

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 – *betweenness*. 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 betweenness 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,

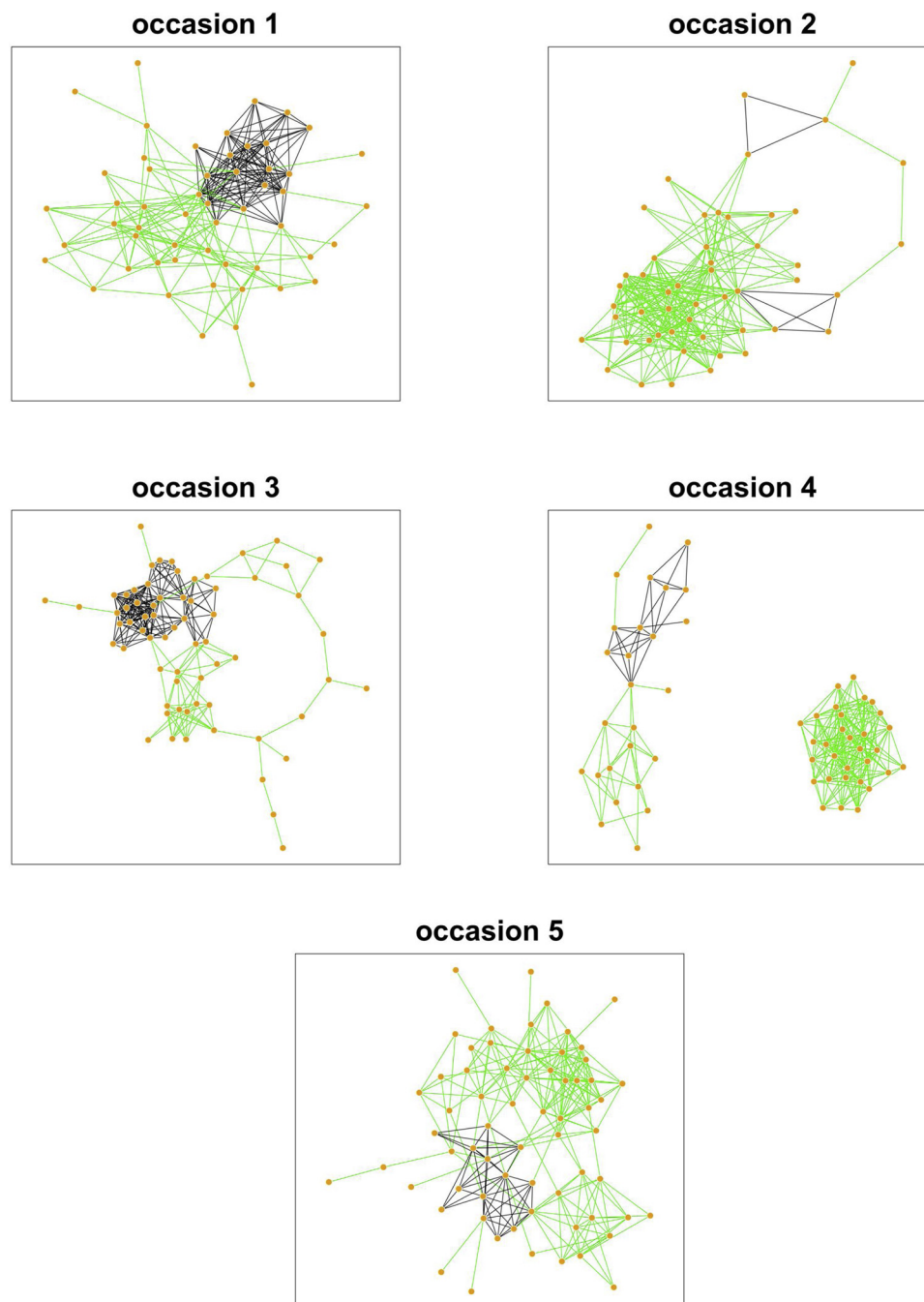


Fig. 1. Visualisation of the network for the Commerson's dolphin population, over five sampling occasions, for the year 2007, showing associations (lines) between individuals (orange circles). For each edge, we calculated the average number of times the corresponding dyad was estimated as being associated ($x = 1$) 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.).

