



Network-Based Diffusion Analysis Reveals Cultural Transmission of Lobtail Feeding in Humpback Whales

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among wild, nonhuman animals than previously appreciated, the initial establishment of behavioral innovations may be a fragile process, in comparison to the transmission of already-common behaviors. If so, this argues not only for the extension of our group-training approach, but also for systematic comparisons between such experiments and those that instead seed new behaviors in individuals, in order to understand why some innovations are short-lived whereas others spread to become new traditions.

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Supplementary Materials

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Materials and Methods

Supplementary Text

Figs. S1 to S4

Tables S1 to S4

References (35–39)

Databases

Movies S1 and S2

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Network-Based Diffusion Analysis Reveals Cultural Transmission of Lobtail Feeding in Humpback Whales

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We used network-based diffusion analysis to reveal the cultural spread of a naturally occurring foraging innovation, lobtail feeding, through a population of humpback whales (*Megaptera novaeangliae*) over a period of 27 years. Support for models with a social transmission component was 6 to 23 orders of magnitude greater than for models without. The spatial and temporal distribution of sand lance, a prey species, was also important in predicting the rate of acquisition. Our results, coupled with existing knowledge about song traditions, show that this species can maintain multiple independently evolving traditions in its populations. These insights strengthen the case that cetaceans represent a peak in the evolution of nonhuman culture, independent of the primate lineage.

Debate about traditions and culture in nonhumans has been fueled by claims of evidence for culture, broadly defined as shared behavior propagated by social learning (1), in a variety of species (2–5), including cetaceans (6). Quantifying cultural transmission in any wild population is difficult, however, because field studies are rarely sufficient to allow for the complete elimination of alternative ge-

netic or ecological explanations (1, 7–9). These problems are exacerbated by the limitations on visibility and accessibility inherent in studying marine mammals, but the group continues to attract interest due, for example, to the strong evidence for cultural transmission of vocal patterns (10, 11). Only a handful of cetacean species have lent themselves to the types of data collection necessary to address questions of cultural transmission (6), and the evidence remains, for the most part, controversial (1).

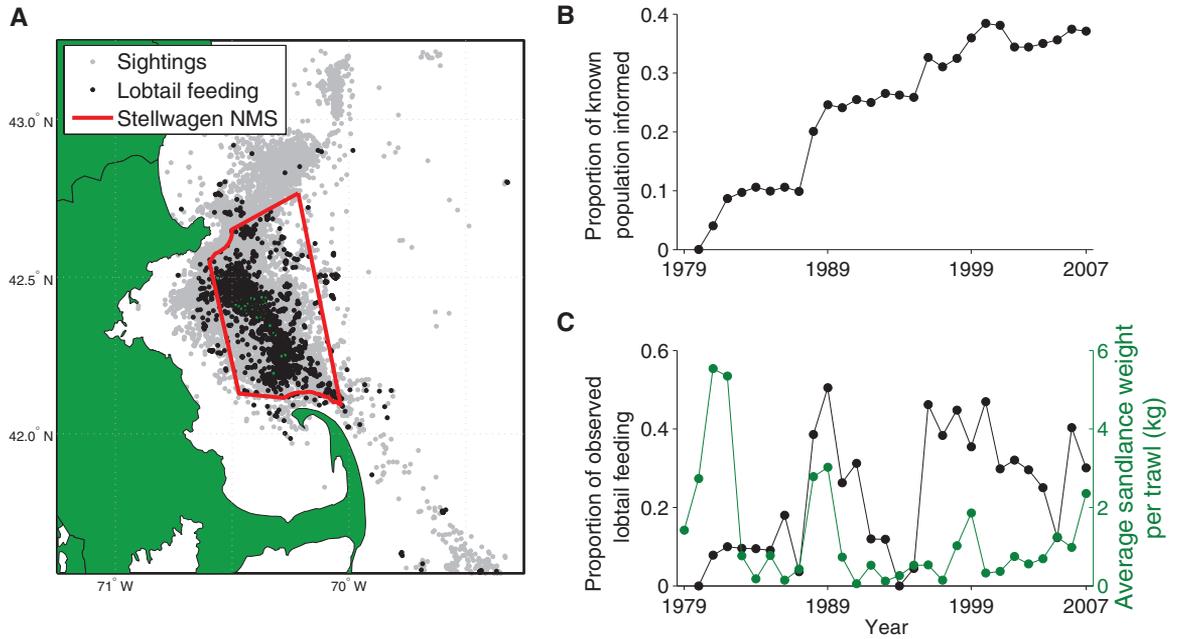
In the Gulf of Maine, bubble-feeding is a common foraging technique used by humpback whales (*Megaptera novaeangliae*), which is characterized by bubble production 20 to 25 m below the surface, underneath and around a prey

