribute significantly to movement decisions. For example,  
529 salinity is known to be an important factor affecting movement and distribution of bull sharks  
530 (Dwyer et al., 2020). Our results confirm that considering temporally dynamic environmental  
531 variables in studies of animal movement is important because movement patterns reflect  
532 dynamic interactions between animals and their physical environment, with environmental  
533 heterogeneity driving movements of individuals and allowing them to remain in optimal  
534 environmental conditions (Avgar et al., 2013; Mueller et al., 2011; Schick et al., 2008).

535

#### 536 *Effects of turtle density on movements*

537 Our study did not find any effect of turtle density on bull shark movements. While we  
538 used available data on turtle density to investigate its influence on movement patterns of bull  
539 sharks in this study based on local people's perception, we acknowledge that turtles are not  
540 the main prey of bull sharks and remain opportunistic items (Cliff & Dudley, 1991). Bull  
541 sharks are known to feed mainly on teleost fish (Trystram et al., 2016) and future studies  
542 could integrate dynamic species-specific fishery data or parallel underwater surveys to  
543 investigate the role of abundance and composition of fish communities in driving predator  
544 movements. Indeed, resource availability and heterogeneity are important drivers of animal  
545 movement, especially for predators (i.e. prey abundance and distribution). Finding prey  
546 requires a predator to make adaptive decisions about which movement patterns to adopt to  
547 feed most profitably given a particular prey distribution (Riotte-Lambert & Matthiopoulos,  
548 2020; Sims et al., 2006). Thus, interpreting predator movements within a prey landscape may  
549 provide a clearer picture of why certain habitats are selected over others.

550

#### 551 *Effects of human densities on movements*

552           While we detected a tendency for more movements through locations with high  
553 human use, the effect sizes were small suggesting human activities did not strongly influence  
554 movement patterns. This is not surprising as nautical human activities and density are spread  
555 fairly evenly along the west coast of the island where the network of receivers was deployed.  
556 In addition, it is now recognized that bull sharks can adapt to urbanized areas and do not  
557 especially avoid these high human density areas and their activities (Hammerschlag et al.,  
558 2022; Werry et al., 2012). The majority of large-bodied terrestrial carnivores tend avoid high  
559 human densities and activities (Tucker et al., 2018, 2023). As opposed to most predators, it is  
560 possible that human activities are not fundamentally avoided by bull sharks because ocean  
561 landscapes maybe affected differently than terrestrial landscapes. This pattern could be  
562 reinforced by the limited suitable habitat available around the island preventing bull sharks  
563 from avoiding most human activities along the coast.

564

565 *Effects of social environment on movements*

566           We found that social factors sometimes had similar effects on movement networks to  
567 environmental variables. While the bull shark has been found to form occasional  
568 aggregations around fish farms (Loiseau et al., 2016) or at artificial provisioning sites  
569 (Bouveroux et al., 2021), it is not recognized as displaying collective behaviours and strong  
570 patterns of spatial segregation have been found in our study population (Mourier et al., 2021).  
571 However, we found that more movements occurred through bull shark hotspots. When  
572 focusing on the behaviour of each sex, we showed that males were less social and tended to  
573 avoid other sharks regardless of their sex. Contrastingly, females' movements occurred  
574 between locations where other females spent a lot of time but avoided areas heavily used by  
575 males. This confirmed previous findings that females show stronger patterns of residency  
576 providing the opportunity to co-occur with other females, while males favour roaming

577 behaviour (Mourier et al., 2021). This gregarious behaviour of females could also suggest the  
578 presence of mating arenas where females gather to choose transient males allowing them to  
579 avoid male harassment during the mating period. Further research investigating the spatio-  
580 temporal interactions between bull sharks is required to better understand their aggregative  
581 and avoidance behaviour. Our results thus confirm that an individual's movements are not  
582 solely driven by environmental features. Individuals share space with other conspecifics,  
583 linking spatial and social processes (Albery et al., 2021; Webber et al., 2023). For example,  
584 the spatial distribution of resources inherently drives the proximity of individuals through  
585 foraging aggregations, influencing many forms of social interaction (Macdonald, 1983). As  
586 such, the distribution of individuals of a species in space generates population structure and  
587 will influence movement decisions at the individual level. In fact, regardless of whether a  
588 species is perceived to be solitary or social, individuals will have to decide whether to join or  
589 avoid other conspecifics distributed unevenly in space. Such decisions will also depend on  
590 social processes driven by individual phenotypes that alter social decisions (e.g. size, sex, or  
591 genetic relatedness).

