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Author for correspondence:
Éadin N. O'Mahony
e-mail: enao1@st-andrews.ac.uk

The diffusion of cooperative and solo bubble net feeding in Canadian Pacific humpback whales

Janie Wray[1,†], Éadin N. O'Mahony[1,2,4,†], Grace Baer[1], Nicole Robinson[5], Archie Dundas[5], Oscar E. Gaggiotti[3], Luke Rendell[3] and Eric M. Keen[1,6]

[1]North Coast Cetacean Society, Alert Bay, British Columbia, Canada
[2]Scottish Oceans Institute, and [3]Centre for Biological Diversity, University of St Andrews, St Andrews, Fife, UK
[4]Section for Molecular Ecology and Evolution, University of Copenhagen Globe Institute, Copenhagen, Capital Region of Denmark, Denmark
[5]Gitga'at Oceans and Lands Department, Hartley Bay, British Columbia, Canada
[6]Sewanee The University of the South, Sewanee, TN, USA

ÉNO, 0000-0002-0755-1329; OEG, 0000-0003-1827-1493; LR, 0000-0002-1121-9142

Animal culture, information and behaviours acquired and shared by social learning are a form of biodiversity with intrinsic and practical value. Cooperative foraging, a mutualistic resource acquisition behaviour observed across diverse taxa, is strongly connected to social networks via behavioural states, cues and often social learning, as it typically involves high interaction rates. Understanding the distribution, diffusion and learning mechanisms of such cooperative behaviours is an important but understudied aspect of nonhuman culture. Bubble net feeding ('bubble netting') is a specialized foraging technique practised by certain humpback whale (*Megaptera novaeangliae*) populations globally. Over 20 years in the northern Canadian Pacific, we observed the diffusion of two forms: cooperative group and independent (or 'solo') bubble netting. Network-based diffusion analysis—a tool to test for social learning—finds strong evidence for social learning of bubble netting when the overall social network is used, even after accounting for traits such as site fidelity and sex (10.6×10^3 to 35.4×10^3 times more support for social versus asocial learning; $p < 0.0001$). A homophily check using pre-acquisition association data returned ambiguous results, likely due to the inherent sociality of this cooperative foraging behaviour. Nonetheless, the rapid diffusion of bubble netting is clearly important for population viability and should inform conservation planning for this threatened population.

1. Introduction

Animal culture, in which information and behaviours are acquired and shared through social learning [1–5], is a form of biodiversity with both intrinsic value and practical importance [1,5–8]. For example, learned behaviours can augment population viability, individual survival, group cohesion and intraspecific diversity, and can also facilitate ecological specialization and resilience to ecosystem change [1,3,6–13]. Cultural traditions, such as learned migratory routes and traditional feeding areas, also affect species' responses to habitat alterations [1]. For these reasons, the importance of animal culture and social learning to biological conservation is receiving increasingly widespread attention [1,8,14–16].

The social learning of foraging techniques can be particularly instrumental to a species's survival and ecological resilience [13]. Innovations can improve efficiency or broaden the prey base, which can reduce vulnerability to shifts in prey supply and distribution [13,17]. The diffusion of new feeding

[†]Janie Wray and Éadin N. O'Mahony share lead authorship.

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strategies through social groups has been described for various taxa, from fish [18,19] to birds [20–22] and mammals [13]. Mammalian examples of socially learned feeding techniques are common among primates [23–29] and cetaceans [7,11,30–33], especially the odontocetes [9,34–37].

Social learning, the foundation of cultural evolution, can be categorized into the occurrence of learning resulting from (i) *observations* of a behaviour or (ii) '*interactions with another animal* or its products' [3] (emphasis added). The diversity of cooperative behaviours in animals, including cetaceans [38–44], suggests interactions could be as potent a factor as observation. Social learning can be understood as a dynamic process of observation of, and simultaneous interaction with, informed individuals and the products of their behaviour (i.e. a process of 'learning by doing').

With few exceptions (i.e. migratory routes of southern right whales *Eubalaena australis* [45], and possibly tread-water feeding in Bryde's whales *Balaenoptera edeni* [46]), the humpback whale (*Megaptera novaeangliae*) is the only baleen whale for which there is currently good evidence of widespread social learning. The cultural evolution of humpback song is widely known [47,48], but humpback whales also innovate and socially learn feeding tactics, such as lobtail feeding in the North Atlantic [30,49] and trap feeding near Vancouver Island, Canada [13]. Other feeding tactics of this generalist predator include lunge feeding [50,51], flick feeding [50,52], bottom feeding [53,54] and bubble net feeding (hereafter 'bubble netting') [44,50,55–60]. It is plausible that these techniques are also socially learned, but to date have not been demonstrated as such.

Bubble netting is performed by humpback whales around the world. The behaviour itself is a multi-step task: diving beneath a shoal of schooling fish or krill and emitting a stream of bubbles through the blowholes while swimming in a spiral or circle creating a curtain 'net' of bubbles, concentrating the prey [61]. Sometimes, this is accompanied by specific vocalizations that may produce increased prey concentration [62]. The feeding bout ends with a vertical or horizontal lunge through the prey patch at or near the surface of the water. Bubble netting is often performed by individual whales [57–59], but it can also be performed cooperatively in groups that show role differentiation [44,50,56,57,60]. While the relative benefits of bubble netting individually versus cooperatively are not well understood, Mastick *et al.* [57] suggest that in larger groups, each individual has decreased exertion, thereby increasing foraging efficiency. Group bubble netting is genuinely cooperative, with coordination and division of labour, not simply a close spatial aggregation of individually feeding whales.