school, followed by a lunge through those bubbles (12, 13). Although this general technique has been documented in other humpback populations (14), in 1980 one whale in the Gulf of Maine was observed performing an innovative modification to this feeding technique that is now known as lobtail feeding (13, 15). Lobtail feeding consists of striking the water's surface one to four times with the ventral side of the fluke, followed by a bubble-feeding sequence. An accelerating rate of diffusion of this behavior, indicated by a sharp increase in the proportional use of lobtail feeding in the years 1981–1989 (Fig. 1), led to the suggestion that social transmission was responsible for its spread (15). Diffusion rate, however, is not a reliable indicator of social transmission (16). Furthermore, it has been suggested that lobtail feeding is a specialization related to foraging on sand lance (15), because it is spatially concentrated on Stellwagen Bank (Fig. 1A), where sand lance gather for spawning (17). In the years immediately preceding the behavior's emergence, the stock of herring, another important prey species, crashed (18), suggesting a role for ecological factors. Because such factors are a common influence on innovation and social learning, these hypotheses are not necessarily mutually exclusive, but it is difficult to measure the relative influence of social and ecological factors on the spread of behavior (1, 9). Network-based diffusion analysis (NBDA) (9, 19, 20), a new method related to network influence models in the social sciences, offers one way forward [see also (5, 21)]. We used NBDA to analyze the spread of the lobtail feeding innovation among humpback whales summering in the Gulf of Maine.

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Fig. 1. Spatial (A) and temporal (B and C) distribution of lobtail feeding. (B) shows the proportion of the known population each year that were also known to be informed, and (C) shows the proportion of observed feeding events each year that were lobtail feeding, along with sand lance abundance in research trawls (27).



NBDA uses an association matrix, which estimates the proportion of time that individuals are associated, to quantify the extent to which social network structure explains the spread of a behavior (9, 19). The underlying assumption is that socially transmitted behaviors should spread at a higher rate between individuals who spend more time associated. We used both discrete time-of-acquisition diffusion analysis (TADA) and the order-of-acquisition extension (OADA) to compare the social association matrix with the order in which informed individuals acquired the trait (9, 22). NBDA models the spread of behavior as a stochastic process in which, at any given time, each naïve individual has a learning rate that determines the likelihood of its learning the behavior at that time. NBDA also allows individual-level data to be incorporated to control for the possibility that factors such as age and gender could affect social learning rates (22).

We analyzed data collated by the Whale Center of New England (WCNE) from observers placed aboard commercial whale-watching vessels. The data set encompasses 27 years (1980–2007) and 73,790 sighting records, in which 653 individuals were sighted 20 or more times in and around the Stellwagen Bank National Marine Sanctuary (Fig. 1A). Lobtail feeding was first recorded in this data set in 1981, although the very first record comes from a separate study in which it was noted once in a sample of 150 feeding events observed in 1980 (13). Over the study period, the proportion of the population known to be informed increased to 37%, indicating that knowledge of this behavior has spread over time (Fig. 1B). The actual use of the lobtail feeding technique, measured as the proportion of observed feeding events in a given year in which lobtail feeding was used, did not follow a monotonic trend, showing instead a pattern of peaks and

Table 1. Summed Akaike weights (ω_i) and maximum-likelihood estimates of social transmission parameters for NBDA models with and without social transmission.

Analysis type	Social transmission model	$\sum \omega_i$	Social transmission parameter estimate	95% CI
Order of acquisition (OADA)	Multiplicative	0.84	30.9	8.2–123.2
	Additive	0.16	32.0	11.3–96.6
	No social transmission	1.8×10^{-23}	(Constrained to 0)	–
Year of acquisition (discrete TADA)	Multiplicative	0.88	2.7	1.2–5.3
	Additive	0.12	3.0	1.1–8.5
	No social transmission	7.7×10^{-7}	(Constrained to 0)	–

troughs. The first observations of lobtail feeding were associated with a peak in sand lance abundance, and a subsequent sharp increase in the use of the behavior was closely tied to a second abundance peak in 1987–1989 (Fig. 1C).

Models including social transmission were overwhelmingly supported in both the OADA and TADA analyses, by between 6 and 23 orders of magnitude as compared to an equivalent set of models in which the social transmission effect was constrained to zero (Table 1). Estimates of the social transmission effect, the factor by which an individual’s learning rate is increased per unit of association with informed individuals as compared to the asocial learning rate of an average individual in the population, ranged from 2.7 to 32.0, with no 95% confidence intervals (CIs) spanning zero. The OADA and TADA models respectively estimated that 87 and 45% of whales that acquired lobtail feeding did so by social transmission, with the latter estimate likely to be highly conservative (22). An alternative explanation for this pattern is that whales who acquired lobtail feeding were subsequently more likely to associate with one another, perhaps through shared attraction to sand lance shoals. When we allowed

for such homophily effects by disregarding all associations recorded after each individual acquired the behavior (22), the ΔAIC (Akaike Information Criterion) between models with and without social transmission was 21.8, corresponding to 54000:1 support for the model with social transmission. These results show that social transmission has had a major role in the spread of lobtail feeding.

