# Adaptation of sperm whales to open-boat whalers: rapid social learning on a large scale?

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Supplementary Material:
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## Abstract:

Animals can mitigate human threats, but how do they do this, and how fast can they adapt? Hunting sperm whales was a major 19th Century industry. Analysis of data from digitized logbooks of American whalers in the North Pacific found that the rate at which whalers succeeded in harpooning (striking) sighted whales fell by about 58% over the first few years of exploitation in a region. This decline cannot be explained by the earliest whalers being more competent, as their strike rates outside the North Pacific, where whaling had a longer history, were not elevated. The initial killing of particularly vulnerable individuals would not have produced the observed rapid decline in strike rate. It appears that whales swiftly learned effective defensive behaviour. Sperm whales live in kin-based social units. Our models show that social learning, in which naïve social units, when confronted by whalers, learned defensive measures from grouped social units with experience, could lead to the documented rapid decline in strike rate. This rapid, large-scale adoption of new behaviour enlarges our concept of the spatio-temporal dynamics of non-human culture.

**Keywords:** social learning, culture, sperm whale, whaling, defensive measures

## 1. Introduction

Social learning can change the behaviour of whole populations, sometimes over large spatial scales [1–3]. However, beyond humans and beyond dialect evolution [4] there is little evidence for large-scale cultural change in behaviour that is rapid (over less than about half a generation).

In the context of a predator-prey interaction that was particularly significant for economic development [5] and marine ecology [6], we investigated a hypothesis that the prey—sperm whales (*Physeter macrocephalus*)—quickly learned effective defensive measures from one another when faced with a novel predator—the open-boat whaler. In the 18th and 19th Centuries, pelagic whalers from Europe and North America spread around the world, exploiting new "grounds" and new species [5,7]. They searched for whales from sail-powered whaleships, with sightings of groups of sperm whales typically interspersed by days or more of searching. Once whales were sighted, whalers rowed whaleboats towards the whales, aiming to "strike" them with hand-thrown harpoons, a process typically lasting tens of minutes to hours (Fig. 1). If whales were killed, they would be towed back to the whaleship for processing ("trying out").

Some historians have suggested that the success rate of open-boat whalers in harpooning sighted whales—the second stage in these whaling operations—dropped substantially during the initial years of industrial exploitation, and that this was due to socially-learned changes in whale behaviour [8,9]. While quantitative data for the earliest years of any new exploitation of wildlife are usually few or absent, the development of pelagic whaling operations in the North Pacific by American whalers during the middle 19th Century is well chronicled in digitized whalers' logbooks [10].

We used these data to quantify the success of whalers in striking (i.e. harpooning) sighted sperm whales during the early years of exploitation. We assessed whether this decline was caused by socially-learned changes in the defensive behaviour of the whales [8,9] (hypothesis HX), evaluating support for several alternative hypotheses using causal models: the first whalers on a ground were particularly proficient (H1); the whalers initially captured especially vulnerable whales (H2); or the whales learned to escape whalers from their own individual experience of encountering them (H3).

## 2. Methods

Detailed methods, together with justifications and a consideration of assumptions, as well as raw data and computer code for analysis, are given in the Supplementary Material. Data come from a compilation and digitization of logbooks of American whalers working between 10-50$^{o}$N in the North Pacific by Maury [11] and the Census of Marine Life [10], giving for each voyage-day (a logged day of searching for whales by a particular vessel; e.g. "Ship-Alexander_06-May-1822") noon position, whether sperm whales were sighted, and how many whales were struck (harpooned) or tried (processed). For this study we needed to determine the date of first exploitation in an area with reasonable accuracy and this was only possible for the North Pacific, with other oceans being exploited earlier, or largely by non-American whalers [5,7,12,13].

We delineated areas by calculating, for each voyage-day $d$ on which sperm whales were sighted, the time lag since the first sighting within $h$=1,000km (based on displacement of photo-identified female sperm whales over lags of years in Southeast Pacific [14]). Then, for each time lag since first sighting in the region, $T$ years, we calculated the mean number of whales struck per sighting day, the "strike rate", $y(T)$: for voyage-days with time lag $T$ since the first sighting in the region, the total number of sperm whales struck divided by the number of voyage-days with sperm whale sightings. To model the observed decrease in strike rate with time lag since first exploitation and estimate the magnitude and temporal scale of the initial decline, we fit a heuristic model of an initial exponential decline in strike rate to a plateau. We also fit causal models corresponding to hypotheses H2, H3 and HX. Equations are in Table 1, and detailed derivations are in the Supplementary Material.

