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1 **Inferring animal social networks with imperfect detection**

2

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13

14 **Abstract**

15 Social network analysis provides a powerful tool for understanding social organisation of
16 animals. However, in free-ranging populations, it is almost impossible to monitor
17 exhaustively the individuals of a population and to track their associations. Ignoring the issue
18 of imperfect and possibly heterogeneous individual detection can lead to substantial bias in
19 standard network measures. Here, we develop capture-recapture models to analyse network
20 data while accounting for imperfect and heterogeneous detection. We carry out a simulation
21 study to validate our approach. In addition, we show how the visualisation of networks and

22 the calculation of standard metrics can account for detection probabilities. The method is
23 illustrated with data from a population of Commerson's dolphin (*Cephalorhynchus*
24 *commersonii*) in Patagonia Argentina. Our approach provides a step towards a general
25 statistical framework for the analysis of social networks of wild animal populations.

26 **Keywords:** Bayesian inference; capture-recapture; multistate models; social networks

27

28 1. INTRODUCTION

29 Knowledge of the social organisation of animal populations is essential to develop
30 sound conservation and management strategies as social structure affects habitat use,
31 information diffusion, as well as the genetic composition and the spread of information and
32 diseases within these populations (Krause and Ruxton, 2002).

33 Social network analysis (SNA; Croft et al., 2008; Whitehead, 2008) has recently
34 known an increasing number of applications to characterize in particular the social structure
35 of animal populations. SNA allows the study of social networks through their visualisation
36 and the calculation of several descriptive statistics, with important applications in ecology,
37 evolution, epidemiology and behavioural ecology (Craft and Caillaud, 2011; Farine and
38 Whitehead, 2015; Krause et al., 2007; Sih et al., 2009; Wey et al., 2008).

39 In free-ranging populations however, individuals may or may not be seen (or
40 recaptured) at various times over a study period. This raises the issue of detectability less than
41 one that makes it difficult to track associations between individuals. In other words, when one
42 or two individuals of a dyad are missed, were they associated or not? Besides being imperfect,
43 detection is often heterogeneous due to variation in individual traits such as, e.g., sex
44 (Tavecchia et al., 2001), social status (Cubaynes et al., 2010; Hickey and Sollmann, n.d.),

45 infection status (Marescot et al., 2018) or pair-bond status (Choquet and Gimenez, 2012;
46 Culina et al., 2013). Overall, ignoring the issue of imperfect and heterogeneous individual
47 detection can lead to substantial bias in estimating the probability of association between
48 individuals (Hoppitt and Farine, 2018; Lusseau et al., 2008; Weko, 2018).

49 To address these issues, Klaich et al. (2011) developed a capture-recapture model
50 where detection probabilities of individuals in dyads varied between individuals that are
51 associated and those that are not. Their approach requires complex probabilistic calculations
52 that make it specific to their case study, and therefore difficult to extend to other situations.
53 Here, we use a state-space modelling (SSM) approach (e.g., Buckland et al., 2004) to
54 acknowledge that data on associations between individuals derived from field studies are
55 imperfect observations of the underlying social structure. Specifically, the SSM approach
56 makes the two-component process underlying network structure explicit: i) the temporal
57 dynamic of associations between individuals and ii) the observations generated from the
58 underlying process in i).

59 We apply the SSM framework to capture-recapture (CR) data (Gimenez et al., 2007)
60 to analyse network data while accounting for imperfect and heterogeneous detection of
61 individuals. We estimate dyad association probability and distinguish the dynamic of
62 associated vs. non-associated states from their partial observation. We carry out a simulation
63 study to assess bias in the association probability. Last, we show how the visualisation and the
64 calculation of standard network metrics can account for detection probabilities. The approach
65 is illustrated with data from a population of Commerson's dolphin (*Cephalorhynchus*
66 *commersonii*) in Patagonia Argentina.

67

68 **2. MODEL DEVELOPMENT**

69 **(a) State-space modelling of capture-recapture data**

70 Following (Klaich et al., 2011), we derived dyad association histories from individual
71 captures and non-captures. For example, let us assume a 4-occasion CR experiment in which
72 two individuals have capture histories ‘1011’ and ‘1001’ where a ‘1’ stands for an individual
73 detection and ‘0’ for a non-detection. We considered that behavioural interactions between
74 individuals occurred within groups (‘gambit of the group’ *sensu* (Whitehead and Dufault,
75 1999)). Let us assume that these two individuals were both detected in the same group at the
76 first occasion but in a different group at the last one, then the association history for this
77 particular dyad is ‘2013’ where ‘0’ stands for none of the two individuals of a dyad are seen,
78 ‘1’ for one individual only of the dyad is seen, ‘2’ for the two individuals of a dyad are seen
79 associated and ‘3’ for the two individuals of a dyad are seen non-associated.