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 $71 \times (71-1)/2 = 2485$ 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, betweenness appeared relatively homogeneous, despite some dolphins with low betweenness and a single animal with very high betweenness (Fig. 2).

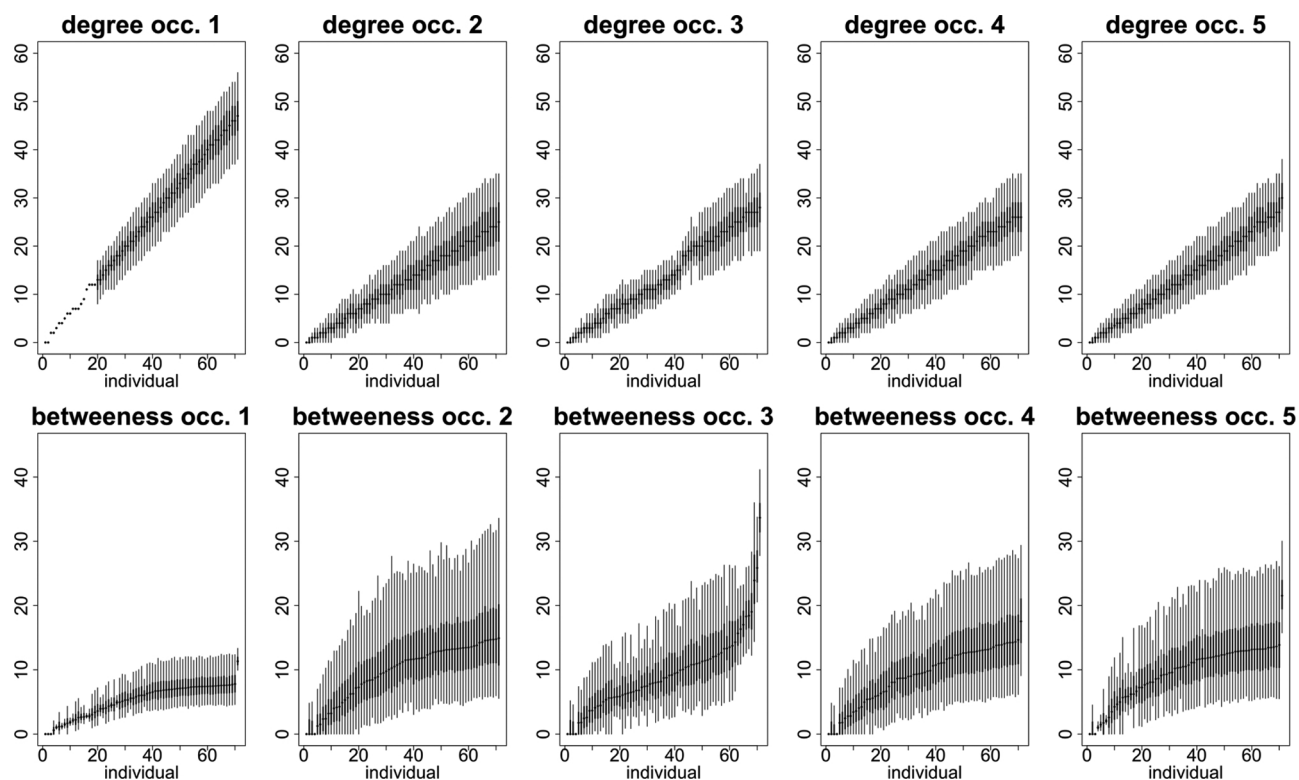


Fig. 2. Local properties of the Commerson's dolphin network. For each individual and for each of the 5 capture occasions, degree (top panels) and betweenness (bottom panels) are summarized with the posterior mean (circle), the 50% (thick line) and 95% (thin line) credible intervals.

