

Supplementary Material for

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

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This PDF file includes:

Detailed Methods

Figs. S1 to S3

Tables S1 to S4

Analyses using $h=500\text{km}$ (Fig. S1; Table S1), $h=2,000\text{km}$ (Fig. S2; Table S2) and whaler-defined grounds (Fig. S3; Table S3) to define regions, in place of $h=1,000\text{km}$ used in main manuscript

Table S4: Analyses exploring the ranges of plausible values for parameters: sighting rate (s), mean group size (g), and mean unit size (u)

Description of data and computer code

Other Supplementary Material for this manuscript include:

NP_data_set_Whitehead_et_al.xlsx

inwhaledatxx.m

runbatch.m

dislimy.m

npwhaldataxxx.mat

groundusey.m

grounds_Sperm.mat

hypsups.m

Detailed Methods

The data

The data come from a compilation and subsequent digitization of logbooks of American whalers by Maury [1] and the Census of Marine Life [2]. These data are indexed by voyage and date, and for each day give noon latitude and longitude, whether the vessel was actively whaling, whether whales were sighted or struck (harpooned), the species of whale, and how many whales were struck. A full, global data set is available at <https://whalinghistory.org/participate/download/>, while an edited version for the North Pacific sperm whale sightings is attached as part of the Supplementary Material (NP_data_set_Whitehead_et_al.xlsx). The units of this data set are voyage-days (e.g. “Ship-Alexander_06-May-1822”). We processed the data used for our primary analyses in several ways: records from Townsend [3] were excluded as there is no associated measure of effort; days when vessels were recorded as not whaling were excluded; “singleton” days without records from the same voyage on the previous or following days were excluded as these may be erroneous; and we only used data from the North Pacific north of 10°N, and south of 50°N.

The restriction to the non-equatorial waters of the North Pacific stems from our goal of examining changes in whaling measures following immediately after the time of first exploitation. We needed data from which we could determine the date of first exploitation in an area with reasonable accuracy. Much of the North Pacific was first exploited after 1818, when we begin to have good logbook coverage (>900 recorded whaling voyage-days per year), and by American whalers, for which we have data from about 10% of the voyages [2]. In contrast, most whaling grounds in the Atlantic, South Pacific and Indian Oceans were first exploited before 1818 or by British whalers with few logbooks available [4–7].

We further restricted the data to records south of 50°N, this being the range of groups of females in the North Pacific, as, except when attending groups of females, adult males typically use higher latitudes and have very different behavior [8,9].

Strike rates

For each voyage-day d on which sperm whales were sighted, we extracted the earliest date in the dataset on which sperm whales were sighted within h km of the logged position on day d . The difference between these two dates gave a time lag since first sighting in the region for sightings on that voyage-day, t_d years. We initially chose $h=1,000$ km based on the estimated root-mean-square displacement of female sperm whales over lags of years in the Southeast Pacific [10], but we also used scenarios with $h=500$ km and $h=2,000$ km. Additionally, in an alternative methodology, we delineated “grounds” roughly following those defined by the whalers [3,11], and for each sighting on a ground calculated the time lag since the first sighting of the species on that ground (see Fig. S3 for ground delineations).

Then, for each time lag since first sighting in the region, T years, we calculated the mean number of whales struck per sighting, called the “strike rate”:

$$y(T) = \frac{\sum d: t_d = T s_d}{n(T)} \quad (1)$$

Where s_d is the number of sperm whales struck on voyage-day d , t_d is the lag since the first sighting in the region on voyage-day d , and $n(T)$ is the number of days that sperm whales were sighted with a lag of T years from the first sighting of the species in the region. This measure (y) estimates the success of whalers at harpooning whales once they had sighted them. We used values of $T \leq 25$ years as $n(T)$ was greater than 30 sighting days for $T=0, \dots, 25$ years (except $T=2$ years where it was 13; Fig. 2) and less than 5 sighting days for all $T > 28$ years. We aggregated data by lag since first sighting (T) to avoid dependencies caused by voyage-days from the same voyage, sometimes on consecutive, or nearly consecutive, days.