80 To analyse these dyadic data, we implemented a SSM formulation (Gimenez et al.,
81 2007) of multistate CR models (Lebreton et al., 2009) for closed populations. We considered
82 two states A and B for ‘dyad associated’ and ‘dyad non-associated’ respectively. We denoted
83 x_t^i , a multinomial trial taking values (1,0) or (0,1) if, at time t , dyad i is in state A or B
84 respectively. Given the underlying states, a dyad may be recaptured in the observations 0, 1, 2
85 or 3 defined above considering imperfect detection. We denoted y_t^i , a multinomial trial taking
86 values (1,0,0,0), (0,1,0,0), (0,0,1,0), (0,0,0,1) if, at time t , dyad i is observed as a 0, 1, 2 or 3.
87 The state–space model relies on a combination of two equations. First, the state equation
88 specifies the state of dyad i at time t given its state at time $t - 1$:

$$x_t^i \sim \text{Multinomial}(1, \Psi x_{t-1}^i)$$

89 where Ψ gathers the probabilities for a dyad of staying associated and non-associated
90 between two successive occasions (Table 1a). We also defined the probability π for a dyad of

91 being in initial state associated. Second, the observation equation specifies the observation of
92 dyad i at time t given its state at time t :

$$y_t^i \sim \text{Multinomial}(1, Px_t^i)$$

93 where P gathers the detection probabilities and of an individual being associated and non-
94 associated in a dyad (Table 1b).

95

96 **(b) Bayesian fitting using MCMC methods**

97 We used Bayesian theory in conjunction with Markov Chain Monte Carlo (MCMC)
98 methods to carry out inference. Inference was based on empirical medians and credible
99 intervals. As a by-product of the MCMC simulations, we also obtained numerical summaries
100 for any function of the parameters, in particular the metrics describing the network structure.

101

102 **(c) Calculating network measures while accounting for imperfect detection**

103 In SNA, a wide range of descriptive statistics can be used to characterize the properties
104 of the structure of a network. Here, we focused on four of them. We used for each animal in
105 the network the number of other animals with which it was associated – *degree* – and the
106 number of shortest paths between pairs of animals that passed through it – *betweenness*. In
107 addition, we quantified the degree to which an animal's immediate neighbours were
108 associated – *cluster coefficient* – and the average of all path lengths between all pairs of
109 animals in the network – *average path length* (Croft et al., 2008). These measures are useful
110 to characterize the properties of a network regarding the spread of disease or information
111 (Craft and Caillaud, 2011; Watts and Strogatz, 1998).

112 A feature of MCMC algorithms is that the dyad states x_t^i 's are treated as parameters to
113 be estimated, just like the transition and detection probabilities. We generated values from the
114 posterior distributions of the dyads' states, which, in turn, were used to visualize the network

115 and characterize its structure over time. Specifically, for each MCMC iteration, we calculated
116 the degree and betweenness for each individual (R package sna; (Butts, 2008)), as well as the
117 clustering coefficient and the average path length (R package igraph; (Csardi and Nepusz,
118 n.d.)), hence obtaining the posterior distribution for each of these metrics. Data and codes are
119 available on GitHub https://github.com/oliviergimenez/social_networks_capture_recapture.

120

121 3. SIMULATION STUDY

122 We conducted a simulation study to assess the bias in parameter estimates. We
123 considered a scenario where detection probabilities were homogeneous. We simulated 100
124 CR datasets with $\pi = 0.2, 0.7$, $\psi^{AA} = 0.1, 0.4, 0.9$ and $\psi^{BB} = 0.1, 0.4, 0.9$ and $p^A = p^B = 0.3, 0.8$
125 (in total, 36 different configurations) and to each simulated dataset we fitted a CR model with
126 homogeneous detection probabilities. We also considered a heterogeneous scenario where all
127 parameters were set to the same values as in the homogeneous scenarios, except the detection
128 probabilities which we set to $p^A = 0.3, p^B = 0.8$ and $p^A = 0.8, p^B = 0.3$ (in total, 36 different
129 configurations). We fitted a model with heterogeneous detection probabilities to these
130 simulated datasets. For both the homogeneous and the heterogeneous scenarios, we calculated
131 the relative bias of all parameters.