Under H2, we assume that the population, of size $P(0)$ at the commencement of whaling, has a proportion $q$ of vulnerable individuals which are struck at a rate $f_1$ when the group containing the individual is sighted, while the less vulnerable animals are struck at a rate $f_2$. If $s$ is the rate of groups (or individuals) being sighted by whalers per voyage-day, then the number of vulnerable animals in the population $t$ days after the commencement of exploitation is $N_1(t)=P(0).q.(1- s.f_1)^t$, and the number of less vulnerable individuals $N_2(t)=P(0).(1-q).(1- s.f_2)^t$, leading to equation H2 in Table 1.

In order to assess learning at the individual or within-unit level as a driver of an initial decline in strike rate (H3), we estimated the proportion of whales that had experience of whalers at different numbers of years after the initiation of whaling, $Z(T)$. $Z(T)$ increases at a rate of $s(1-Z(T))$ per day. Integrating over $T$ gives $Z(T)=1-e^{-s\cdot 365\cdot T}$, leading to equation H3 in Table 1.

Studies of living animals in the Pacific Ocean have found groups to be made up of on average two kin-based social units of females and their young, that generally remain grouped for around 7-14 days [15]. To model a rapid form of social learning (HX), we assumed that a group being approached by whalers would act like an experienced group if any of the units that made it up had previous experience with whalers. Then, the probability that at least one unit in the group had experience of whaling becomes $Z'(T)=1-e^{-(g/u)\cdot s\cdot 365\cdot T}$, where g is the group size and u the unit size. This leads to equation HX in Table 1.

We estimated $g$=21.75, $u$=10.5 from literature and $s$=0.000313 sightings.group$^{-1}$.day$^{-1}$ using population estimates (see Detailed Methods in Supplementary Material). We assessed the fit of each model using adjusted $R^2$, and the relative support of the causal models using the Akaike information criterion [16]. To evaluate the results' robustness, we systematically changed $g$, $u$, and $s$ to outer plausible values, varied $h$, and alternatively used whaler-defined grounds as regions (Supplementary Material).

## 3. Results

The data set included 77,749 operational voyage-days, with sperm whale sightings on 2,405 voyage-days. The heuristic model indicated a 58% drop in strike rates over time lag scales of 2.4yr after which they stabilized (Fig. 2; Table 1).

To assess hypothesis H1, whaler competency, we used the full global data set. When outside the North Pacific, whalers that entered a North Pacific region 0-4 years after the initial sighting had similar rates of trying out whales per sighting day (0.80, SE=0.08) as those entering the North Pacific 5-9 years after the initial sighting (0.77, SE=0.09; strike rates were not available outside the North Pacific, so we used try rates). That the earliest whalers in the North Pacific and those that followed later had similar success when in other oceans, where the sperm whales had typically been exploited for longer, argues against decreasing whaler competence driving the fall in strike rate.

Under hypothesis H2, differential vulnerability, an initial decline in strike rates will occur if a population is stratified by vulnerability to whaling and the most vulnerable animals are taken first. These vulnerable individuals might include the young, the old, the sick, the foolhardy, the belligerent, or mothers attempting to protect calves. Our model of H2 produces a decline in strike rate, but it is not as steep as indicated by the real data (Fig. 2), fitting considerably worse than the social learning model (HX) (Table 1). Furthermore, the parameters of the best-fitting model (Table 1) indicated that all vulnerable individuals (2.2% of population) would have been struck when first sighted, while non-vulnerable individuals were struck at a rate of 0.016 per sighting. This extreme contrast in vulnerability seems unrealistic. Alternative formulations of the vulnerable individual model that we can imagine (e.g. more than 2 categories of vulnerability, continuous measure of vulnerability) would tend to reduce the rate of initial decline in strike rate. Thus, a stratification of the population by vulnerability to whalers is not supported as the sole cause of the initial decline in strike rate.

The final two potential causes of the fall in strike rate that we considered (H3, HX) assume that whales, individually or socially, learn behaviour that is adaptive for avoiding being struck. A model in which strike rates fell following the first experience of a social unit to whalers (H3) produces virtually the same decline as the vulnerable individual model (H2; Fig. 2). However, in common with the vulnerable individual model, the decline in strike rate due to within-unit learning seems insufficient (with a poorer fit than HX). Realistic modifications to the within-unit learning model that we can imagine, such as imperfect learning from the first encounter with whalers, will tend to reduce the rate of initial decline in strike rate. Thus, learning as individuals or within social units is not supported as the sole cause of the initial decline in strike rate. In contrast the between-unit social learning model (HX) fits the data better than all other causal models (Fig. 2; Table 1), producing a rapid decline in strike rate as units learn defensive measures from one another.