To describe and quantify the decline in strike rates, y , with time lag since first sighting in the region, T , shown in Fig. 1 (and Figs S1-3), we fitted a descriptive model, that included parameters to estimate an initial exponential decline to a plateau:

$$y(T) = a_1 + a_2 \cdot e^{-a_3 T} \quad (2)$$

Here a_1 is the height of the plateau, $a_1 + a_2$ is the initial strike rate. Then the proportional decline in success over the initial whaling period is estimated by $a_2 / (a_1 + a_2)$; and the time scale of the decline is indicated by $1/a_3$.

Hypothesis H1: proficiency of initial whalers

A potential explanation for any initial decline in strike rate is that the first whalers in the region were generally more competent than those who followed later. Using the full global data set, we calculated rates at which whales were “tried” (processed) per sighting day (the global data set lists numbers tried, but not numbers struck, although these are similar in the North Pacific data set). We compiled two sets of voyages, those that had sightings 0-4 years from the initial regional sighting in the North Pacific, and those that had sightings 5-9 years from the initial regional sighting in the North Pacific. We compared try rates for these two sets of voyages when they were in other parts of the globe. If the initial decline in strike/trying rates in the North Pacific was caused by the first whalers on a ground being more competent, then, when outside the North Pacific, the try rates of the initial whalers in the North Pacific should also be higher than later whalers.

Hypothesis H2: differential vulnerability of whales

Differential vulnerability of whales to whalers is another potential explanation for an initial decline in strike rate. Under hypothesis H2, 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. We developed a causal model of this phenomenon. It assumes that the population, initially of size $P(t=0; t \text{ in days})$ at the

commencement of whaling, has a proportion q of vulnerable individuals which are struck at a rate f_1 per individual on days when the group containing the individual is sighted, while the less vulnerable animals are struck at a rate f_2 . Then, assuming struck whales are killed, that reproduction and natural mortality are small or roughly balance out, and that the rates of groups (or individuals) being sighted by whalers per voyage-day, s , are the same through the years of exploitation, then the number of vulnerable individuals in the population decreases by a mean proportion of $s.f_1$ per day, and $s.f_2$ for the less vulnerable individuals. 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 $N_2(t) = P(0).(1-q).(1 - s.f_2)^t$. Under this differential vulnerability scenario, the strike rate per group sighted T years into exploitation is:

$$y(T) = g \frac{f_1 N_1(365 \cdot T) + f_2 N_2(365 \cdot T)}{N_1(365 \cdot T) + N_2(365 \cdot T)}$$

Where g is the mean group size. And so,

$$y(T) = g \frac{f_1 q (1 - s f_1)^{365 \cdot T} + f_2 (1 - q) (1 - s f_2)^{365 \cdot T}}{q (1 - s f_1)^{365 \cdot T} + (1 - q) (1 - s f_2)^{365 \cdot T}} \quad (3)$$

As to the assumptions listed above: if not all struck whales were killed, the reduction in the population of vulnerable individuals would be slower, as would the decline in strike rates (the opposite of the trend shown in Fig. 2); a natural growth or decline in the population size at the commencement of whaling would be constrained to be small given the life history characteristics of sperm whales (likely $< \pm 0.01/\text{yr}$; [12]), and so have minimal effect on changes in the proportion of vulnerable individuals; and whaling effort, and so sighting rates per group, generally increased during the first years of exploitation, so increasing the rate at which vulnerable individuals were killed, and reducing the decline in strike rate due to this phenomenon. Thus, anticipated departures from the assumptions of the vulnerable individual model will have had little effect, or led to a less severe decline in sighting rates than modelled.