132 For the homogeneous scenarios, the bias decreased when detection increased (Table
133 2). Bias was negligible on detection, around +5% on the transition probabilities and around -
134 13% on π in scenario 19 with $\psi^{BB} = 0.4$. When $\psi^{BB} = 0.9$ in scenario 31, the bias in π
135 decreased by a factor 2. For the heterogeneous scenarios, the bias was negligible, except for
136 scenario 31 in which the proportion of associated dyads was low and all dyads tended to
137 remain non-associated.

138

139 4. CASE STUDY

140 To illustrate our methodological approach, we used a real-world example as a case
141 study. We used photo-identification data on a population of Commerson's dolphin (*C.*
142 *commersonii*) that was monitored in the coastal waters near the Chubut River mouth
143 (43°20`_S, 65°00`_W) in the Patagonian coast (Coscarella et al., 2003). Commerson's
144 dolphins are particularly abundant in the area during the austral spring (Coscarella et al.,
145 2010). The mean residence time in the sampling area was 15 days (SE = 6.4), therefore we
146 sampled 5 times in October 2007 to unravel which individual was associated with which,
147 while arriving and leaving the area together (Coscarella et al., 2011). Two individuals were
148 considered associated when they were photo-identified during the same encounter, while they
149 were considered not associated otherwise (Coscarella et al., 2011).

150 Over the study, a total of 71 dolphins were detected which led to $71 * (71 - 1) / 2 = 2485$
151 association histories. Based on previous analyses (Klaich et al., 2011), we considered time-
152 dependent state-independent individual detection probabilities. Individual detections varied
153 between 11% and 44% (Table 4). The probability of staying associated was 33% while that of
154 staying non-associated was 57% with very little overlap in the credible intervals (Table 4),
155 suggesting a high turnover in the dynamic of associations and a fission-fusion social
156 organization.

157 Along the five sampling occasions, the estimated network showed changes in its
158 structure (Figure 1). At occasions 1, 2, 3 and 5, the estimated network had a single component
159 with a higher number of associated dyads at occasion 1 than at occasions 2, 3 and 5. Although
160 the number of dyads was higher at occasion 1, all networks were fully connected (i.e. none
161 individual or group of individuals were isolated from other individuals). At occasion 4, the
162 network estimated had two components, isolated from each other (i.e. none of the individuals
163 from one component was associated with any of the individuals in the other component). This

164 suggests that at least two groups might exist having preferential associations between
165 individuals inside each group.

166 Average path length was lower on the first sampling occasion than in the subsequent
167 ones, while the reverse pattern was observed for the clustering coefficient (Table 4). These
168 estimated values also suggest high individual connectivity and that the estimated social
169 network has features related to a small-world type network. At the individual level, degree
170 was heterogeneous (Figure 2), with individuals spreading all over the range of its distribution
171 (Figure 2). In contrast, betweenness appeared relatively homogeneous, despite some dolphins
172 with low betweenness and a single animal with very high betweenness (Figure 2).

173

174 **5. DISCUSSION**

175 We have proposed a new statistical approach combining network analyses with CR
176 models formulated as state-space models. Our framework has several appealing advantages.
177 First and most importantly, ignoring imperfect and possibly heterogeneous detection may lead
178 to biased results about the structure and dynamics of associations (see Figure 1). Our CR
179 model provides a robust method to estimate social networks. Second, in addition to social
180 status, our model can easily incorporate individual-level traits such as age or sex through
181 regression-like functions. This opens an avenue towards investigating the relationships
182 between the phenotype and social position of individuals. Third, our method provides
183 unbiased and precise estimates of relevant metrics to characterise the properties of social
184 networks (see the Simulation study section), the whole process being controlled for imperfect
185 and heterogeneous detection. Another appealing feature of our approach is the quantification
186 of uncertainty associated to network measures under the form of Bayesian credible intervals
187 (Table 2 and Figure 2). Last, the social organisation can be visualised over time while

188 accounting for imperfect detection, providing the opportunity for testing socio-ecological
189 hypotheses in free-ranging animal populations. For example, the rapid turnover of the free
190 ranging Commerson's dolphin groups has been previously proposed (Coscarella et al., 2011),
191 and here we could identify this turnover within the fission-fusion society model.