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.

Competing interests

The authors declare no competing interests.

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*Stomach contents of long-finned pilot whales (*Globicephala melas*) from southern Chile*

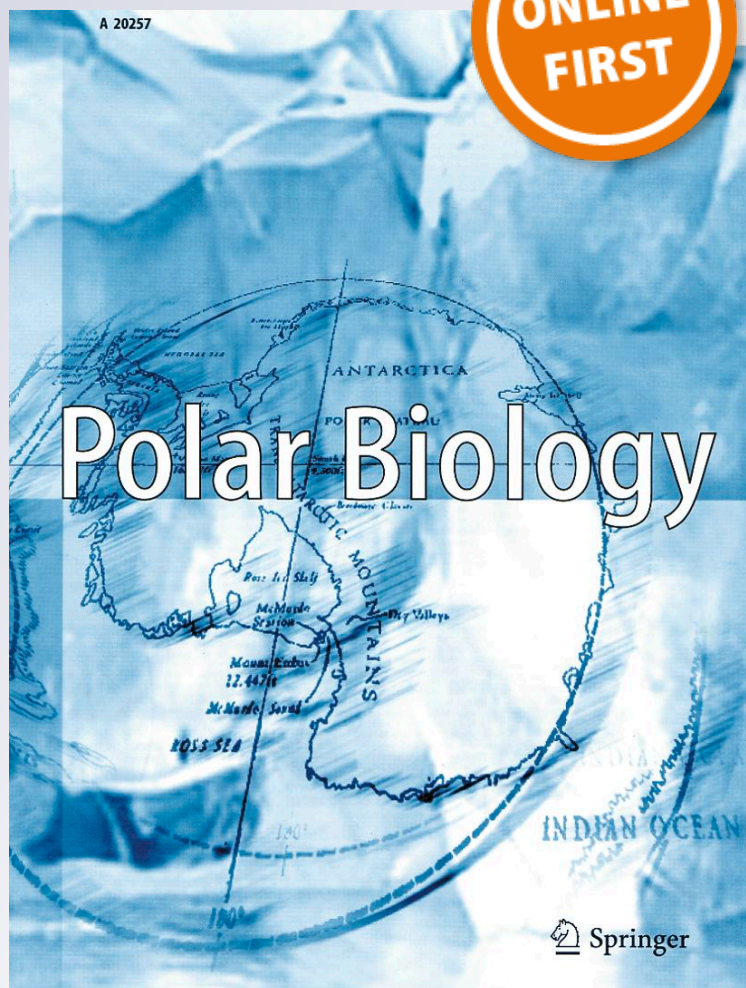
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Stomach contents of long-finned pilot whales (*Globicephala melas*) from southern Chile

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Abstract The widely distributed long-finned pilot whale (*Globicephala melas*) has been reported off the Chilean coast, from Iquique (20°12'S) south to Navarino Island (55°15'S; 67°30'W), but little is known about its biology or ecology in the region. Here, we report on the prey of this species, identified by stomach content analyses from animals stranded on Holget Islets, Beagle Channel, southern Chile in August 2006. The stomachs of seven individuals (six females and one male) contained cephalopod remains. The prey composition found in these southern Chilean pilot whales was similar to that described in other parts of the world and the Southern Ocean. This is the first report on the feeding habits of this species from Chile.

Keywords *Globicephala melas* · Beagle Channel · Mass stranding · Stomach content · Cephalopods · Southern Ocean

Introduction

Marine mammal feeding is often poorly understood due to environmental and behavioral challenges: observations are difficult (feeding usually takes place below the surface), researcher presence can disturb animals' foraging behavior, and feeding events may occur quickly (Heithaus and Dill 2002). Some aspects of feeding, such as diet, are possible to study by the analysis of digestive tracks of stranded individuals and analyses of prey hard structures that resist the digestion process, such as bones and cephalopod beaks (Perrin and Geraci 2002). Mass stranding events offer the rare opportunity of collecting data from many individuals, which gives a better representation of the feeding habits of those species.

