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Author for correspondence:
Johann Mourier
e-mail: johann.mourier@gmail.com

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Conservation biology

Learning and robustness to catch-and-release fishing in a shark social network

Johann Mourier[1,2,3], Culum Brown[3] and Serge Planes[1,2]

[1]PSL Research University: EPHE-UPVD-CNRS, USR 3278 CRIOBE, 66860 Perpignan, France
[2]Laboratoire d'excellence 'CORAIL', EPHE, PSL Research University, UPVD, CNRS, USR 3278 CRIOBE, Papetoai, Moorea, French Polynesia
[3]Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia

JM, 0000-0001-9019-1717

Individuals can play different roles in maintaining connectivity and social cohesion in animal populations and thereby influence population robustness to perturbations. We performed a social network analysis in a reef shark population to assess the vulnerability of the global network to node removal under different scenarios. We found that the network was generally robust to the removal of nodes with high centrality. The network appeared also highly robust to experimental fishing. Individual shark catchability decreased as a function of experience, as revealed by comparing capture frequency and site presence. Altogether, these features suggest that individuals learnt to avoid capture, which ultimately increased network robustness to experimental catch-and-release. Our results also suggest that some caution must be taken when using capture–recapture models often used to assess population size as assumptions (such as equal probabilities of capture and recapture) may be violated by individual learning to escape recapture.

1. Introduction

It has been demonstrated that individuals play different roles in animal social networks [1,2], altogether maintaining connectivity and social cohesion in populations. These functions will have several implications for population vulnerability to environmental and anthropogenic perturbations [2,3]. In the end the consequences of removing individuals from a population through natural mortality or human harvest (i.e. exploitation or culling) may vary depending on the role of each individual's contribution to group integrity. Association of individuals with different attributes will shape the network, with a few individuals holding structurally important positions in their population and thereby influencing processes such as mating, information flow and parasite or disease transmission [2,4]. Assuming that individuals play similar roles in their population would have dramatic consequences on population dynamic modelling. For instance, the removal of a matriarch from an elephant social group can disrupt population dynamics by the loss of social knowledge [5].

Unlike mammal species, sharks have traditionally been assumed to show some form of social structure only in some particular situations like mating, feeding or migrations. However, it has been recently discovered that several species of sharks showed more complex levels of sociality than previously expected, having social preferences [6] and personalities [7,8], and are capable of social learning [9]. However, little is known about the varying importance of each individual within social groups and its significance in terms of vulnerability of shark networks to anthropogenic impacts. Sharks are increasingly targeted by fisheries [10] and are subject to culling policies in response to shark–human interactions [11]. Integrating individual characteristics and variable contribution into a social network may also contribute to improving conservation biology strategies.

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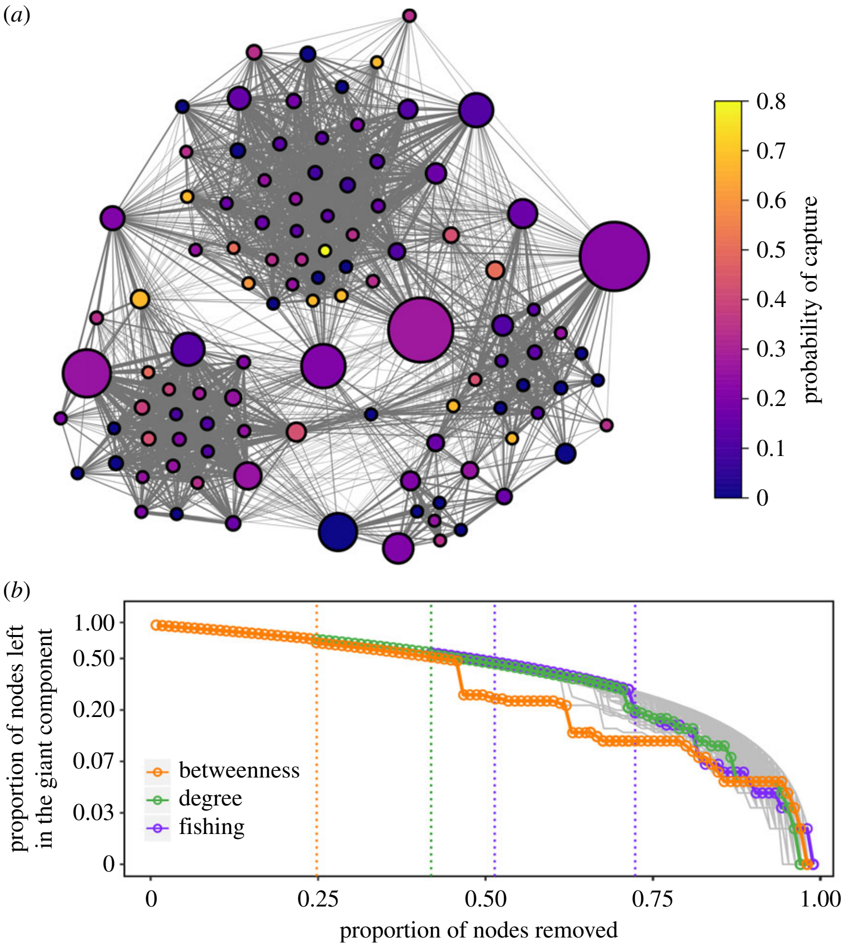