192 When inspecting the results of the dolphin case study, there are advantages in adopting
193 a CR approach to infer social networks. First, when it comes to visualizing the network, we
194 illustrate in Figure 1 what we would obtain with a standard approach with in black edges,
195 while the green edges correspond to the dyads that are estimated to be associated with the new
196 approach by correcting for imperfect detection. Clearly, the structure and dynamics of the
197 network are different depending on whether we ignore imperfect detection (black edges only)
198 or we consider the model-based estimated network (edges of both colors). Second, regarding
199 network metrics, the only way to estimate degree and betweenness for all occasions when
200 non-detections occur (Figure 2) is to resort to a CR approach to account for missing values.”

201 Our CR model requires data on individuals that can be uniquely identifiable.
202 Identifying individuals can be achieved by using non-invasive marking (such as coat patterns,
203 body scars, or genetic profiling for mammals; e.g., Cubaynes et al., 2010; Marescot et al.,
204 2018; Santostasi et al., 2016) or invasive marking (such as rings for birds, colouring for
205 insects or passive integrated transponders for fishes; e.g., Băncilă et al., 2018; Buoro et al.,
206 2010; Lagrange et al., 2014). The model also needs data on interactions or associations. Here,
207 we rely on the ‘gambit of the group’ method which states that all individuals within a group of
208 animals observed at a point in time are associated (Farine and Whitehead, 2015).

209 Our model relies on several assumptions. First, we have considered closed populations
210 while demographic process might occur in animal populations. The extension of our model to
211 open populations is feasible (Lebreton et al., 2009) to incorporate survival and dispersal,

212 therefore allowing to assess the influence of social structure on fitness. Second, we assumed
213 that association states were correctly assigned while some uncertainty might occur due to
214 incomplete information. In the SSM framework, incorporating uncertainty in state assignment
215 is relatively straightforward (Gimenez et al., 2012; Pradel, 2005). Third, we assumed
216 independence of the association histories to form the SSM likelihood. To account for an
217 individual effect, random effects can be incorporated in CR models (Choquet et al., 2013;
218 Choquet and Gimenez, 2012, 2010), which opens a promising avenue towards a general
219 statistical framework for the analysis of animal social networks (Cross et al., 2012; Van Duijn
220 et al., 2004).

221 Overall, we hope our proposal will foster applications of social network analysis to
222 free-ranging animal population in behavioural ecology to describe social behaviour and social
223 dynamics, in evolution ecology to explore the fitness consequences of the social positions of
224 individuals and in epidemiological ecology to determine the implications of network structure
225 and dynamics in the spread of diseases.