Hypothesis H3: within-unit learning

In order to assess the potential for learning of defensive measures as a driver of an initial decline in strike rate, we estimated the proportion of whales that had experience of whalers at different time lags in years (T) after the initiation of whaling, $Z(T)$. $Z(T)$ increases at a rate of $s(1 - Z(T))$ per day. Integrating over T gives $Z(T) = 1 - e^{-s \cdot 365 \cdot T}$. If f_1 is the strike rate on naïve animals without experience of whalers and f_2 (lower than f_1 because of learning defensive measures) the strike rate on animals with whaling experience, then:

$$y(T) = g [f_1 e^{-s \cdot 365 \cdot T} + f_2 (1 - e^{-s \cdot 365 \cdot T})] \quad (4)$$

This causal model assumes a binary response to whalers based on experience. Behavioural responses will have varied among both naïve and experienced animals and social units, but the modelled binary vulnerabilities can be thought of as expressing mean values for the two classes of animal/unit. Further, the model assumes that all learning of defensive measures occurs from individual experience of whalers (model HX considers a violation of this assumption), and that there is one immediate change in behaviour following the first exposure to whalers. If defensive behaviour became generally more effective with additional exposures, then the decline in strike rates would be lessened from that modelled.

Model HX: between-unit social learning

To model a rapid form of social learning, 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. Thus, members of naïve social units without any experience of being approached by whalers took effective defensive measures if they were grouped with another unit which had such experience. The strike rate under these assumptions then becomes:

$$y(T) = g \left[f_1 e^{-3 \cdot \left(\frac{g}{u}\right) \cdot 365 \cdot T} + f_2 \left(1 - e^{-\left(\frac{g}{u}\right) \cdot s \cdot 365 \cdot T} \right) \right] \quad (5)$$

Where u is the mean unit size, and so g/u is the mean number of units present in an encounter.

The decline in strike rates would be less than that modelled if not all animals/units fully adopted the more effective defensive measures when grouped with experienced animals. An increased decline beyond that modeled could result from learning defensive measures against whalers from other units outside the whaling experience, or various forms of social mixing between experienced and naïve animals (discussed in the Main Text).

Fitting models

We fitted the descriptive and causal models indicated by equations (2-5) to the data using the `fitnlm` function in MATLAB with data points weighted by $\sqrt{n(T)}$, estimating parameters f_1 , f_2 , and q , evaluating the proportion of variance accounted for by each model using adjusted R^2 , and assessed the relative support of these different hypotheses using AIC. Minimum AIC indicated the best supported model, and ΔAIC , the difference between AIC for a particular model and the best supported model indicates support for the particular model ($\Delta AIC > 4$ indicating very little support compared to the model with the lowest AIC in the set [13]). We used estimates of mean group size $g=21.75$ (mean of two estimates for SE Pacific sperm whales in Table 6.3 of [8]), $u=10.5$ [8], and $s=10 \cdot \text{mean}(n(T)) / (170,000/g)$, as our database included about 10% of the voyages [2], and the population in the North Pacific study area was about 170,000 individuals (using proportion of pre-whaling global population in study area, scaled by chlorophyll production; see [14]), giving $170,000/g$ groups. This leads to $s=0.000313 \text{ sightings.group}^{-1} \cdot \text{day}^{-1}$. We examined the robustness of our results to these

parameter choices by systematically changing $g=16.75, 26.75$; $u=7.5, 13.5$; and $s=0.000156, 0.000626$. These values are roughly outer limits for plausible values of these parameters based on current studies of living sperm whales in different parts of the Pacific and elsewhere (g, u ; [8]) or uncertainty about pre-whaling population densities (s ; [14]).

In the Main Text, we present results for the $h=1,000\text{km}$ scenario to determine time lags since first sighting in a region. Results for $h=500\text{km}$, $h=2,000\text{km}$, and using whaler-defined grounds are presented in Figs S1-S3, and Tables S1-S3. Model fits with different input parameter values are shown in Table S4. Results vary little depending on which scenario or set of input parameters was used.

