Inferring animal social networks with imperfect detection

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ABSTRACT

Social network analysis provides a powerful tool for understanding social organisation of animals. However, in free-ranging populations, it is almost impossible to monitor exhaustively the individuals of a population and to track their associations. Ignoring the issue of imperfect and possibly heterogeneous individual detection can lead to substantial bias in standard network measures. Here, we develop capture-recapture models to analyse network data while accounting for imperfect and heterogeneous detection. We carry out a simulation study to validate our approach. In addition, we show how the visualisation of networks and the calculation of standard metrics can account for detection probabilities. The method is illustrated with data from a population of Commerson's dolphin (*Cephalorhynchus commersonii*) in Patagonia Argentina. Our approach provides a step towards a general statistical framework for the analysis of social networks of wild animal populations.

1. Introduction

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

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

In free-ranging populations however, individuals may or may not be seen (or recaptured) at various times over a study period. This raises the issue of detectability less than one that makes it difficult to track associations between individuals. In other words, when one or two individuals of a dyad are missed, were they associated or not? Besides being imperfect, detection is often heterogeneous due to variation in individual traits such as, e.g., sex (Tavecchia et al., 2001), social status (Cubaynes et al., 2010; Hickey and Sollmann, 2019), infection status (Marescot et al., 2018) or pair-bond status (Choquet and Gimenez,

2012; Culina et al., 2013). Overall, ignoring the issue of imperfect and heterogeneous individual detection can lead to substantial bias in estimating the probability of association between individuals (Hoppitt and Farine, 2018; Lusseau et al., 2008; Weko, 2018).

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

We apply the SSM framework to capture-recapture (CR) data (Gimenez et al., 2007) to analyse network data while accounting for imperfect and heterogeneous detection of individuals. We estimate dyad association probability and distinguish the dynamic of associated vs. non-associated states from their partial observation. We carry out a simulation study to assess bias in the association probability. Last, we show how the visualisation and the calculation of standard network metrics can account for detection probabilities. The approach is

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illustrated with data from a population of Commerson's dolphin (*Cephalorhynchus commersonii*) in Patagonia Argentina.

2. Model development

2.1. State-space modelling of capture-recapture data

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

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

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

where Ψ gathers the probabilities for a dyad of staying associated and non-associated between two successive occasions (Table 1a). We also defined the probability π for a dyad of being in initial state associated. Second, the observation equation specifies the observation of dyad i at time t given its state at time t:

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

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

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	$p^B p^B$

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

2.2. Bayesian fitting using MCMC methods

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

2.3. Calculating network measures while accounting for imperfect detection

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

A feature of MCMC algorithms is that the dyad states x_t^i's are treated as parameters to be estimated, just like the transition and detection probabilities. We generated values from the posterior distributions of the dyads' states, which, in turn, were used to visualize the network and characterize its structure over time. Specifically, for each MCMC iteration, we calculated the degree and betweeness for each individual (R package sna; Butts, 2008), as well as the clustering coefficient and the average path length (R package igraph; Csardi and Nepusz, 2006),

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

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]		

hence obtaining the posterior distribution for each of these metrics. Data and codes are available on GitHub https://github.com/oliviergimenez/social_networks_capture_recapture.

3. Simulation study

We conducted a simulation study to assess the bias in parameter estimates. We considered a scenario where detection probabilities were homogeneous. We simulated 100 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 (in total, 36 different configurations) and to each simulated dataset we fitted a CR model with homogeneous detection probabilities. We also considered a heterogeneous scenario where all parameters were set to the same values as in the homogeneous scenarios, except the detection 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 configurations). We fitted a model with heterogeneous detection probabilities to these simulated datasets. For both the homogeneous and the heterogeneous scenarios, we calculated the relative bias of all parameters.

For the homogeneous scenarios, the bias decreased when detection increased (Table 2). Bias was negligible on detection, around +5% on the transition probabilities and around -13% on π in scenario 19 with $\psi^{BB} = 0.4$. When $\psi^{BB} = 0.9$ in scenario 31, the bias in π decreased by a factor 2. For the heterogeneous scenarios, the bias was negligible, except for scenario 31 in which the proportion of associated dyads was low and all dyads tended to remain non-associated (Table 3).