226

227 FIGURES

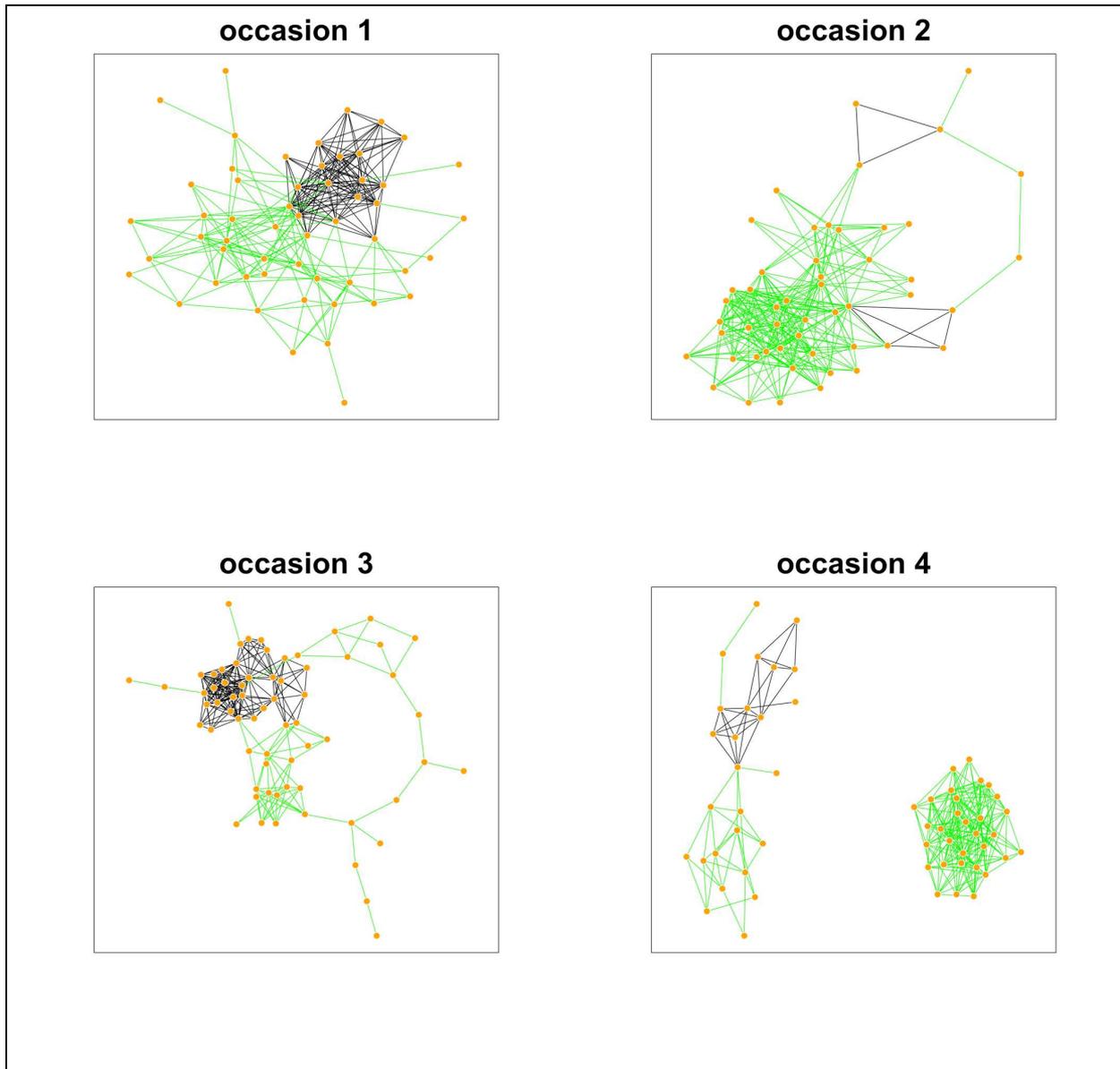
228

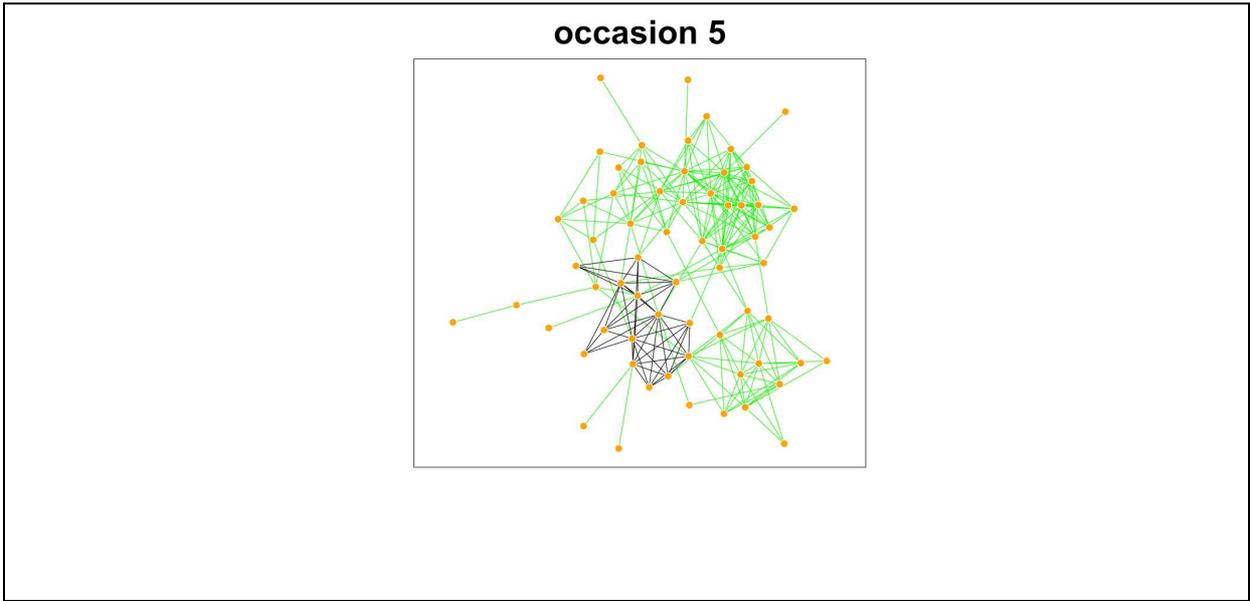
229 **Figure 1.** Visualisation of the network for the Commerson's dolphin population, over five
230 sampling occasions, for the year 2007, showing associations (lines) between individuals
231 (orange circles). For each edge, we calculated the average number of times the corresponding
232 dyad was estimated as being associated ($x = 1$) over the total number of MCMC simulations.
233 Then, we displayed only the edges for which this number was larger than the 0.90 quantile of
234 the distribution of x . Black edges are for observed dyads (also corresponding to $x = 1$ for
235 simulations) while green edges are for dyads that are estimated to be associated (with