Given that cooperation usually involves coordinated actions that can include division of labour [43,63], stable social associations could, through familiarity, lead to additional improvements in foraging efficiency [43]. It has been suggested that groups of bubble netting humpback whales have role specialization across foraging bouts (where a 'foraging bout' is considered to be one iteration of the casting of a bubble net with subsequent lunge feeding) [57]. Conceivable roles include the production of the bubble net itself, the herding of shoaling fish into the net, and vocalizing [44]. The humpback whales foraging in the Kitimat Fjord System (KFS) of northern British Columbia (BC), Canada, show high variability in bubble netting group size, and some individuals switch between cooperative group and solo forms of bubble netting [56]. Given this behavioural plasticity and the inherent sociality of cooperation, testing for social learning requires an assessment of the effect of homophily, where behavioural similarity will result in preferential social connection [64]. It is important in such cases to untangle as best as possible whether homophily is structuring the social network [65], or if the social network is predicting the diffusion of the cooperative behaviour through social learning. This can be challenging to achieve, but network-based diffusion analysis (NBDA) [66] using temporally dynamic networks offers a way to isolate social associations prior to the acquisition of the behaviour, thereby reducing the impact of homophily on inferences about social transmission [30].

We have previously shown bubble netting to be a behavioural trait underpinning the structure of the social network of an annually resident population of humpback whales [56]. Here we test for the statistical signals of social learning of this behaviour, paying particular attention to the inherent sociality of its cooperative form. The behavioural plasticity and social learning of novel behaviours within this locally expanding population may contribute to its ability to recover from a history of commercial whaling [60,67], which resulted in the catch of an estimated 29 000 humpback whales across the North Pacific in the twentieth century [68]. Understanding the mechanisms of resilience of local populations in light of increasing anthropogenic stressors is particularly important given more recent evidence of a decline in the North Pacific-wide population [69]. We tested for evidence of social learning and homophily of bubble netting using a NBDA on a dataset of humpback whale sightings from 2004 to 2023, under the null hypothesis of no association between social network links an individual has to informed individuals and that individual's apparent learning rate of bubble netting.

2. Methods

(a) Data collection

Humpback whale photo-identifications and behavioural observations were collected from 2004 to 2023 (n = 20 years) within the marine territories of the Gitga'at, Kitasoo/Xai'xais and Haisla First Nations in the KFS (52.8–53.5° N, 129.6–128.5° W; figure 1), BC, Canada. This work was carried out in close collaboration with the Oceans and Lands Department of the Gitga'at First Nation and with the explicit permission of each Nation (box 1). Whales were observed from shore- and vessel-based platforms. The vessel-based survey methods we used are detailed in previous publications [56,67]. Briefly, pre-planned survey routes were conducted between 2004 and 2023 using a 7 m skiff as weather permitted from April to November. When humpback whales were detected, groups were approached with caution, all individuals were counted, location and behaviour noted, and identification photographs of the underside of their tail flukes were collected with standard DSLR cameras and telephoto lenses, following established protocols for this species (e.g. [70]). Fluke photograph capture was non-systematic to maximize the number of whales identified.

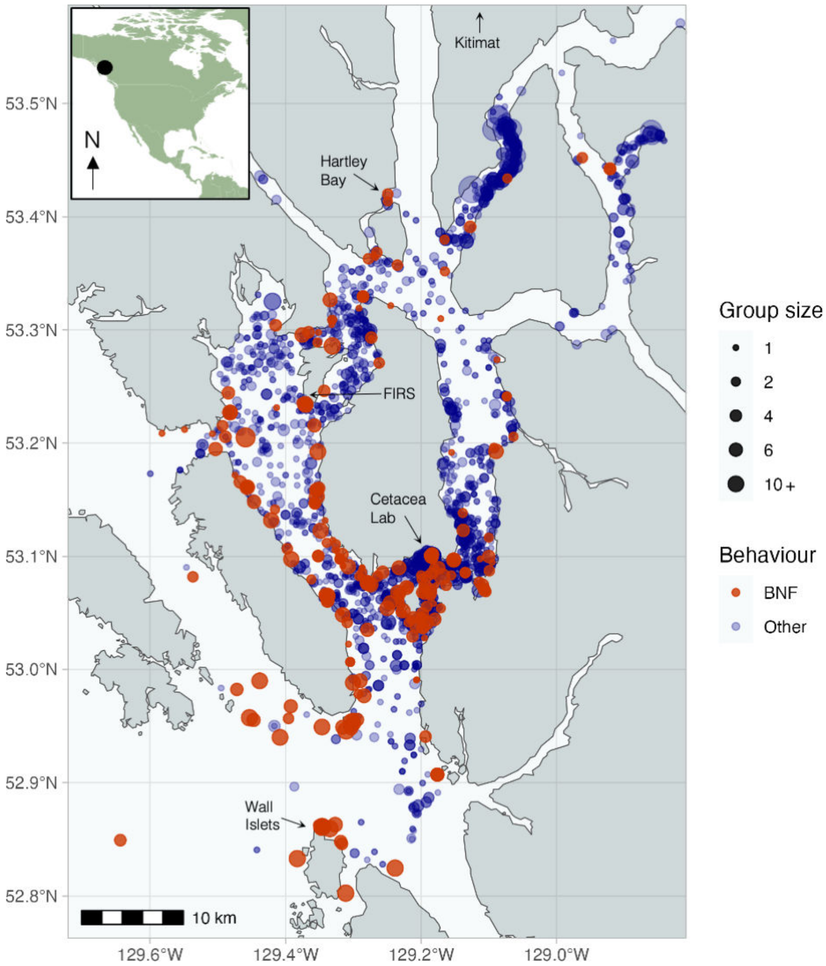

Figure 1. Humpback whale sightings, colour-coded and sized by behavioural state (orange represents sightings of bubble netting, while blue represents sightings of any other behavioural state), in the Kitimat Fjord System, British Columbia, Canada, within the marine territories of the Gitga'at, Kitasoo/Xai'xais and Haisla First Nations. Field stations and population centres are labelled.