The long-finned pilot whale (*Globicephala melas*, Traill 1809) is a widely distributed cetacean. In the Northern Hemisphere (*G. m. melas* subspecies), it is found only in the Atlantic Ocean north of 20°N; however, they are more extended in the Southern Hemisphere (*G. m. edwardii* subspecies), where they range in the southern South Pacific, South Atlantic, and mostly across the Southern Ocean (Olson and Reilly 2002). Off South America, this species has been recorded along the coast of Chile from Iquique (20°12'S) south to Navarino Island (55°15'S; 67°30'W) in the Cape Horn area, and also near the offshore island of San Ambrosio (26°20'37"S; 79°53'28"W) (Aguayo-Lobo et al. 1998). In the southwestern South Atlantic, this species has been recorded from southern Brazil, Uruguay, along the coast of Argentina (Bastida and Rodríguez 2003; Crespo et al. 2008), and around the Falkland (Malvinas) Islands (Otley et al. 2008; www.falklandsconservation.com/wildlife/FISStateOfTheEnvRpt08.pdf). It has also been reported around the South Shetland Islands, in the Antarctic Peninsula area (Aguayo-Lobo et al. 1998).

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The long-finned pilot whale frequently suffers mass strandings (Olson and Reilly 2002; Perrin and Geraci 2002). A significant number of the strandings result in high mortality of the whales involved. During these events, important biological and ecological aspects of the species may be gathered, including diet. Stomach content analyses after necropsy have revealed that cephalopods are the main prey item for the long-finned pilot whale in different parts of its worldwide distribution, such as Argentina (Clarke and Goodall 1994), Brazil (Santos and Haimovici 2001), Falkland (Malvinas) Islands (H. Otley pers. comm.), Australia (Gales et al. 1992), New Zealand (Beatson et al. 2007a, b; Beatson and O'Shea 2009), along the USA, Atlantic coast (Gannon et al. 1997) and the coast of Normandy, English Channel (De Pierrepont et al. 2005).

In Chile, little is known about the biology and ecology of this species due to the limited number of records of both sightings and strandings. Some single strandings have been reported (Venegas and Sielfeld 1978), but only three mass strandings had been recorded. The first occurred in March 1979, on Windhond Bay (55°15'S; 67°30'W), Navarino Island (Venegas and Sielfeld 1980) involving 125 individuals. The second occurred at Poseidón Bay (52°17'S; 69°13'W), in the Strait of Magellan, in August 1982 including 61 pilot whales (C. Venegas pers. comm.). The third, of 13 individuals, was on Holger islets (54°56'S; 67°15'W), Beagle Channel, in August 2006 (Olavarria unpublished data). Only in the latter case were stomach content samples collected. Their analyses are reported here. Our aim was to get new insights into the prey species composition of long-finned pilot whales from southern Chile, to complement the sparse information in the Southern Ocean.

Materials and methods

The stranding and sample collection

On August 8, 2006, a group of 13 long-finned pilot whale stranded along the coasts of the Holget islets, Beagle Channel, in southern Tierra del Fuego. The stranding was found by the crew of a Chilean Navy helicopter patrolling the area. Due to the remoteness of the area, 5 days passed before it was possible for one of us (CO) to visit the area. Of the 13 whales, one had floated into the Beagle Channel, where fishermen found and flensed it. Additionally, a single pilot whale was found in the easternmost part of the Beagle Channel, on the coast of Estancia Moat the same month. This pilot whale is believed to be from the same stranding. Only skeletal remains were collected (RNP Goodall pers. comm.).