236 probability 0.69, 0.39, 0.42, 0.42 and 0.40 for capture occasion 1, 2, 3, 4 and 5 respectively)

237 but for which one or the two individuals were not detected.

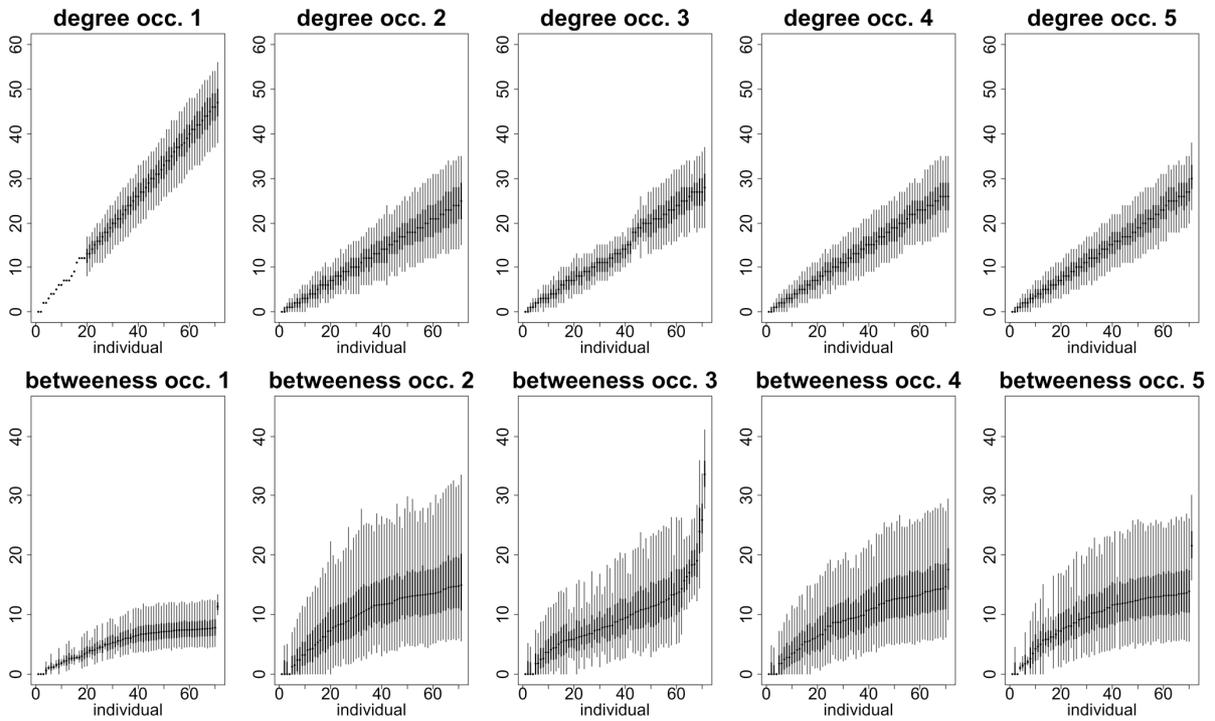
238





239

240 **Figure 2.** Local properties of the Commerson’s dolphin network. For each individual and for
 241 each of the 5 capture occasions, degree (top panels) and betweenness (bottom panels) are
 242 summarized with the posterior mean (circle), the 50% (thick line) and 95% (thin line) credible
 243 intervals.