BOX 1: Positionality and reflexivity statement.

We comprise an international group of researchers with a range of expertise in various biological disciplines who are collaborating on this project on humpback whales foraging within the traditional territories of the Gitga'at First Nation, the Kitasoo and Xai'xais First Nations, the Gitxaała First Nation and the Haisla First Nation. We have an equal gender balance but a diverse set of backgrounds and perspectives. Authors N.R. and A.D. are Gitga'at members who have been dedicated to the study and protection of marine mammals in Gitga'at territory for approximately two decades. Author J.W. is the co-founder and CEO of the North Coast Cetacean Society (NCCS) and E.M.K., É.N.O. and G.B. are researchers within NCCS, which has been collaborating with the Gitga'at First Nation as an organization since 2001, when permission to conduct research in the territory was granted and specific research agreements established. Authors E.M.K., É.N.O., G.B., J.W., L.R. and O.E.G. recognize our intersecting social identities—we are all white and either living and working as settlers in Canada, or based at research institutions in Europe, from where we travel to spend time working with the Gitga'at in their unceded territory. We are striving to decolonize our research practices and acknowledge that we have much work to do on this still. Authors E.M.K., É.N.O., L.R. and O.E.G. work in an academic system which affords us unearned privileges through its significant history of colonization. All authors recognize that the biological sciences strive for objectivity, but we collectively believe it is critical in the process to decolonise ecology and evolution research that we address our inherent biases and belief systems. We therefore wish to state that we are motivated by a deep care for Earth's biodiversity, and in particular hope to see cetacean species co-existing with our own in perpetuity. We advocate for other researchers within ecology and evolution research to self-reflect on their own positionalities and relationships to land and community. We thank the Gitga'at Oceans and Lands Department and the Gitga'at community for their continued support and collaboration on whale research and conservation.

Shore-based observations occurred at Cetacea Lab (53°6′17.31″ N, 129°11′37.72″ W) from 2014 to 2016, the Wall Islets (52°51′29.10″ N, 129°20′28.53″ W) from 2014 to 2016, and Fin Island Research Station (FIRS; 53°13′18.94″ N, 129°22′34.77″ W) from 2018 to 2023 (figure 1). At these stations, observers carried out systematic scans of the aquatic viewshed at regular intervals from sunrise to sunset from May to October. Groups were noted if they came within 500 m of shore, and identification photographs were taken and catalogued.

(b) Data analysis

For analysis, we defined a *sampling period* as a single calendar day of photo-identification effort, which usually consisted of up to 16 h of active monitoring at shore-based stations and 2–10 h of surveying during vessel-based effort. An *encounter* is defined as a unique observation of a unique group (i.e. if a group of the same social composition was observed twice in one day, as determined through photo-identification, it is only included once; if certain whales from a previous group are seen with other whales in a separate group later in the same day, both encounters are included). A *group* is defined here as individuals that come within two body lengths of each other and coordinate their swimming, diving and/or ventilation behaviour for at least one surfacing [56,71]. We use the term *population* here to refer to the local population of humpback whales documented within the KFS, unless otherwise specified as referring to the entire North Pacific population. Bubble netting behaviour was easily identifiable due to its many indications at the surface (bubble rings, vertical lunges and often conspicuous group sizes). Females were identified when they arrived with a calf and additional sex information was obtained from blow samples [72]. All identification photographs were scored for quality, and only high-quality photographs were used for annual catalogues of identified individuals, as described in [67]. Dyadic association weights were determined with the Simple Ratio Index (SRI) [73] based on the recommendations of Hoppitt & Farine [74] and Weko [75]. The social network across the 20-year study period was visualized using all individuals observed on at least five occasions using the R package 'igraph' [76]. Social associations and behavioural expression of bubble netting occurred over the same period (2004–2023). A sighting threshold of five occasions was applied to remove spurious and extreme association data from very small sample sizes (electronic supplementary material, figure S1) [77].

We used a NBDA [66,78] to test for evidence of cultural transmission of bubble netting in whales encountered 5 or more times (both group and solo events included). The underlying premise of NBDA is that socially learned behaviours tend to spread more quickly among individuals who spend more time together, and that heightened rates of trait performance will increase the likelihood of behavioural transmission among associated conspecifics [66,79]. NBDA models the rate at which 'naive' whales (i.e. those never before observed performing the behaviour) are first observed bubble netting as a function of their associations with 'informed' individuals. The likelihood of the model's fit is then compared to a null model of asocial learning (i.e. independent discovery or invention), where the social transmission parameter is fixed at zero [78].

We built models using a multiplicative order-of-acquisition diffusion analysis (OADA), as we do not know the exact times of acquisition of the target behaviour and therefore assign a ranked bubble netting acquisition order onto whales in the order in which we documented them performing the behaviour [78]. Newly informed individuals from the same detection window were assigned the same ranked order (i.e. they were tied to each other). All individuals observed bubble netting in the study's first year during their first sighting ($n = 12$, representing 7% of the individuals seen five or more times and known to perform the behaviour at the end of the study) were assigned a rank as 'demonstrator', assumed to seed the population with the behaviour, and therefore were removed from the order of acquisition. We chose three individual level variables (ILVs) to include in the models. (i) All models include the total number of sightings of that individual, standardized to a mean of zero and standard deviation of one, to account for sampling bias in our dataset. Models were then built using a combination of (ii) site fidelity, as measured by the Standardized Site Fidelity Index (SSFI, range 0–1) [80], and (iii) sex. We included these to explore their impact on estimated social transmission. We chose to use multiplicative models because of our underlying assumption that each ILV would affect social and asocial learning rates equally (e.g. there is no biological evidence we know of to suggest that one biological sex might be better at learning socially—or, alternatively, at asocial innovation—than the other). Models were compared using ΔAIC, and the lowest ranking model was used to further test for the effect of homophily.