Figure 1. (*a*) Social network of a population of blacktip reef sharks in Moorea. Nodes represent individual sharks ($n = 105$) sighted more than three times between 2008 and 2010 with node colour representing individual probability of capture and node size proportional to betweenness. Link thickness is proportional to the association index HWI. (*b*) Fragmentation of the network under random and targeted attacks. The proportion of nodes left in the largest cluster is displayed against the proportion of nodes sequentially removed from the population according to betweenness (orange), degree (green) and catchability (purple). Grey curves indicate 1000 random removal scenarios.

We used the social network of a free-ranging population of blacktip reef sharks (*Carcharhinus melanopterus*) that show preferred associations and network assortment [6] to assess the role of individuals in maintaining cohesion in the network by examining network properties. The study was conducted in combination with an experimental catch-and-release programme enabling us to infer individual differences in catchability and their consequences for network robustness. This programme enabled us to simultaneously test the learning capability of shark toward their catchability and question estimates of population size inferred from catch-and-release programmes.

2. Material and methods

(a) Field observations and network construction

Between 2008 and 2010, observation surveys were conducted along a 10 km portion of the northern reef of Moorea Island (French Polynesia). The surveys consisted of 40 min dives at seven sites during which individual blacktip reef sharks were identified using photo-identification. Shark assortment by space use was shown to be significantly weaker than random expectation [6]. Using R package *asnipe* [12], we calculated dyadic association strengths from the spatio-temporal co-occurrences, the proportion of time two individuals were observed together at the same site and time, using the half-weight index (HWI) [13]. Note that sharks displayed social behaviours such as following or parallel swimming [6] and a social interaction was therefore recorded as two individuals at the same time in the diver's field of view.

(b) Experimental captures

Shark fishing sessions using rod and reel and barbless hooks were conducted initially to obtain tissue samples for genetic analysis [14]. Each shark was identified by photo-identification of dorsal fin [6], sexed and measured [15]. Fishing sessions were conducted directly after underwater surveys to avoid perturbations of the experimental set-up and assess the response of sharks known to be present during fishing. Fishing effort was maintained until sharks failed to respond to the bait (generally less than 30 min).

(c) Network properties and node removal

We investigated network properties to assess the degree of vulnerability to the removal of individuals. Individual variation in centrality was calculated using the following statistics [16]: (i) *betweenness centrality* measures how important a node is for connecting disparate parts of a network and, (ii) node *degree* (i.e. the number of direct neighbours an individual has in the network) measures individual gregariousness. Moreover, individuals were ranked according to their probabilities of capture (number of captures divided by the number of sessions the individual was observed).

We then investigated network homophily to test whether individuals preferentially associate with others similar in traits. Assortative mixing by node degree, for example, indicates preferential associations among individuals of similar level of gregariousness. We assessed assortment by degree and probability of capture using the R package *assortnet* [17].