In the Supplementary Material we examine the effects of changing our definition of “region” and of variation in the parameters of the models within plausible limits. In all scenarios the between-unit social learning model fit better than other causal models. With a few exceptions, considered below in the discussion of the between-unit learning hypothesis, violations of the assumptions of the causal models would tend to decrease the steepness of the initial decline in strike rates, and thus the fit of the model to the data.

## 4. Discussion

While a combination of H1-H3 might produce a steep decline in strike rate, social learning of defensive measures between social units (HX) is the best-supported explanation for the rapid decline in strike rate following the first sperm whale sighting within a region. The whalers themselves wrote of defensive methods that they believed the whales were adopting, including communicating danger within the social group, fleeing—especially upwind—or attacking the whalers [17,18] (Fig. 1). Deep dives would also have been effective. But, perhaps the most straightforward change would be for sperm whales to cease their characteristic defensive behaviour against their most serious previous predator, the killer whale, *Orcinus orca*. Gathering in slow-moving groups at the surface and fighting back with jaws or flukes often works against killer whales [19,20], but will have only assisted the relatively slow-moving, surface-limited, harpoon-bearing open-boat whalers.

There are other behavioural changes that the whales may have made in response to whaling, but their impact on strike rates is less clear. There is some evidence that sperm whales formed larger groups in response to whaling [15], but this would likely have increased rather than decreased strike rates. They may have learned to avoid the whalers before the whalers detected them, but this should generally have reduced the mean detection range of the whalers and so increased the strike rate. However, if whales fleeing at long ranges made themselves more visible by blowing hard and showing their bodies forcefully, so increasing the number of sightings with groups that were not easily struck, this might have additionally decreased the strike rate.

Thus, there are learned behavioural changes that the sperm whales could have made to reduce strike rates, and some anecdotal witness that they did so. However, learning as individuals or within social units is not supported as the sole cause of the initial decline in strike rate. To achieve the observed reduction in strike rate through behavioural change, some mechanism must have allowed naïve whales without experience of whalers to receive the benefits of experience.

We suggest that naïve social units learned defensive measures from grouped experienced social units and adopted them. Encounters with whalers typically lasted hours, and sperm whales through their echolocation and communication systems can probably sense and coordinate behaviour over ranges of several km. Other processes could have enhanced the social learning process. If groups were particularly likely to split between or within social units after experience with whalers, and then to join other units, this will have increased the probability that a naïve animal was grouped with an experienced individual during its first encounter with whalers.

Our analysis provides substantial support for rapid (<20% generation time) social learning over large spatial scales. The ability of sperm whales, or potentially other species, to rapidly change behaviour in the face of a new anthropogenic threat by making use of social learning has implications for the population significance of new threats, and their assessment. Data from the earliest exposures may not generalize to later periods, and vice versa.

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**Author contributions:** HW conceived the study and carried out the analyses; TDS curated the data; TDS and LR provided input to the analyses; all authors wrote and revised the manuscript.

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**Fig. 1.** Sperm whaling in the North Pacific from the ship *Canton* (by Oliver Wilcox, whaler; New Bedford Whaling Museum).