To determine the influence of each ILV on social learning, we calculated the summed Akaike weights ($\sum w_{\mathrm{i}}$) across all models, the model-averaged parameter estimate with 95% confidence intervals calculated according to equation (6.12) in [81] (see electronic supplementary material for equation). Effect sizes are calculated as $e^{(\beta/\sigma)}$ for continuous variables (standardized sightings and site fidelity SSFI), where β is the model-averaged parameter estimate and σ is the s.d. of the unstandardized data. Effect size is calculated as $e^{(2\beta)}$ for the categorical variable sex, where sex is 1 for male, −1 for female and 0 as unknown.

(i) Homophily and immigration

Given the inherent sociality of cooperative bubble netting, we tested for the putative bias that post-acquisition social associations might have on our ability to test for social transmission. A standard OADA-type model as above uses one overarching static social network, composed of dyadic social association strengths (in our case SRI values) spanning the length of the study period. However, as this approach does not differentiate between encounters before and after the acquisition events in calculating the social network, it does not distinguish homophily—where animals that share a behaviour tend to be around each other more, perhaps simply because they target the same resource or cooperate in the targeting of the shared resource. To do this, we needed to target individuals that (i) acquired the behaviour during the study and (ii) had a reasonable estimate available of their pre-acquisition social network. Therefore, to test for the effect of homophily in this context, we temporally halved the sightings data into two time periods (2004–2013 and 2014–2023) and calculated a new social network (a matrix of dyadic SRI scores) at each acquisition event that occurred in the second half of the study, where the individual had been seen at least 5 times before being observed bubble netting. We did this to ensure sufficient data for each iterative social network, as even the earliest acquisition event would include the entire first half of the study's sighting history. Each iterative social network therefore included the full first half of the study period plus the additional time to acquisition (resulting in several

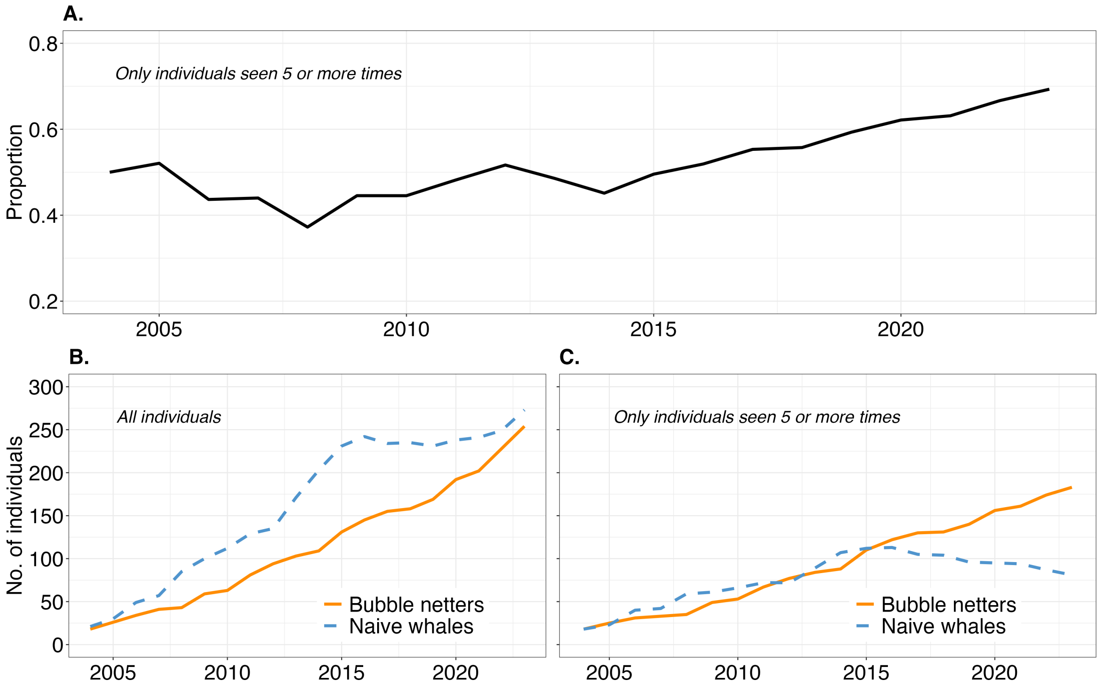

Figure 2. (A) The proportion of whales who are known to bubble net in the NCCS catalogue each year showing an accelerating spread in the second half of the study period. (B) Cumulative number of individuals added to the catalogue by year, including all whales ever identified (regardless of whether they were resighted in later years). Counts are split by whether individuals are known to bubble net feed (solid orange) or not (dashed blue). (C) The number of individuals known to the catalogue each year that have been seen five or more times, split as in (B).

static social networks for each newly informed individual that acquired the behaviour in the second half of the study period combined as a time series to create a dynamic social network through time). This dynamic social network was then incorporated into a final OADA model with the format of the most parsimonious static network (i.e. the lowest AICc scoring model of ILV combinations). We included as seeded demonstrators all whales seen bubble netting in the first half of the study period as well as any individuals seen bubble netting on their first sighting in the second half of the study period. Ties were treated as before, with whales observed bubble netting for the first time together being given the same rank in the order of acquisition. All analyses were conducted in R v. 4.3.1 [82] using custom scripts and R package 'NBDA' [79].