592

### 593 *Effects of interspecific competition on movements*

594 In our study we tested the influence of another large predator, the tiger shark, on the  
595 movements of bull sharks. Our results indicated the presence of patterns of avoidance  
596 between bull and tiger sharks. Bull shark movements were affected by the presence of tiger  
597 sharks with female bull sharks directing their movements towards locations with lower tiger  
598 shark occupancy while male sharks showed the opposite pattern. The tiger shark is an apex  
599 predator that is larger than the bull shark and potentially dominant. It is therefore plausible  
600 that bull sharks avoid interactions with tiger sharks. Female bull sharks, being larger than  
601 males, could also compete with tiger sharks. Therefore, one plausible explanation to this

602 pattern is spatial and foraging niche separation between both species (Niella et al., 2021). We  
603 previously highlighted that male and female bull sharks displayed patterns of spatial  
604 segregation (Mourier et al., 2021; Niella et al., 2022), which could also explain the difference  
605 in interaction opportunities with tiger sharks based on habitat utilization and movement  
606 patterns. Indeed, bull sharks rely more on coastal food sources than tiger sharks which feed  
607 on more coastal-pelagic and deep-water prey (Le Croizier et al., 2020; Trystram et al., 2016),  
608 thus supporting our results and implying local spatial segregation between the two species.  
609 These patterns of interference interactions are relatively common in large sharks, as  
610 competitive species generally show spatial (Papastamatiou et al., 2018), temporal (Lear et al.,  
611 2021) and trophic niche (Matich et al., 2017) partitioning to limit the negative effect of  
612 competition and promote co-existence of predators. Similar avoidance strategies are found  
613 between competing carnivores in terrestrial ecosystems. Indeed, lions (*Panthera leo*)  
614 usually remain in areas rich in prey, while subordinated carnivores like leopard (*P. pardus*)  
615 and cheetah (*Acinonyx jubatus*) overlap with the home range of lions but use fine-scaled  
616 avoidance behaviours, and small species like African wild dog (*Lycaon pictus*) employ  
617 multiple tactics to avoid all other competitors (Vanak et al., 2013). Coexistence of multiple  
618 carnivore species is typically explained by dietary niche separation as a consequence of  
619 avoiding intraguild competition. Another potential explanation is the avoidance of tiger  
620 sharks by females during summer corresponding to the parturition season (Pirog et al., 2019)  
621 in order to avoid tiger shark predation on bull shark neonates.

622 Our results thus complement previous studies suggesting that interactions among  
623 large predators involve a complex interplay of competition and predation, as large carnivores  
624 can suppress populations of smaller carnivores through direct predation, resource  
625 competition, or via other forms of interference competition. This may result in spatial and/or  
626 temporal avoidance, reductions in the density of the subordinate species, or even competitive

627 exclusion from certain habitats (Berger & Gese, 2007; Linnell & Strand, 2000; Prugh et al.,  
628 2009; Prugh & Sivy, 2020).

629

### 630 *Conclusion*

631 To investigate the drivers of movements of a marine predator, we used a network-  
632 based approach of movement between fixed stations and employed Exponential Random  
633 Graph Model in a way that could account for the dynamical nature of site attributes visited by  
634 individual animals within a flexible framework that could be extended to test hypotheses  
635 related to the structure of the network itself (extending beyond what is easily possible using  
636 more conventional statistical approaches). While this modelling framework performed well in  
637 our study, it could be refined further to test similar research questions at different spatial and  
638 temporal scales. For example, one promising model is the separable temporal exponential-  
639 family random graph model (tERGM), which treats the formation and dissolution of ties in  
640 parallel at each time step as independent ERGMs (Carnegie et al., 2015; Krivitsky &  
641 Handcock, 2014) and can provide a more realistic view of movement networks (e.g.,  
642 including consecutive individual monthly or daily networks). This would make it possible to  
643 better integrate the temporal interdependency of environmental changes in explaining animal  
644 movement patterns.

645 Our results fit into a broader picture illustrating that animal movements arise from  
646 complex interactions of individuals with their physical environment as well as with both  
647 surrounding conspecific and heterospecific individuals. By including a diverse set of  
648 variables that may influence bull shark movements within our analyses, we demonstrate that  
649 to fully explain animal movement patterns requires the incorporation of multiple variables  
650 associated with environmental heterogeneity, human footprint and the distribution of  
651 individuals in space, both of the same species and other members of the community. A main

652 finding was that, although environmental conditions were important factors influencing  
653 movement of bull sharks, interactions with other individuals in their surroundings was also  
654 important to consider, opening new perspectives at the socio-spatial interface for these  
655 marine predators.

656

### 657 **Data availability**

658 Data and R codes used in this study are available at

659 SEANOE: <https://doi.org/10.17882/99080>

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661

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