244

245

Table 1. Transition matrices used in the state and observation equations of the state-space CR network model. States A and B are for associated and non-associated. Parameters p and ψ are the detection and transition probabilities.

a) State matrix

Previous occasion	Current occasion	
	A	B
A	ψ^{AA}	$1 - \psi^{AA}$
B	$1 - \psi^{BB}$	ψ^{BB}

b) Observation matrix P

Current occasion	Current occasion			
	0	1	2	3
A	$(1 - p^A)(1 - p^A)$	$2p^A(1 - p^A)$	$p^A p^A$	0
B	$(1 - p^B)(1 - p^B)$	$2p^B(1 - p^B)$	0	$p^B p^B$

251 **Table 2.** Bias in parameter estimates for the homogeneous scenarios.

scenario	p	π	ψ^{AA}	ψ^{BB}	bias p	bias π	bias ψ^{AA}	bias ψ^{BB}
1	0.3	0.2	0.1	0.1	0.50	26.49	120.98	58.77
2	0.8	0.2	0.1	0.1	0.08	9.46	4.37	1.36
3	0.3	0.7	0.1	0.1	-0.33	-1.23	142.04	22.83
4	0.8	0.7	0.1	0.1	-0.21	-3.23	8.91	-0.04
5	0.3	0.2	0.4	0.1	0.07	14.73	27.30	53.03
6	0.8	0.2	0.4	0.1	-0.04	1.02	-1.65	4.74
7	0.3	0.7	0.4	0.1	0.60	-10.96	65.19	26.16
8	0.8	0.7	0.4	0.1	-0.04	-0.37	-8.88	0.79
9	0.3	0.2	0.9	0.1	0.29	4.46	-23.10	37.30
10	0.8	0.2	0.9	0.1	0.11	2.29	-5.57	7.26
11	0.3	0.7	0.9	0.1	-0.25	0.30	-14.44	28.57
12	0.8	0.7	0.9	0.1	0.07	-0.55	-7.99	3.91
13	0.3	0.2	0.1	0.4	-0.74	54.58	45.20	24.95
14	0.8	0.2	0.1	0.4	-0.08	6.23	2.19	4.71
15	0.3	0.7	0.1	0.4	0.27	-25.83	29.36	7.66
16	0.8	0.7	0.1	0.4	-0.11	-11.71	3.05	1.72
17	0.3	0.2	0.4	0.4	0.45	14.96	10.59	21.80
18	0.8	0.2	0.4	0.4	-0.09	3.22	-1.45	-0.27
19	0.3	0.7	0.4	0.4	0.64	-13.37	5.67	5.96
20	0.8	0.7	0.4	0.4	0.02	0.24	-1.44	-0.71
21	0.3	0.2	0.9	0.4	-0.26	8.35	-17.84	-28.74
22	0.8	0.2	0.9	0.4	0.01	1.28	-1.62	-1.72
23	0.3	0.7	0.9	0.4	0.45	-1.59	-10.12	-5.75
24	0.8	0.7	0.9	0.4	-0.08	-0.52	-2.47	-0.54
25	0.3	0.2	0.1	0.9	0.94	38.86	21.21	-1.08
26	0.8	0.2	0.1	0.9	0.08	8.48	2.90	0.87
27	0.3	0.7	0.1	0.9	0.11	-47.67	10.35	-2.45
28	0.8	0.7	0.1	0.9	-0.34	2.48	1.29	-0.87
29	0.3	0.2	0.4	0.9	-0.46	11.66	-4.68	-16.83
30	0.8	0.2	0.4	0.9	-0.22	2.55	-0.36	-1.68
31	0.3	0.7	0.4	0.9	-0.27	-6.82	-7.96	-7.75
32	0.8	0.7	0.4	0.9	0.04	-1.00	-0.86	-1.29
33	0.3	0.2	0.9	0.9	1.18	3.33	-30.90	-55.94
34	0.8	0.2	0.9	0.9	0.12	0.47	-1.45	-2.53
35	0.3	0.7	0.9	0.9	-0.74	-3.30	-20.09	-38.39
36	0.8	0.7	0.9	0.9	-0.16	-1.19	-0.85	-1.26

253 **Table 3.** Bias in parameter estimates for the heterogeneous scenarios.