3. Results

A total of 7485 photo-identifications were collected during 4053 encounters across 20 years of survey effort (1356 days of sampling, 2004–2023). Of the 526 identified individual whales, 250 were encountered on at least 5 occasions. Fifty-eight per cent of all 526 whales were encountered across multiple years (32% in 5 or more years, 15% in 10 or more years). Of the 250 whales encountered on 5 or more occasions, 97% were encountered in multiple years (68% in 5 or more years and 32% in 10 or more years). Bubble netting was observed in 254 individuals (48% of the identified population, hereafter referred to as 'bubble netters') on 635 occasions. The form of bubble netting observed was similar to that described in southeast Alaska [50,55], in which one individual in the group (or in rare cases more than one) produces a distinct tonal moan (400–600 Hz) that has come to be known as a 'feeding call' [50]. Solo bubble netting does not always include the production of a feeding call. Pacific herring (*Clupea pallasii*) was the only prey observed during cooperative feeding events or indicated from the collection of prey remains.

Of all 254 bubble netters, 32% ($n = 82$) were bubble netting during our first encounter of them. Of these, 65 individuals (25.6% of all bubble netters) were observed cooperatively bubble netting on first encounter. The remaining 17 individuals (6.7% of all bubble netters) were observed solo bubble netting on first encounter. Therefore, most individuals seen bubble netting on first encounter were doing so cooperatively. The large majority of all the bubble netting events observed were cooperative: 92.4% of all 635 bubble netting events documented during the 20-year study period (cooperative bubble netting video available in electronic supplementary material). Of the 17 individuals first seen in a solo bubble netting context, six (35%) were subsequently observed participating in cooperative bubble netting. Given a lesser prevalence of solo bubble netting overall, with a total of 167 solo bubble netting events documented (7.6% of all bubble netting events), these were performed by a comparatively high number of unique individuals, 93 individuals in total. Of the remaining 172 bubble netters, who were first seen in non-feeding contexts, 151 (88%) of these were cooperatively bubble netting when first observed in a bubble netting context.

When data were filtered to whales seen at least 5 times, 179 individuals were seen bubble netting on 614 occasions (72% among whales encountered at least 5 times). The size of bubble netting groups ranged from 1 to 16 (median = 3), with 30% of encounters involving groups of at least 5 whales. Of the 179 bubble netters that were seen at least 5 times in the study period, 151 of them were encountered before they were seen bubble netting for the first time (electronic supplementary material, figure

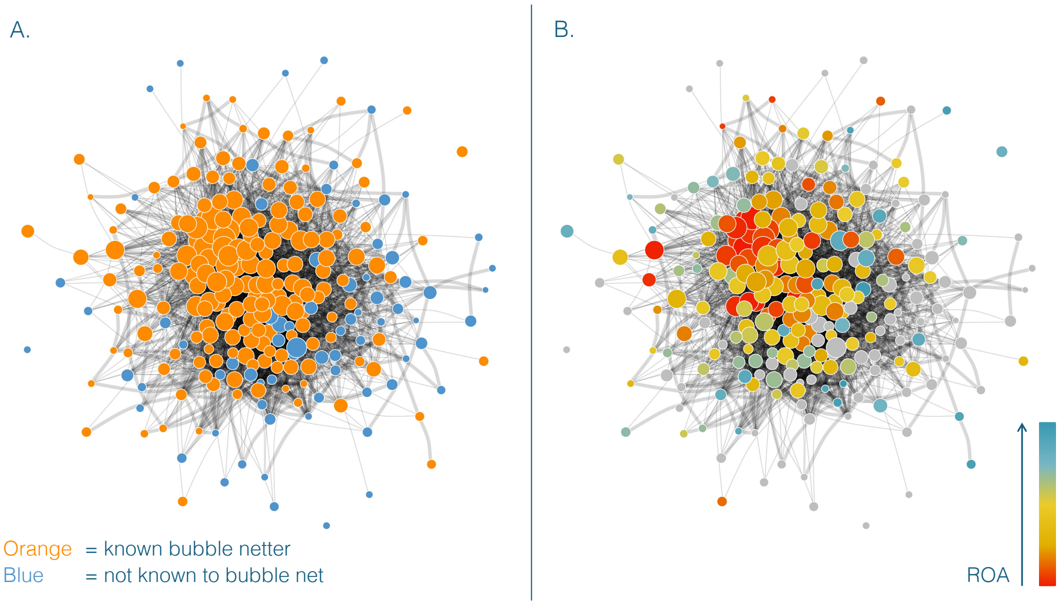

Figure 3. Humpback whale network of social associations (≥5 encounters), weighted by the Simple Ratio Index where thicker edges are social associations significantly more likely than by random chance ($p < 0.05$). The networks are colour-coded by (A) known bubble netting activity (orange nodes are known bubble netters, while blue nodes are not known to bubble net), and (B) observed ranked order of acquisition (ROA) of the bubble netting strategy that we observed in humpback whales in the Kitimat Fjord System (warm colours are early acquisition events, moving to the cooler colours which occurred later in the study period). Grey nodes represent whales not known to bubble net. Nodes are scaled by the total number of sightings for each individual, with more sightings increasing the size of the node, and clustered according to the magnitude of their social association measures.