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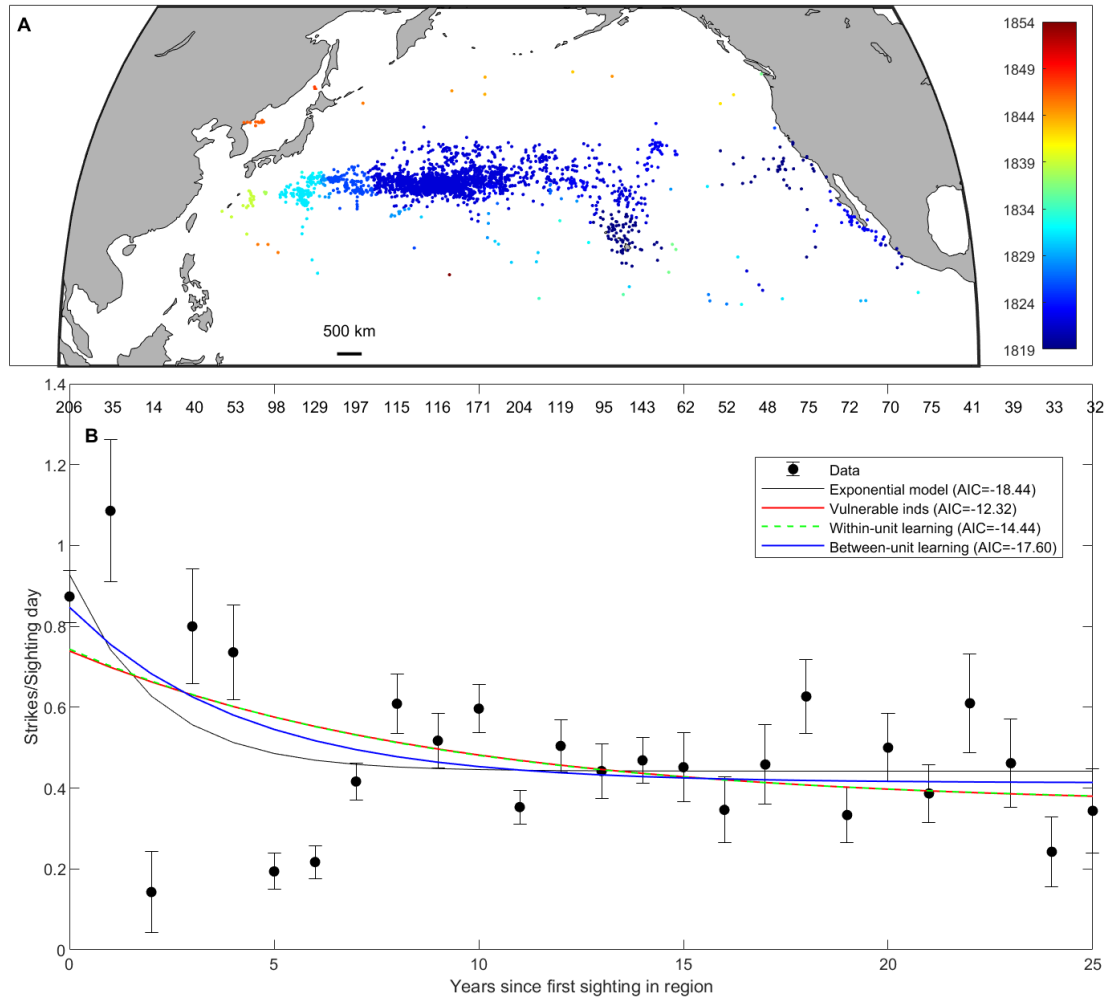


Fig. S1. Success of whalers in striking sighted sperm whales with time lag since first sighting in region (scale of $h=500$ km). A: Locations of sperm whale sightings in the North Pacific with estimated date of first sighting in region. B: Strike rate with time lag since first sighting of sperm whales in region (number of voyage-days above each lag; standard errors from Poisson approximation may be biased narrow due to dependencies), together with fitted models.