In the field, the sex and several morphological measurements were recorded, and samples were obtained. Sex identification was confirmed later by DNA analysis from skin samples (Gilson et al. (1998); Olavarria unpublished data). Necropsies performed on seven of the 13 individuals allowed for collection of the stomach content from six females and one male. The examination of intestines revealed prey remains in only one individual (in the rectum). Weather and time constraints prevented the examination of other individuals.

All prey remains from stomach and intestine contents were stored in 95 % ethanol until laboratory analyses. Samples were washed with water and retained using a 1-mm sieve (Beatson et al. 2007a). Cephalopod beaks and a few eye lenses were found after washing; however, only individual beaks were used in further analyses given the lack of references for identifying species using eye lenses. Beaks were cleaned using a soft brush and separated into upper or lower beak categories. The species identification was performed by comparison with key references (Clarke 1986; Kubodera et al. 1998; Lu and Ickeringill 2002; Xavier and Cherel 2009). Rostral and hood length (RL and HL, respectively) were measured according to Xavier & Cherel (2009) protocol, using a ruler under a microscope (uncertainty of the rule was ± 0.5 mm). The mantle length (ML) and total weight (TW) were estimated using the regression equations in Xavier and Cherel (2009).

Results

A total of 148 mandibles were taken from the stomachs and intestines of the 7 pilot whales and 86 % of those were identified. The remaining 14 % could not be identified due to being partially broken, poor development of structures and/or the lack of representation in the taxonomic keys of Southern Ocean cephalopod species.

The majority of squid beaks were found in the stomachs of only two whales (ID numbers 801 and 805) (Table 1). Three cephalopod species were identified: *Chiroteuthis veranyi*, *Martialia hyadesi* and *Moroteuthis ingens*. A few beaks from the genus *Moroteuthis* formed a fourth group, which was not possible to identify to species level. *Martialia hyadesi* and *Moroteuthis ingens* were the most abundant prey species. For the last two species, the RL and HL values (and the estimated ML and TW) show that a range of prey sizes were consumed by these long-finned pilot whales (Tables 2, 3).

Discussion

The diet of long-finned pilot whales stranded in southern Chile seems to be comprised exclusively by cephalopods.

Table 1 Prey composition and frequency in stomach contents of *G. melas* on the Holger Islets, Beagle Channel, southern Chile

Individual pilot whale	801	803	804	805	805 Rectum ^a	806	807	809
Sex	F	F	F	F	F	F	F	M
Length of whale (cm)	444	439	259	423	423	465	410	515
Chiroteuthidae								
<i>Chiroteuthis veranyi</i>					2			
Ommastrephidae								
<i>Martialia hyadesi</i>	17	2	1	20	1	1		
Onychoteuthidae								
<i>Moroteuthis ingens</i>	20	1		19	3	15	1	4
<i>Morotheuthis</i> sp.				7	1			
Unidentified	2	2	3	4	1		1	
Total upper cephalopod beaks	22	3	2	18	3	4	0	0
Total lower cephalopod beaks	17	2	2	32	5	12	2	4

^a The only individual with prey remains in the intestine

Table 2 Cephalopod beak measurements from *G. melas* stranded on the Holger Islets, Beagle Channel, southern Chile

Cephalopod species	Upper beak				Lower beak			
	<i>N</i>	Mean (mm)	Range (mm)	SD	<i>N</i>	Mean (mm)	Range (mm)	SD
<i>Moroteuthis ingens</i>								
RL	25	5.76	9.50–2.50	1.60	32	8.73	11.50–1.00	1.96
HL	25	16.20	26.00–7.00	4.68	32	6.57	9.00–1.80	1.28
<i>Martialia hyadesi</i>								
RL	7	5.03	8.00–2.00	2.36	28	6.97	9.50–3.00	1.58
HL	7	14.00	20.50–5.50	6.22	28	6.23	8.00–3.00	1.23

Table 3 Mean mantle length (ML) and total weight (TW) estimated from lower beak rostral length (LRL; following regression equations in Xavier and Chereil 2009) for cephalopod species from *G. melas* stranded on Holger Islets, Beagle Channel, southern Chile