Table 1. Results of multiplicative order of acquisition diffusion analysis (OADA), testing for evidence of social learning in the diffusion of bubble netting throughout humpback whales of the Kitimat Fjord System, British Columbia, Canada. All models treat whales observed bubble netting in year one of the study (2004) to have already acquired the trait before the study began. All models include the standardized number of sightings as an individual level variable (ILV), in order to correct for potential sampling bias. All models assume ILVs to affect the social and asocial learning rates to be equal (multiplicative modelling; see text for details).

static models	AICc	ΔAIC	w_i	MLE (ST)	95% C.I.	% ST[a]	LRT[b]	p-value[b]
OADA with std. sightings	1561.28	0.00	0.36	4.01	1.42–10.66	55.6%	20.60	***
OADA with std. sightings & sex	1561.32	0.04	0.36	4.70	1.71–12.53	58.8%	22.64	***
OADA with std. sightings, SSFI & sex	1562.99	1.71	0.15	4.98	1.79–13.56	59.9%	23.05	***
OADA with std. sightings & SSFI	1563.19	1.90	0.14	4.13	1.45–11.11	56.2%	20.76	***

[a] %ST = Percentage social transmission.
[b] LRT = Likelihood ratio test for social transmission and associated p-value.

S2). There was a relatively steady increase over time in the proportion of the NCCS catalogue that were known bubble netters (figure 2A).

An important pattern emerges when the set of known individuals in the study is split based on whether they have been seen bubble netting up to that point (i.e. becoming informed individuals; figure 2B,C). When this data is visualized with all whales, regardless of number of sightings (figure 2B), we see a steady increase in both bubble netters (solid orange) and non-bubble netters (dashed blue), suggesting an immigration of informed individuals, as opposed to social learning upon arrival to the KFS. However, when the less sampled (or more transient) individuals are removed (i.e. those seen less than 5 times in total), the pattern changes: we see a steady increase in both bubble netters and non-bubble netters until 2014, at which point the number of non-bubble netters reverses its trend and begins to decline (figure 2C). Given this measure is summative and the behavioural state a binary either/or, the only explanation for this decline is that whales already known to the catalogue are beginning to bubble net having not done so previously. The decline in non-bubble netters is explained by naive individuals becoming informed and switching into the bubble netter category. This suggests a rapid diffusion of the behaviour throughout the population, coinciding with the severe northeast Pacific Marine Heatwave (2014–2016 [83]), which negatively affected regional prey availability and consequently the humpback whale populations [69,84–86].

When analysing the overall social network, social transmission was strongly favoured in all static NBDA models of bubble netting, with all models of social learning scoring a lower AIC than the equivalent asocial model. The social network used for these models, based on SRI scores, is visualized in figure 3, with thicker edges depicting social associations significantly more likely than by random chance ($p < 0.05$). The four social models, differing only in their ILVs, ranged from 10.6×10^3 to 35.4×10^3 times more support than their asocial counterparts (likelihood ratio test (LRT) results in table 1; $p < 0.0001$). The estimated proportions of acquisition events that result from social transmission (%ST) [79] vary little across models (min = 55.6%; max =

Table 2. Individual level variables summed Akaike weights ($\sum w_i$) across all models, the model-averaged parameter estimate with 95% confidence intervals calculated according to equation (6.12) in [81]. Effect sizes are calculated as $e^{(\beta/\sigma)}$ for continuous variables (sightings and site fidelity SSFI), where β is the model-averaged parameter estimate and σ is the standard deviation of the unstandardized data. Effect size is calculated as $e^{(2\beta)}$ for the categorical variable sex where sex is 1 for male, −1 for female and 0 as unknown.

variable	$\sum w_i$	estimate	95% CI	effect size	interpretation
std. sightings	NA[a]	0.59	0.37 to 0.82	1.02	the apparent learning rate increases by a factor of 1.02 per standard deviation (which equates to a 46.8% increase in apparent learning rate for every additional 18 sightings, i.e. the median number of sightings)
sex	0.50	−0.10	−0.29 to 0.09	0.82	being male was associated with an 18% reduction in apparent learning rate
SSFI	0.29	0.13	−0.75 to 1.02	3.50	compared with an animal with zero site fidelity, an animal with complete fidelity has a 15.7% greater apparent learning rate; calculated as (effect size ^ median(SSFI))

[a] NA: a priori decision to include this parameter in every model and therefore the summed Akaike weights are irrelevant and simply sum to 1.

59.9%), indicating that the model estimates for social learning are not reliant on the inclusion of particular combinations of ILVs. To interpret the effect of each ILV on social learning, we calculated the model-average parameter estimates using the summed Akaike weights ($\sum w_i$; table 2). For every additional 18 sightings of an individual (the median number of sightings in the study), there was a 46.8% increase in apparent learning rate, so it was important to try and account for that in all models. There was an 18% reduction in apparent learning rate associated with being male. Compared to an animal with zero site fidelity, an animal with complete fidelity has a 15.7% greater apparent learning rate.

However, the dynamic OADA, which was built to test for the effect of homophily, showed inconclusive results: the model estimated 30.1% of acquisition events occurred by social transmission (%ST). A likelihood ratio test showed that including a social parameter did not significantly improve model fit over the asocial version (LRT = 1.47, $p = 0.22$), probably because learning to bubble net feed, regardless of how, leads to homophilous formation of social ties due to its inherent sociality in the cooperation form of the behaviour. It is important to note that, due to the temporal halving of the dataset and construction of the dynamic social network as described in §2(b), this homophily test had a restricted dataset of 51 individuals acquiring the behaviour, representing 30.5% of the 167 acquisition events of the full dataset, reducing its overall statistical power.