scenario	p^A	p^B	π	ψ^{AA}	ψ^{BB}	bias p^A	bias p_B	bias π	bias ψ^{AA}	bias ψ^{BB}
1	0.3	0.8	0.2	0.1	0.1	0.59	-0.24	4.67	5.86	5.61
2	0.3	0.8	0.7	0.1	0.1	0.18	-0.39	-6.01	1.17	12.27
3	0.3	0.8	0.2	0.4	0.1	-0.16	-0.65	-2.13	-6.94	2.94
4	0.3	0.8	0.7	0.4	0.1	0.84	-0.49	-25.65	-2.16	4.77
5	0.3	0.8	0.2	0.9	0.1	-0.02	-2.53	-15.23	-6.76	1.87
6	0.3	0.8	0.7	0.9	0.1	0.67	-14.33	-131.51	-8.99	8.40
7	0.3	0.8	0.2	0.1	0.4	-0.11	0.34	2.82	9.96	6.86
8	0.3	0.8	0.7	0.1	0.4	1.55	0.30	-0.32	2.34	0.53
9	0.3	0.8	0.2	0.4	0.4	-0.65	-0.69	0.88	-2.29	2.30
10	0.3	0.8	0.7	0.4	0.4	1.41	-1.75	-3.50	-2.06	7.67
11	0.3	0.8	0.2	0.9	0.4	0.49	-0.06	2.86	-3.88	-0.25
12	0.3	0.8	0.7	0.9	0.4	0.81	-4.39	-11.31	-1.57	2.71
13	0.3	0.8	0.2	0.1	0.9	4.24	-0.21	0.26	27.14	-1.08
14	0.3	0.8	0.7	0.1	0.9	1.63	-0.22	-0.49	1.94	-2.15
15	0.3	0.8	0.2	0.4	0.9	7.33	-0.96	-1.02	-1.77	0.34
16	0.3	0.8	0.7	0.4	0.9	-0.05	-0.38	-1.43	-1.41	-0.78
17	0.3	0.8	0.2	0.9	0.9	-1.53	-0.24	0.43	-8.22	-0.36
18	0.3	0.8	0.7	0.9	0.9	0.84	-0.48	0.53	-1.08	-1.45
19	0.8	0.3	0.2	0.1	0.1	-0.39	-0.01	11.75	4.63	3.82
20	0.8	0.3	0.7	0.1	0.1	0.03	-0.63	4.72	1.48	7.67
21	0.8	0.3	0.2	0.4	0.1	0.47	0.73	16.29	3.33	3.73
22	0.8	0.3	0.7	0.4	0.1	0.52	-1.16	-0.14	1.50	5.51
23	0.8	0.3	0.2	0.9	0.1	0.00	0.04	17.21	-2.35	2.46
24	0.8	0.3	0.7	0.9	0.1	-0.13	1.98	-8.68	0.17	4.71
25	0.8	0.3	0.2	0.1	0.4	-0.94	0.38	2.54	11.96	-26.02
26	0.8	0.3	0.7	0.1	0.4	-0.79	-0.64	-0.89	1.91	-11.83
27	0.8	0.3	0.2	0.4	0.4	-0.91	-0.14	5.53	8.95	-3.96
28	0.8	0.3	0.7	0.4	0.4	-0.52	0.57	-0.87	1.32	-3.13
29	0.8	0.3	0.2	0.9	0.4	-0.48	1.01	2.13	-3.45	0.13
30	0.8	0.3	0.7	0.9	0.4	-0.48	0.58	-1.17	0.17	-1.46
31	0.8	0.3	0.2	0.1	0.9	-30.02	21.00	27.86	112.23	-196.71
32	0.8	0.3	0.7	0.1	0.9	-1.90	0.23	2.38	1.93	-8.34
33	0.8	0.3	0.2	0.4	0.9	-9.87	2.22	7.98	27.76	-6.73
34	0.8	0.3	0.7	0.4	0.9	-1.40	0.28	0.70	1.65	-1.85
35	0.8	0.3	0.2	0.9	0.9	0.14	-0.29	0.86	-8.69	-1.06
36	0.8	0.3	0.7	0.9	0.9	0.22	0.16	-0.41	-0.32	-1.45

1 **Table 4.** Parameters estimates (posterior medians) with 95% credible intervals for the Commerson's dolphin case study.

Parameter	Estimate with 95% credible interval				
	Occasion 1	Occasion 2	Occasion 3	Occasion 4	Occasion 5
Average path length	1.31 [1.25; 1.38]	1.65 [1.54; 1.79]	1.61 [1.57; 1.66]	1.60 [1.55; 1.65]	1.61 [1.56; 1.66]
Clustering coefficient	0.68 [0.61; 0.74]	0.36 [0.27; 0.45]	0.42 [0.39; 0.45]	0.39 [0.35; 0.43]	0.40 [0.36; 0.43]
Individual detection	0.27 [0.26; 0.28]	0.11 [0.10; 0.12]	0.44 [0.42; 0.45]	0.17 [0.16; 0.18]	0.20 [0.19; 0.21]
Staying associated			0.33 [0.17; 0.50]		
Staying non-associated			0.57 [0.48; 0.69]		

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12 **Competing interests**

13 The authors declare no competing interests.