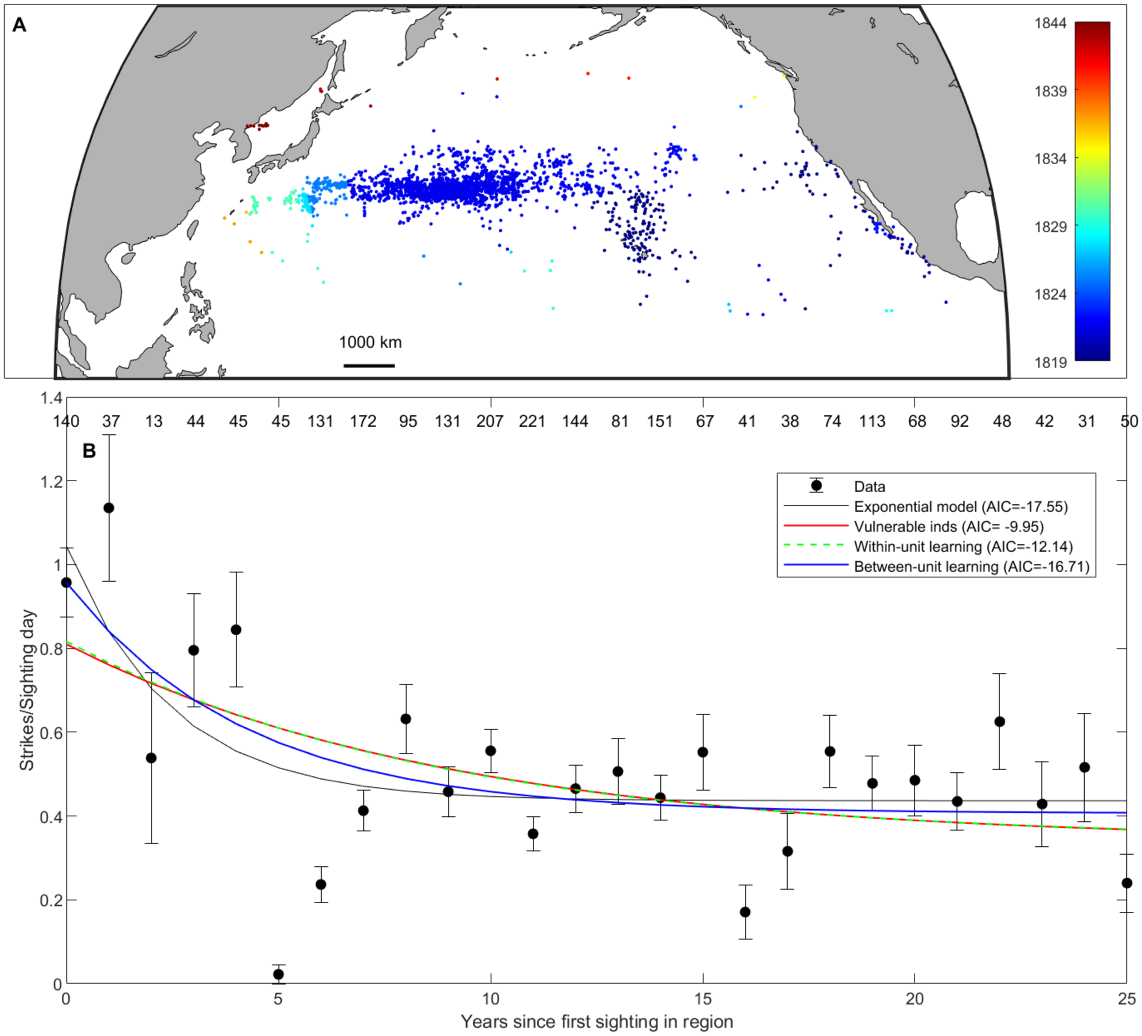

**Fig. 2. A**: Sperm whale sightings with estimated date of first sighting in region (scale of 1,000 km). **B**: Strike rate with time lag since first sighting in region (number of voyage-days above each lag; standard errors from Poisson approximation may be biased narrow due to dependencies), with fitted models (Table 1).

**Table 1**. Models fit to strike rates (*y* strikes/sighting day) with time lag (*T* years) after first sighting in region (*s* = rate of groups being sighted by whalers per day; *g* = mean size of group; *u* = mean size of social unit; see Supplemental Material for derivation of models, and parameter estimates).

| | | | Parameter estimates (SE): | | |
|---|---|---|---|---|---|
| Model | AIC | Adjusted $R^2$ | Strike rate on vulnerable /naïve animals ($f_1$) | Strike rate on less vulnerable/ experienced animals ($f_2$) | Proportion of vulnerable animals ($q$) |
| *Heuristic:* | | | | | |
| Exponential<br>$y = a_1 + a_2 \cdot e^{-a_3 T}$ | -17.55 | 0.42 | - | - | - |
| *Causal:* | | | | | |
| Vulnerable individuals (H2)<br>$y = g\dfrac{f_1 q(1 - sf_1)^{365 \cdot T} + f_2(1 - q)(1 - sf_2)^{365 \cdot T}}{q(1 - sf_1)^{365 \cdot T} + (1 - q)(1 - sf_2)^{365 \cdot T}}$ | -9.95 | 0.28 | 1.000 (0.000) | 0.016 (0.003) | 0.022 (0.007) |
| Within-unit learning (H3)<br>$y = g[f_1 e^{-s \cdot 365 \cdot T} + f_2(1 - e^{-s \cdot 365 \cdot T})]$ | -12.14 | 0.28 | 0.038 (0.005) | 0.016 (0.003) | - |
| Between-unit learning (HX)<br>$y = g\left[f_1 e^{-(\frac{g}{u}) \cdot s \cdot 365 \cdot T} + f_2\left(1 - e^{-(\frac{g}{u}) \cdot s \cdot 365 \cdot T}\right)\right]$ | -16.71 | 0.40 | 0.044 (0.005) | 0.019 (0.002) | - |