4. Case study

To illustrate our methodological approach, we used a real-world example as a case study. We used photo-identification data on a population of Commerson's dolphin (*C. commersonii*) that was monitored in the coastal waters near the Chubut River mouth (43∘20`_S, 65∘00`_W) in the Patagonian coast (Coscarella et al., 2003). Commerson's dolphins are particularly abundant in the area during the austral spring (Coscarella et al., 2010). The mean residence time in the sampling area was 15 days (SE = 6.4), therefore we sampled 5 times in October 2007 to unravel which individual was associated with which,
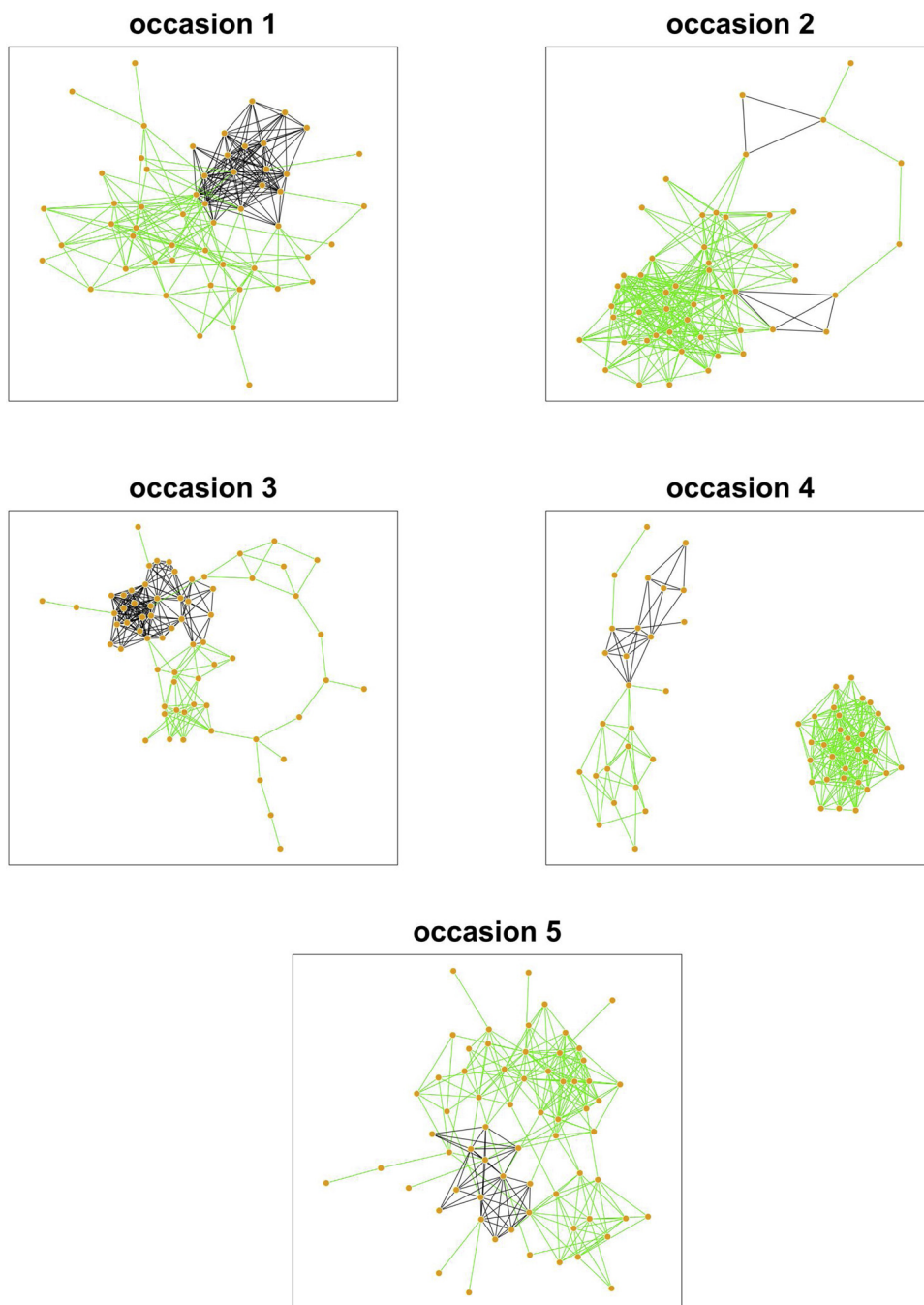
occasion 1