Species	<i>N</i>	LRL (mm)		ML (mm)		TW (gr)	
		Mean	SD	Mean	SD	Mean	SD
<i>M. ingens</i>	32	8.73	1.96	311.71	47.80	850.94	267.36
<i>M. hyadesi</i>	28	6.97	1.58	307.45	46.57	578.89	236.21
<i>C. veranyi</i>	1	4.5		121.47		45.61	

This is consistent with studies undertaken in other parts of the Southern Ocean, where this group is the main prey for the species (Gales et al. 1992; Clarke and Goodall 1994; H Otley pers. comm.; Beatson et al. 2007a, b; Beatson and O'Shea 2009). Some of the studies have shown a proportion of fish in their diet (Gales et al. 1992; H. Otley pers. comm.; R. N. P. Goodall, pers. comm.), which were not found here. This could be the result of a difference in diet preference or of sampling.

The three species identified here as prey of long-finned pilot whales have been found distributed in Chilean waters (Vega 2009). *Moroteuthis ingens* is found south of 39°S, but more commonly south of 42°S off Chile (Vega 2009).

In other locations, this species has been reported in sub-antarctic waters north of the Antarctic Convergence (Roper et al. 1985). *M. ingens* has been also found south of the subtropical convergence off Patagonia and New Zealand; however, it probably has a circumantarctic distribution (Kubodera et al. 1998). The full bathymetric range of distribution of this epipelagic oceanic species is unknown (Vega 2009), although it has been recorded at 400 m (Roper 1981). *Martialia hyadesi* is found south of 40°S in the southwestern South Atlantic, South Pacific and Southern Ocean (Roper et al. 1985; Nesis 1987; Wormuth 1998; Vega 2009). Its bathymetric distribution in the southwestern South Atlantic indicates that mainly lives in waters

deeper than 250 m (González et al. 1997). *Chiroteuthis veranyi* has been reported for Peru and northern and central Chile south to 40°–45°S (Nesis 1972, 1987; Rocha 1992; Alexeyev 1994). It has been suggested that near the Cape Horn, this species could have an Atlantic origin. The bathymetric distribution of adults shows that they live in the mesopelagic and bathypelagic zone to depths of up to 2,000 m (Nesis 1972, 1987).

Two out of the three species of cephalopods found in our study had been reported as prey of the long-finned pilot whale before, *M. ingens* from Falkland (Malvinas) Islands (H. Otley pers. comm.) and *C. veranyi* in New Zealand (Beatson et al. 2007b) and off Brazil (Santos and Haimovici 2001). They also have been reported as prey of other marine predators. *M. ingens* is common in the diet of the king penguin (*Aptenodytes patagonicus*), wandering albatross (*Diomedea exulans*), royal albatross (*Diomedea epomophora*) and southern opah (*Lampris immaculatus*) (Clarke and Goodall 1994; Cherel et al. 1996; Cherel and Klages 1998; Cherel and Weimerskirch 1999; Jackson et al. 2000; Xavier and Cherel 2009). *C. veranyi* is present in the diet of a wide range of predators, such as albatrosses, petrels, fish, dolphins, toothed whales and seals (Xavier and Cherel 2009). This species is not usually an important prey item, except in the case of the Patagonian toothfish at the Kerguelen Islands (Cherel et al. 2004). *Martialia hyadesi* has been commonly found in the diet of albatrosses, petrels, penguins, fish, toothed whales and sharks, but has not previously been reported as prey of long-finned pilot whales (Cherel and Klages 1998; Croxall et al. 1999; Waugh et al. 1999; Xavier et al. 2003; Xavier and Cherel 2009).

Cephalopods are important prey items of several species of marine mammals, and the analysis of their stomach contents helps to better understand the trophic interactions in the marine environment. The data presented here contribute to the understanding of a particularly poorly understood region.

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