We calculated the clustering coefficient, i.e. the number of ties between neighbours divided by the maximal possible number of ties, as an indicator of path redundancy within the network. We constructed a null model by performing permutations on the group matrix, swapping individuals between associations while controlling for the number of observations and group size [18], and restricting swaps within site and sampling periods (i.e. weeks). We then compared the observed clustering coefficient to those from 1000 random networks. The number of values outside of the 95% range of the distribution provides the p-value.

A node removal procedure was performed to emphasize network properties and investigate the vulnerability of the network under three scenarios: (i) we first removed individuals one by one starting with sharks of highest betweenness centrality to test for the presence of a few individuals connecting the different clusters of the network; (ii) then we removed individuals one by one according to decreasing node degree to test for the importance of gregariousness for network robustness; (iii) and finally we removed individuals one by one with higher capture probabilities (i.e. fishing scenario) first to infer the vulnerability of the network to shark capture. For each scenario and each removal step, the number of individuals left in the largest component of the network was inferred. A drop in size indicates fragmentation of the network into smaller components. Each scenario was then compared with a null model consisting of 1000 random removal procedures.

(d) Modelling shark capture

Finally, we investigated factors influencing shark capture using a generalized linear mixed model (GLMM) to examine the effects of sex, size, node degree, betweenness, number and order of sightings for each individual on their probability of capture using a binomial error structure with a logit link function. Individual ID was input as a random factor in the model. The model was built using function *glme()* in R package lme4 [19] and model selection was conducted using single-term deletions with a likelihood ratio test based (LRT) backward selection [20].

3. Results and discussion

The network was built with 105 individual sharks observed at least three times (range 3–20) during 136 sampling periods (i.e. weeks), all connected within a single social network component (figure 1*a*). The threshold of three observations for each shark was chosen to remove transient sharks from the network and to enable the computation of capture rate for each individual. Sharks displayed assortative mixing by degree ($r = 0.286 \pm 0.018$) but not by betweenness ($r = -0.006 \pm 0.016$). Assortment by gregariousness is a common characteristic of many animal social networks [1]. We also identified some individuals with high betweenness (figure 1*a*) that linked sub-communities and provided social cohesion to the global community. Assortment by probability of capture was rather weak ($r = 0.063 \pm 0.019$), suggesting that catchability does not play an important role in association patterns.

The removal of individuals under a fishing scenario demonstrated that reasonable levels of fishing pressure are unlikely to induce a rapid break in connectivity within the network (figure 1*b*). Even after removing more than 25% of the individuals, the network did not fragment under targeted nor random removal and maintained a large component encompassing most individuals (figure 1*b*). Unlike some other networks, which disintegrate quickly following removal of high-betweenness nodes [3], the largest component of the present shark network shrank faster than it would do under random removal only after more than 25% of individuals had been removed ($p < 0.001$; figure 1*b*), demonstrating the presence of multiple redundant relationships between individuals. Similarly, the network was slightly more robust to the removal of nodes with highest degree as the network fragmented faster than random after more than 42% of individuals were removed. Removing individuals according to their catchability revealed that the network was highly robust to fishing as it remained structured and was more robust than random until up to 72% of individuals were removed ($p < 0.001$; figure 1*b*). In addition, the network had a clustering coefficient significantly higher than expected by chance ($C_{obs} = 0.72$, mean $C_{random} = 0.70$; $p < 0.001$), confirming a high level of redundancy in social connections between any two sharks which increases the resilience of the network [1]. Interpretation of our results however should consider that our approach does not allow for the potential of adaptation and restructure after individual removal [21]. For instance, missing central animals might be replaced by others which our simulation cannot predict.

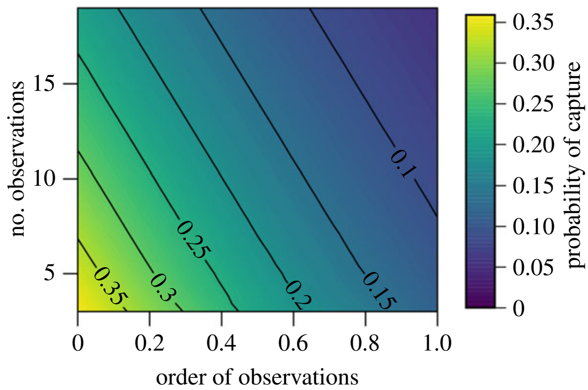

Figure 2. Probability of capture decreases across time as a result of experience gained by individuals through repeated observations.