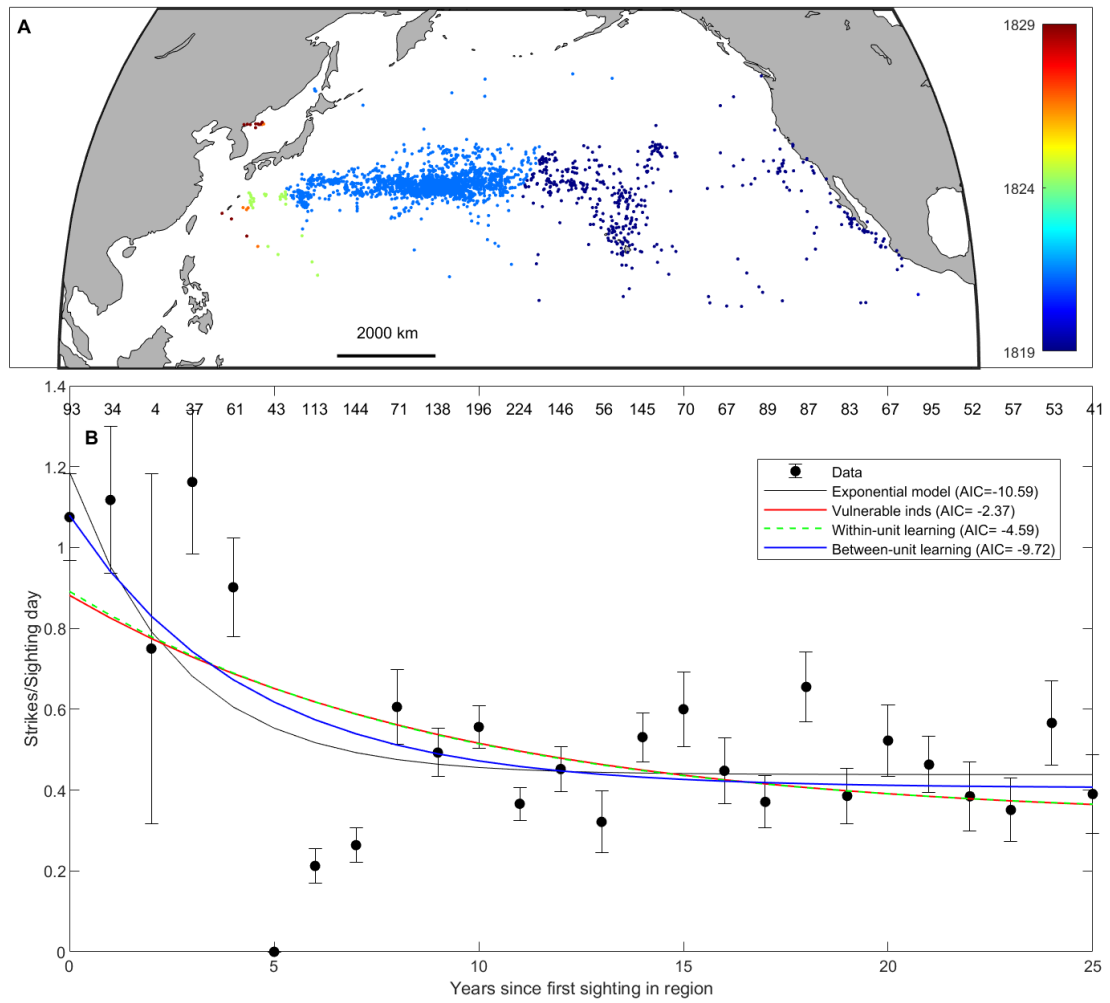


Fig. S2. Success of whalers in striking sighted sperm whales with time lag since first sighting in region (scale of $h=2,000$ km). A: Locations of sperm whale sightings in the North Pacific with estimated date of first sighting in region. B: Strike rate with time lag since first sighting of sperm whales in region (number of voyage-days above each lag; standard errors from Poisson approximation may be biased narrow due to dependencies), together with fitted models.