4. Discussion

We aimed to test for the role of social transmission in the observed spread of a foraging behaviour in humpback whales. A NBDA of the 20 year dataset showed strong support for social transmission. However, when data were restricted to test for the effect of homophily, the analysis supported asocial and social learning equally. It is difficult to determine whether this is due to a lack of power from a restricted dataset or whether bubble netting is really learned individually followed by a strong homophily effect in the context of cooperation. A third possibility is a confounding in the NBDA because the behaviour, cooperative bubble netting, is itself social. This latter fact, however, along with tracking of the dynamics of the behavioural spread and the overwhelming prevalence of cooperative over solo bubble netting in our data, suggests significant social components. Irrespective of the precise learning trajectories, our analysis clearly shows that the diffusion of bubble netting is very strongly linked with the social structure of this expanding population and is potentially ecologically significant insofar as it affects the distribution and ecological impact of humpbacks foraging in the KFS. We expect the rapid diffusion of primarily cooperative bubble netting to have cascading effects on ecological niche partitioning, and beyond this, a likely effect on the population's ability to recover to pre-whaling numbers.

Our study took place at the end of a period of population expansion (the North Pacific has since experienced a decline [69]) so it is plausible that population movements are a factor in the spread of this behaviour, rather than learning. However, using almost 4000 identification photographs, Calambokidis *et al.* [87] found little interchange between different feeding grounds of humpback whales in the North Pacific, and we have found high rates of return and residency amongst the whales foraging in the KFS (electronic supplementary material, figure S2). This suggests informed individuals are not simply immigrating to the study region from other feeding grounds and thereby 'importing' the bubble netting behaviour from elsewhere, and instead supports the hypothesis that some whales are learning the behaviour onsite. There is an increasing proportion of bubble netters in our research catalogue (figure 2A), and a clear switching of better-sampled individuals from a naive to an informed status regarding bubble netting ability (figure 2C). Whales infrequently seen (less than 5 times) masked this trend of behavioural diffusion, so it is important to account for this in network analyses (figure 2B).

(a) Disentangling homophily and social learning in a cooperative behaviour

We must be cautious with the interpretation of the results from the NBDA, primarily due to the confounding results between the primary NBDA models showing very strong support for social learning (between 10 000 and 35 000 times more support for the social versus asocial models; $p < 0.0001$) compared with the dynamic social network used to test for the bias of homophily, which is inconclusive (LRT = 1.47, p = 0.22). It might be premature to conclude that bubble netting is in fact socially learned, despite it being inherently social in most instances (92% of bubble netting events occurred in cooperative groups of two or more whales). The results of the homophily test may suggest that, in fact, homophily is reflected in the social network, such that we find very strong support for social learning when not correcting for its effects. However, this homophily test is vulnerable to failing precisely *because* bubble netting occurs socially, and so we would expect bubble netters to bias their social associations towards other bubble netters (i.e. homophily) to feed cooperatively. This suggests that a NBDA might, in this context where the behaviour relies on inherent sociality and cooperation, have less power to detect the signals of social learning.

Disentangling homophily from social learning can be challenging. Literature on homophily in social network analyses shows that homophily shapes network topology and can either promote diffusion of the innovation or result in the behaviour becoming localized in community clusters within the social network [88,89]. Previous work on the social network of this same population of humpback whales demonstrated that the population clustered into seven communities with a greater network structure strength (i.e. modularity), a fewer number of communities than expected by chance [56]. The most differentiated community had the highest proportion of bubble netters, while the least differentiated community had the lowest proportion, illustrating how homophilic cooperative clusters could develop in this context.

A literature review of applications of NBDA was conducted, with Google Scholar and Web of Science searches on the term ‘network-based diffusion analysis’ carried out on 17 October 2024. Study titles were screened for applications of NBDA and behaviours were examined on whether they were individual or group behaviours. The review demonstrated that, to our knowledge, all behaviours tested with this tool which find support for social learning are learned socially but performed individually (detailed in electronic supplementary material). In cetaceans, examples include lobtail feeding in humpback whales [30] and sponge tool use in Indo-Pacific bottlenose dolphin matrilines (*Tursiops aduncus*) [90]. All behaviours tested are performed individually, regardless of learning strategy or specific analytical test. It remains to be seen if and how the problems of using NBDA when the social network is largely defined by associations taking place during the behaviour of interest can be resolved, but the answer will be relevant to contexts beyond humpback whale cooperative bubble netting, such as to the well-documented occurrence of cooperative mud ring feeding in common bottlenose dolphins [42,91] and in Guiana dolphins (*Sotalia guianensis*) in Brazil [92]. One obvious way around this conundrum would be to use a social network constructed from observations outside the feeding context to predict the spread of the social behaviour, but in our case, this was not possible because while they are on a feeding ground, the whales are doing little else.

Even if individuals were to first acquire the solo bubble netting behaviour asocially, for them to ultimately feed cooperatively, there must be a phase of learning to cooperate that is heavily influenced by social interactions. It seems highly likely from this argument that the development from a naive individual, through to a fully cooperating bubble netter, involves some degree of social learning. If bubble netting is learned in a solo context, followed by homophily leading to involvement in the cooperative form, the division of tasks inherent in the cooperative form means that any transition from solo to cooperative bubble netting involves some learning about how and when tasks should be performed. This aspect of the learning must be social because it involves learning facilitated by the behaviour of others. Given the likely limitations of visible demonstrations of the behaviour in a temperate marine environment (due to limited visibility both of the species itself but also in the water column generally), we envision the social learning process involving some level of trial and error (i.e. learning by doing), possibly the use of passive acoustics (given that other cetacean species can imitate through their use; e.g. [93]), as well as interactions with various aspects of the bubble net feed.