Individual changes in catchability through learning were observed from a capture–release–recapture protocol (e.g. population surveys or capture-and-release fishing). GLMM revealed that individual probability of capture was only marginally driven by sex, size, degree or betweenness of sharks. However, probability of capture decreased with an increasing number of sightings as well as with individual's experience of capture (figure 2 and tables 1 and 2). In this framework, learning makes the network increasingly robust to catch-and-release fishing pressure. In addition to the fact that blacktip reef sharks are relatively robust to injuries [22], their population structure appeared robust to reasonable levels of fishing pressure. Learning in response to being captured should particularly be taken into consideration when using mark–recapture models based on fishing sampling. We show here that learning may induce important bias in such an analytical framework as the assumption that individuals have the same probability of being caught may be violated. In some teleost species catchability quickly dropped in a few days of sustained fishing pressure in a catch-and-release scenario [23,24]. Similarly, sharks may learn from previous non-lethal interaction with fisheries (e.g. where sharks are by-catches and are released in the water) [25].

In conclusion, our results not only reveal interesting learning capacities in sharks but also improve our understanding

Table 1. Model selection using single-term deletions with a likelihood ratio test based (LRT) backward selection. Selected model based on the likelihood ratio test is indicated in bold. Variables: Capture = probability of capture; OrdS = order of sightings; Nobs = number of observations; Deg = network degree; Betw = network betweenness; Sex = sex; Size = size. AIC, Akaike information criterion; logLik, log likelihood.

	description	d.f.	AIC	logLik	*p*
model 1	Capture ~ OrdS × Nobs + Deg + Betw + Sex + Size + (1|*ID*)	9	672.51	−327.26	0.051
model 2	Capture ~ OrdS + Nobs + Deg + Betw + Sex + Size + (1|*ID*)	8	674.31	−329.16	0.696
model 2	Capture ~ OrdS + Nobs + Deg + Sex + Size + (1|*ID*)	7	672.47	−329.23	0.581
model 3	Capture ~ OrdS + Nobs + Deg + Sex + (1|*ID*)	6	670.77	−329.38	0.429
model 4	Capture ~ OrdS + Nobs + Deg + (1|*ID*)	5	669.39	−329.70	0.313
model 5	**Capture ~ OrdS + Nobs + (1|*ID*)**	**4**	**668.41**	**−330.20**	**0.039**
model 6	Capture ~ OrdS + (1|*ID*)	3	670.66	−332.33	

Table 2. General linear mixed model results of factors that influence probability of capture of sharks for the selected model. Explanatory variables include number of sightings and order of sightings. Significant differences were evaluated with maximum-likelihood ratio index (χ^2, $p < 0.05$; table 1) using a backward selection procedure.

	estimate	std error	*F*-value	*p*-value
(intercept)	−0.28203	0.24901		
number of sightings (Nobs)	−0.04921	0.02438	4.0732	0.0436
order of sightings (OrdS)	−1.52289	0.29801	26.3912	3.22×10^{-7}

of shark social networks revealing that social path redundancy (i.e. the presence of multiple links between two individuals) and individual learning abilities reinforce population robustness to removal. Expanding this approach to other populations will benefit conservation of threatened species (including sharks) by estimating the removal threshold after which the cohesion of the population may collapse and may also contribute to human–wildlife management. Although the effect of reduction in connectivity within the population is poorly understood, connectivity in animal populations has previously been identified as an important evolutionary feature maintaining genetic health of populations [26].

Ethics. This work was approved by the Direction à l'Environnement (DIREN) of French Polynesia and Ministère de la promotion des langues, de la culture, de la communication et de l'environnement de Polynésie française under Arrêté 9324 of 30 October 2015.

Data accessibility. Data are available at: http://dx.doi.org/10.5061/dryad.gg859 [27].

Authors' contributions. All authors contributed to the study and first draft; J.M. and S.P. designed the experiment; J.M. collected and analysed the data, supported by C.B. and S.P. All authors approved the final version of the manuscript agree to be held accountable for the content therein.

Competing interests. We have no competing interests.

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