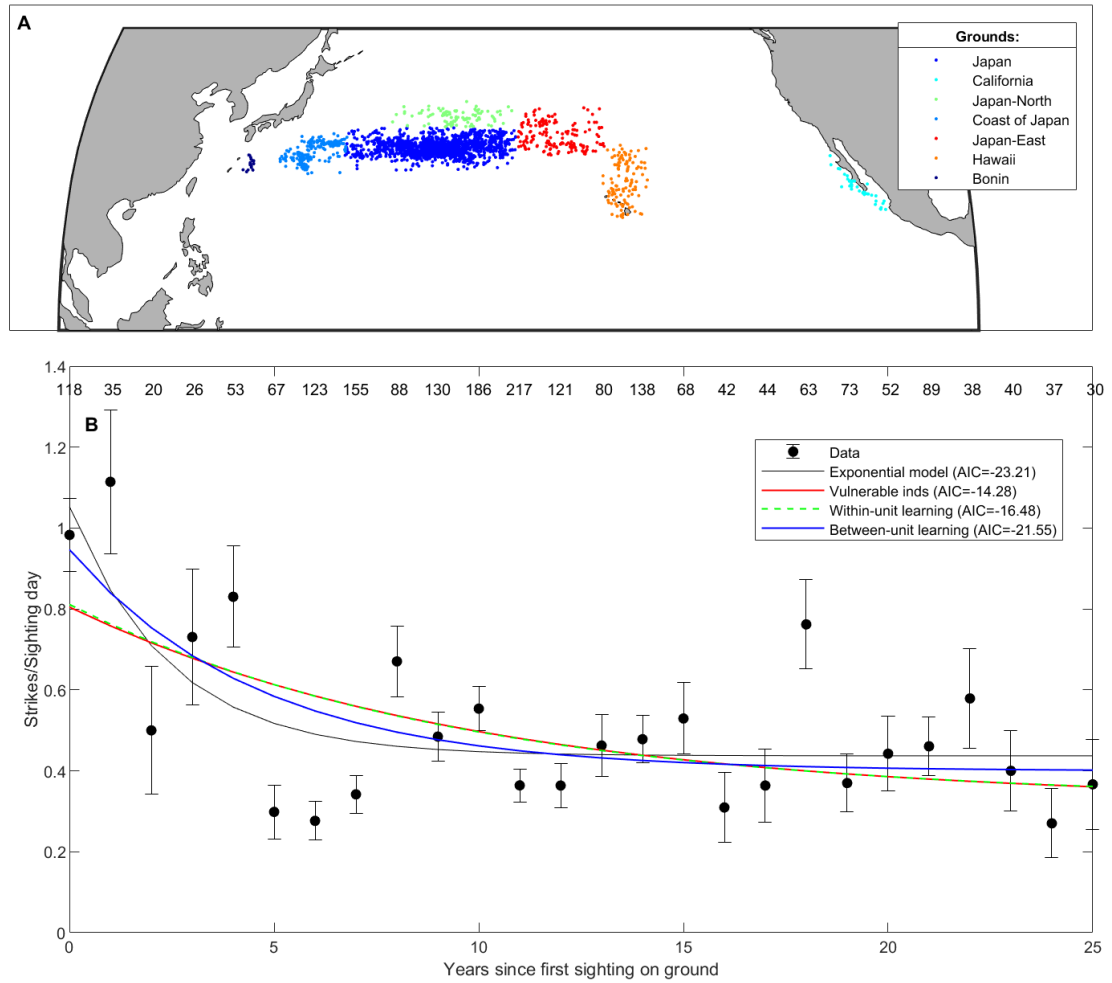


Fig. S3. Success of whalers in striking sighted sperm whales with time lag since first sighting on assigned grounds. **A:** Locations of sperm whale sightings in the North Pacific on each ground. **B:** Strike rate with time lag since first sighting of sperm whales on a ground (number of voyage-days above each lag; standard errors from Poisson approximation may be biased narrow due to dependencies), together with fitted models.