(b) Social cohesion

Due to the inherent sociality of cooperative group bubble netting, repeated expression of the behaviour in the same group plausibly strengthens social cohesion and reinforces homophily in a positive feedback loop—the more practice with a specific group, the more accustomed to each other and therefore the more efficient the feeding. In a related study, the bubble netters of this same population were shown to have population-distinctive social behaviours [56]. Compared to the remainder of the population, known bubble netters were involved in longer-lasting and stronger social relationships, exhibited strong social preferences, were more socially connected, and exhibited greater centrality within the social network [56]. Bubble netters also exhibited higher rates of annual return and remained in the fjord system for longer durations each year [56]. These patterns underline that irrespective of the mechanism, social learning or homophily, the spreading bubble netting trait has a fundamental importance to the population’s social structure or vice versa. Understanding the full effect of homophily on the diffusion of behaviours and the underlying social networks can be challenging, particularly because it can simultaneously accelerate the diffusion of a trait by helping to attain a critical mass, while also restricting the trait to homophilic groups within the network, depending on the strength of homophily at play [88]. Nonetheless, in addition to this example of humpback whales foraging in the KFS, it has been shown in another marine mammal species (populations of bottlenose dolphins in Laguna, Brazil and Shark Bay, Australia), that homophilic preferences tend to extend beyond the active performance of a behaviour to mediate the social network more generally [94,95].

(c) Solo bubble netting

The co-occurrence of solo and cooperative bubble netting is an example of behavioural plasticity in this population. Unlike the steady growth in numbers of informed individuals visible in figure 2, the increase of new soloists (i.e. individuals observed solo bubble netting at least once) is slow until a sharp peak in the latter years of the study period (electronic supplementary material, figure S3). This could be attributed to decreased prey availability or increased prey patchiness within the KFS in 2022 and 2023, given that we see the majority of these soloists switch back and forth between cooperatively and individually bubble netting (74% of whales known to solo bubble net have also been seen taking part in the cooperative form). A study relating prey abundance and distribution would therefore be an important next step.

(d) Ecological resilience

The North Pacific population of humpback whales had been steadily increasing at a relatively fast rate of 8% per year [70] until recent evidence of a drastic 20% decline in population size from 2012 to 2021 [69]. What sets humpback whales apart in their ability to rebound to pre-whaling numbers, which is not observed in cetacean species with whom they share a habitat [96–99], might be explained by the interactions of their behavioural plasticity and their sociality [56], underpinning rapid cultural evolution [47]. Since bubble netters can exploit schools of fish that naive humpback whales cannot capture as effectively on their own [100], the diffusion of this behaviour has implications for this population's ecological niche, carrying capacity and resilience to environmental perturbations within Pacific Canada [56,101]. An increased rate of diffusion of the bubble netting behaviour coincided with the Pacific Marine Heatwave of 2014–2016 (figure 2), which negatively impacted prey nutritional value and availability [102,103]. Perhaps bubble netting, which primarily targets Pacific herring, remained a more reliable foraging strategy compared with other foraging behaviours, or, due to decreased overall prey availability, an increasing number of individuals diversified their foraging tactics to maintain sufficient energy intake. Individuals who have learned to bubble net can exploit distinct prey types (in the present case, euphausiids and herring) with highly disparate ecologies and phenologies, and do so both cooperatively and individually [55,96]. Such behavioural plasticity results in a resource base to be used more efficiently, which perhaps increases local carrying capacity. This, presumably, expands the viable foraging niche and can be the basis for further behavioural innovations.

In these ways, diffusion of techniques within social networks can bolster the recovery and resilience of a depleted population. Indeed, the dynamic nature of humpback whale culture may have played an important role in this species's recovery from commercial whaling [70]. Cultural resilience may also play an important role in the future as humpback whales, like most cetaceans, face declines in habitat quality and population size [69,104–106]. Targeted efforts to protect a culturally distinct segment of a population may yield disproportionate benefits to diversity and resilience overall, but localized cultural loss can have an equally outsized effect [6]. In the KFS, a forecasted increase in large vessel traffic is expected to cause an increase in humpback whale ship-strike mortalities [107]. Should these mortalities affect core knowledge-holding, bubble netting individuals, a greater impact than expected may be seen on the seasonally resident population. For this reason, epicentres of distinct learned behaviours within management jurisdictions, such as the KFS in the Canadian Pacific, are strategic priority areas for conservation efforts [1,6]. To date, the consideration of cultural strains is rarely accounted for in conventional conservation frameworks [108–110], but their importance is expected to grow as anthropogenic perturbations deteriorate marine ecosystems worldwide [104,105,111].

(e) Concluding remarks

We conclude that the spread of bubble netting in this population is intimately linked to its social network given the inherent sociality in its cooperative form. We highlight issues around NBDA tests for social learning in a context of cooperation, as opposed to the social learning of behaviours performed alone. Furthermore, we show that the diffusion of bubble netting throughout northern British Columbia is not merely another example of this species's predisposition for behavioural innovation; it is also a reminder that species recovery is more than a numerical process. As humpback whales undergo large fluctuations in population size in the northeastern Pacific [70,111], the distribution of behavioural knowledge will be an important factor in their recovery if it has been lost and is now being restored.

Ethics. This work was carried out under the Department of Fisheries and Oceans research permit DFO XR 83 2014 and XMMS12022.

Data accessibility. Code and data are available on GitHub [112] and on Dryad [113].

Supplementary material is available online.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. J.W.: data curation, funding acquisition, project administration, writing—review and editing; É.N.O.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, validation, visualization, writing—original draft, writing—review and editing; G.B.: data curation, funding acquisition, writing—review and editing; N.R.: data curation; A.D.: data curation; O.E.G.: investigation, supervision, writing—review and editing; L.R.: conceptualization, investigation, methodology, supervision, writing—review and editing; E.M.K.: conceptualization, data curation, investigation, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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