occasion 2

Fig. 1. Visualisation of the network for the Commerson's dolphin population, over five sampling occasions, for the year 2007, showing associations (lines) between individuals (orange circles). For each edge, we calculated the average number of times the corresponding dyad was estimated as being associated ($x = 1$) over the total number of MCMC simulations. Then, we displayed only the edges for which this number was larger than the 0.90 quantile of the distribution of x. Black edges are for observed dyads (also corresponding to $x = 1$ for simulations) while green edges are for dyads that are estimated to be associated (with probability 0.69, 0.39, 0.42, 0.42 and 0.40 for capture occasion 1, 2, 3, 4 and 5 respectively) but for which one or the two individuals were not detected. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

occasion 3

occasion 4

occasion 5

while arriving and leaving the area together (Coscarella et al., 2011). Two individuals were considered associated when they were photo-identified during the same encounter, while they were considered not associated otherwise (Coscarella et al., 2011).

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

Along the five sampling occasions, the estimated network showed changes in its structure (Fig. 1). At occasions 1, 2, 3 and 5, the estimated network had a single component with a higher number of associated dyads at occasion 1 than at occasions 2, 3 and 5. Although the

number of dyads was higher at occasion 1, all networks were fully connected (i.e. none individual or group of individuals were isolated from other individuals). At occasion 4, the network estimated had two components, isolated from each other (i.e. none of the individuals from one component was associated with any of the individuals in the other component). This suggests that at least two groups might exist having preferential associations between individuals inside each group.

Average path length was lower on the first sampling occasion than in the subsequent ones, while the reverse pattern was observed for the clustering coefficient (Table 4). These estimated values also suggest high individual connectivity and that the estimated social network has features related to a small-world type network. At the individual level, degree was heterogeneous (Fig. 2), with individuals spreading all over the range of its distribution (Fig. 2). In contrast, betweeness appeared relatively homogeneous, despite some dolphins with low betweeness and a single animal with very high betweeness (Fig. 2).
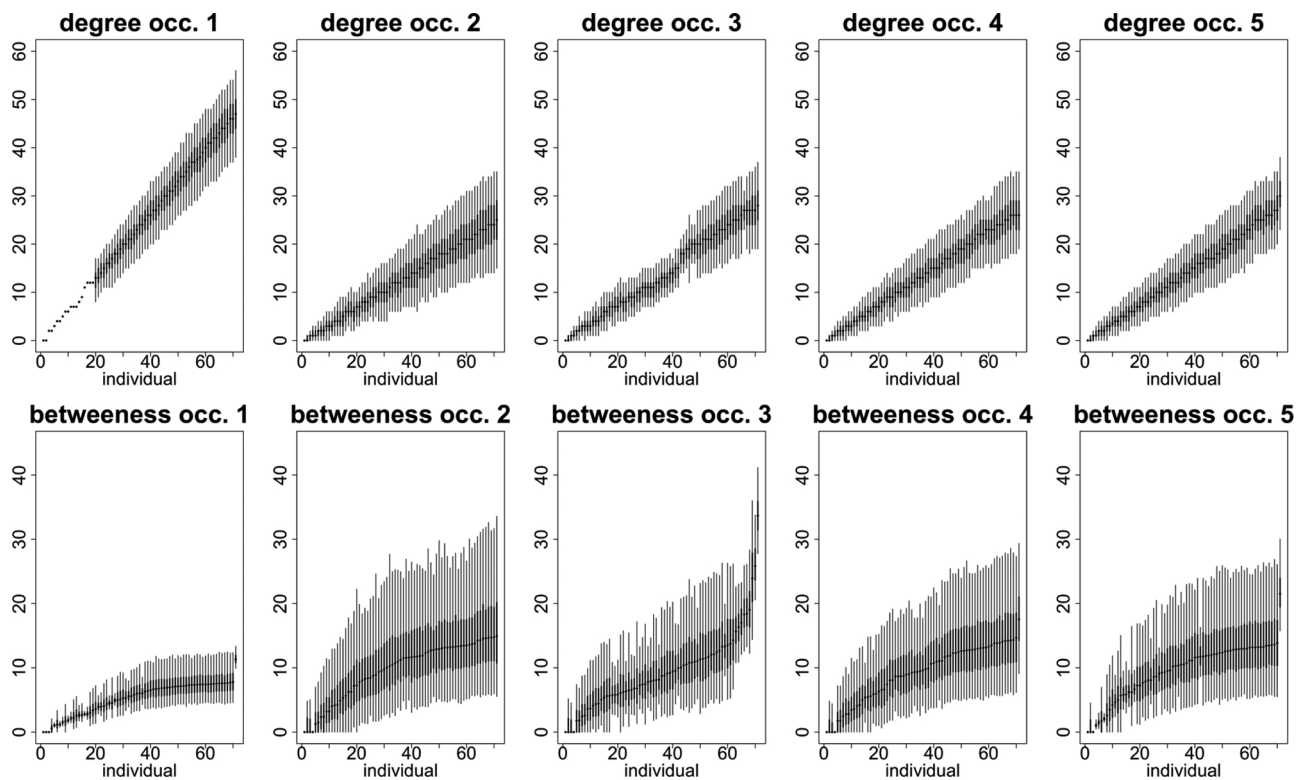
Fig. 2. Local properties of the Commerson's dolphin network. For each individual and for each of the 5 capture occasions, degree (top panels) and betweeness (bottom panels) are summarized with the posterior mean (circle), the 50% (thick line) and 95% (thin line) credible intervals.