Table S1. Descriptive and causal models fit to strike rates (y) of whalers at different time lags after the first sighting in the region (defined by $h=500\text{km}$)

Model	AIC	Adjusted R ²	Parameter estimates (SE):		
			Strike rate on vulnerable /naïve animals (<i>f</i> ₁)	Strike rate on less vulnerable/ experienced animals (<i>f</i> ₂)	Proportion of vulnerable animals (<i>q</i>)
<i>Descriptive:</i>					
Exponential $y = a_1 + a_2 \cdot e^{-a_3 T}$	-18.44	0.33	-	-	-
<i>Causal:</i>					
Vulnerable individuals (H2) $y = g \frac{f_1 q (1 - s f_1)^{365 \cdot T} + f_2 (1 - q) (1 - s f_2)^{365 \cdot T}}{q (1 - s f_1)^{365 \cdot T} + (1 - q) (1 - s f_2)^{365 \cdot T}}$	-12.32	0.22	1.000 (0.000)	0.016 (0.003)	0.018 (0.006)
Within-unit learning (H3) $y = g [f_1 e^{-s \cdot 365 \cdot T} + f_2 (1 - e^{-s \cdot 365 \cdot T})]$	-14.44	0.23	0.034 (0.004)	0.016 (0.003)	-
Between-unit learning (HX) $y = g \left[f_1 e^{-\left(\frac{g}{u}\right) \cdot s \cdot 365 \cdot T} + f_2 \left(1 - e^{-\left(\frac{g}{u}\right) \cdot s \cdot 365 \cdot T} \right) \right]$	-17.60	0.31	0.039 (0.005)	0.019 (0.002)	-

Table S2. Descriptive and causal models fit to strike rates (y) at different time lags after the first sighting in the region (defined by $h=2,000\text{km}$)

Model	AIC	Adjusted R ²	Parameter estimates (SE):		
			Strike rate on vulnerable/naïve animals (f_1)	Strike rate on less vulnerable/experienced animals (f_2)	Proportion of vulnerable animals (q)
<i>Descriptive:</i>					
Exponential					
$y = a_1 + a_2 \cdot e^{-a_3 T}$	-10.59	0.42	-	-	-
<i>Causal:</i>					
Vulnerable individuals (H2)					
$y = g \frac{f_1 q (1 - s f_1)^{365 \cdot T} + f_2 (1 - q) (1 - s f_2)^{365 \cdot T}}{q (1 - s f_1)^{365 \cdot T} + (1 - q) (1 - s f_2)^{365 \cdot T}}$	-2.37	0.27	1.000 (0.000)	0.015 (0.003)	0.026 (0.008)
Within-unit learning (H3)					
$y = g [f_1 e^{-s \cdot 365 \cdot T} + f_2 (1 - e^{-s \cdot 365 \cdot T})]$	-4.59	0.28	0.041 (0.006)	0.015 (0.003)	-
Between-unit learning (HX)					
$y = g \left[f_1 e^{-\left(\frac{g}{u}\right) \cdot s \cdot 365 \cdot T} + f_2 \left(1 - e^{-\left(\frac{g}{u}\right) \cdot s \cdot 365 \cdot T} \right) \right]$	-9.72	0.41	0.050 (0.006)	0.019 (0.002)	-

Table S3. Descriptive and causal models fit to strike rates (y) at different time lags after the first sighting on defined grounds (see Fig. S3)

Model	AIC	Adjusted R ²	Parameter estimates (SE):		
			Strike rate on vulnerable /naïve animals (<i>f</i> ₁)	Strike rate on less vulnerable/ experienced animals (<i>f</i> ₂)	Proportion of vulnerable animals (<i>q</i>)
<i>Descriptive:</i>					
Exponential $y = a_1 + a_2 \cdot e^{-a_3 T}$	-23.21	0.47	-	-	-
<i>Causal:</i>					
Vulnerable individuals (H2) $y = g \frac{f_1 q (1 - s f_1)^{365 \cdot T} + f_2 (1 - q) (1 - s f_2)^{365 \cdot T}}{q (1 - s f_1)^{365 \cdot T} + (1 - q) (1 - s f_2)^{365 \cdot T}}$	-14.28	0.32	1.000 (0.000)	0.015 (0.003)	0.022 (0.006)
Within-unit learning (H3) $y = g [f_1 e^{-s \cdot 365 \cdot T} + f_2 (1 - e^{-s \cdot 365 \cdot T})]$	-16.48	0.32	0.037 (0.004)	0.015 (0.003)	-
Between-unit learning (HX) $y = g \left[f_1 e^{-\left(\frac{d}{u}\right) \cdot s \cdot 365 \cdot T} + f_2 \left(1 - e^{-\left(\frac{d}{u}\right) \cdot s \cdot 365 \cdot T} \right) \right]$	-21.55	0.44	0.044 (0.005)	0.018 (0.002)	-

Table S4. Models fit to strike rates at different time lags after the first sighting in the region ($h=1,000\text{km}$) for different input values for sighting rate (s sightings.group⁻¹.day⁻¹), mean group size (g), and mean unit size (u), roughly encompassing the ranges of plausible values of these parameters. Model fit is indicated by AIC, with lower AICs indicating better-fitting models.

Input parameters:	Standard	Decrease u	Increase u	Decrease g	Increase g	Decrease s	Increase s
s	0.000313	0.000313	0.000313	0.000313	0.000313	0.000156	0.000626
g	21.75	21.75	21.75	16.75	26.75	21.75	21.75
u	10.50	7.50	13.50	10.50	10.50	10.50	10.50
Model:	AIC:						
Exponential	-17.55	-17.55	-17.55	-17.55	-17.55	-17.55	-17.55
Vulnerable individuals	-9.95	-9.95	-9.95	-8.69	-11.12	-7.31	-14.29
Within-unit learning	-12.14	-12.14	-12.14	-10.89	-13.34	-9.41	-16.49
Between-unit learning	-16.71	-18.25	-15.09	-13.33	-18.43	-12.33	-18.40

Description of data and computer code

NP_data_set_Whitehead_et_al.xlsx

Data set used for primary analysis (edited from that at whalinghistory.org)

MATLAB files:

inwhaledatxx.m

Reads in data from Excel file, removes times when not whaling, singleton days and duplicates, outputs as MATLAB data file npwhal.datxxx.mat.

runbatch.m

Makes plots and provides results for scenario described in main test (Fig.2, Table 1) as well as variants in Supplementary Material (Figs S1-3, Tables S1-3), calling functions dislimy.m, groundusey.m and hypsup.m.

dislimy.m

Uses npwhal.datxxx.mat to make plots of positions of sightings, indexed by colour for date of first sighting in region (defined using range, h), aggregates data by time lag since first sighting in region, plots strike rate versus time lag, and adds descriptive model of initial exponential decline to plot.

groundusey.m

Uses grounds_Sperm.mat (a version of npwhal.datxxx.mat with information on grounds added: grnn: names of grounds; qq: voyage-day in which ground) to make a plot of positions of sightings, indexed by colour for ground, aggregates data by time lag since first sighting in region, plots strike rate versus time lag, and adds descriptive model of initial exponential decline to plot.

hypsup.m

Examines support for causal hypotheses (vulnerable individuals, within-unit learning, between-unit learning) using non-linear models for initial decline in strike rate, and adds curves for each model to plots of strike rate versus time lag produced by dislimy.m or groundusey.m.