5. Discussion

We have proposed a new statistical approach combining network analyses with CR models formulated as state-space models. Our framework has several appealing advantages. First and most importantly, ignoring imperfect and possibly heterogeneous detection may lead to biased results about the structure and dynamics of associations (see Fig. 1). Our CR model provides a robust method to estimate social networks. Second, in addition to social status, our model can easily incorporate individual-level traits such as age or sex through regression-like functions. This opens an avenue towards investigating the relationships between the phenotype and social position of individuals. Third, our method provides unbiased and precise estimates of relevant metrics to characterise the properties of social networks (see the Simulation study section), the whole process being controlled for imperfect and heterogeneous detection. Another appealing feature of our approach is the quantification of uncertainty associated to network measures under the form of Bayesian credible intervals (Table 2 and Fig. 2). Last, the social organisation can be visualised over time while accounting for imperfect detection, providing the opportunity for testing socio-ecological hypotheses in free-ranging animal populations. For example, the rapid turnover of the free ranging Commerson's dolphin groups has been previously proposed (Coscarella et al., 2011), and here we could identify this turnover within the fission-fusion society model.

When inspecting the results of the dolphin case study, there are advantages in adopting a CR approach to infer social networks. First, when it comes to visualizing the network, we illustrate in Fig. 1 what we would obtain with a standard approach with in black edges, while the green edges correspond to the dyads that are estimated to be associated with the new approach by correcting for imperfect detection. Clearly, the structure and dynamics of the network are different depending on whether we ignore imperfect detection (black edges only) or we consider the model-based estimated network (edges of both

colors). Second, regarding network metrics, the only way to estimate degree and betweenness for all occasions when non-detections occur (Fig. 2) is to resort to a CR approach to account for missing values.

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

Our model relies on several assumptions. First, we have considered closed populations while demographic process might occur in animal populations. The extension of our model to open populations is feasible (Lebreton et al., 2009) to incorporate survival and dispersal, therefore allowing to assess the influence of social structure on fitness. Second, we assumed that association states were correctly assigned while some uncertainty might occur due to incomplete information. In the SSM framework, incorporating uncertainty in state assignment is relatively straightforward (Gimenez et al., 2012; Pradel, 2005). Third, we assumed independence of the association histories to form the SSM likelihood. To account for an individual effect, random effects can be incorporated in CR models (Choquet et al., 2013; Choquet and Gimenez, 2012; Gimenez and Choquet, 2010), which opens a promising avenue towards a general statistical framework for the analysis of animal social networks (Cross et al., 2012; Van Duijn et al., 2004).

Overall, we hope our proposal will foster applications of social network analysis to free-ranging animal population in behavioural ecology to describe social behaviour and social dynamics, in evolution ecology to explore the fitness consequences of the social positions of individuals and in epidemiological ecology to determine the

implications of network structure and dynamics in the spread of diseases.

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