The social network in the population was consistent with previous descriptions of humpback social structure (14, 23), being characterized by many relatively weak associations. The social network of individuals sighted at least 20 times showed a mean number of associates at any one time, also known as mean node strength, of 1.04 (range 0.02 to 4.14) measured by the half-weight association index (22, 24), and the average number of identified associates for the 653 individuals was 51 (range 1 to 210). Modeling the network as a system of springs (25) shows informed individuals (defined as those observed lobtail feeding at least once) concentrated at the well-connected center of the network (Fig. 2).

In the OADA analysis, the nonsocial characteristic with the largest effect on an individual’s rate of learning lobtail feeding was the proportion

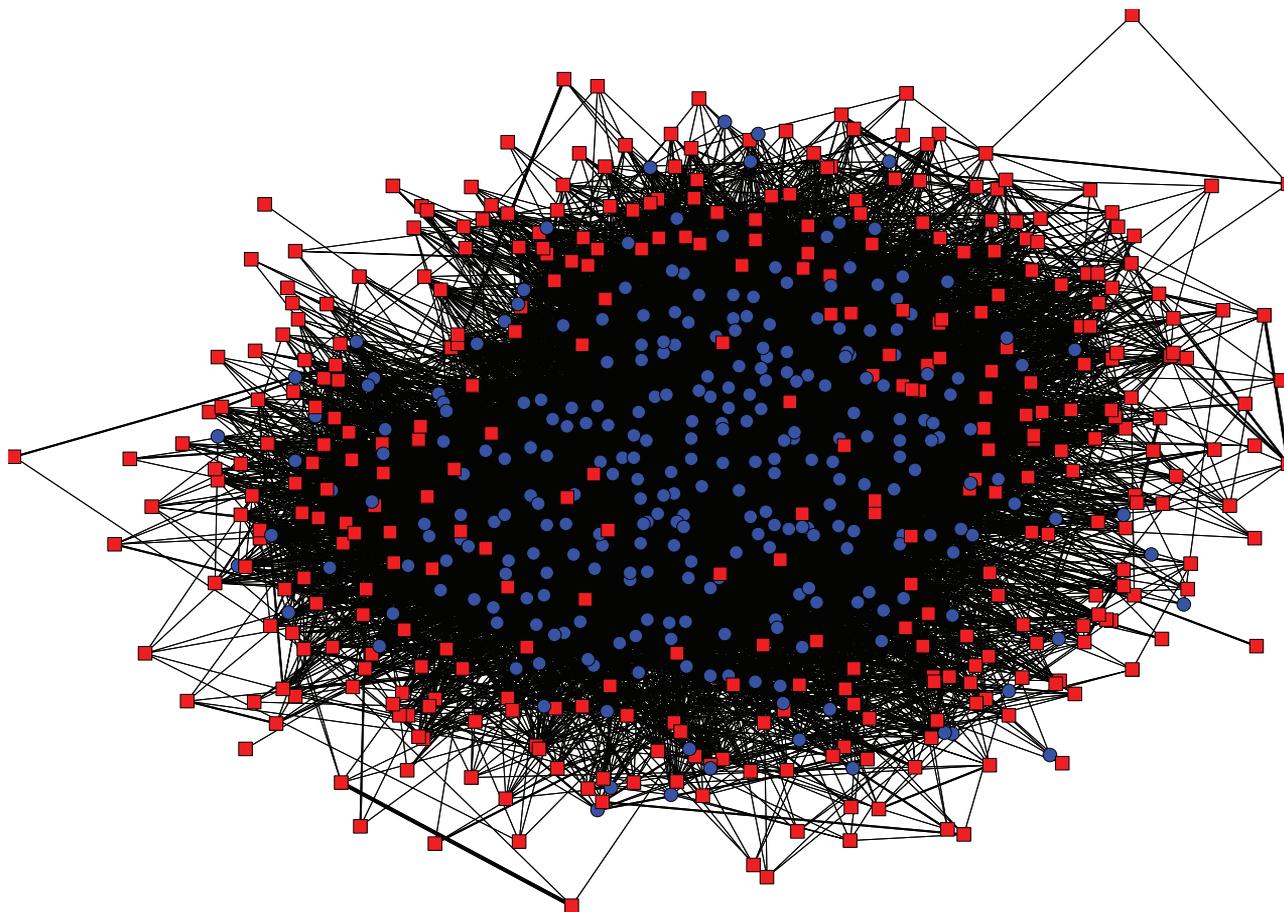


Fig. 2. Social network of whales sighted at least 20 times. Blue nodes are individuals observed lobtail feeding, red nodes are those never observed lobtail feeding. The network was laid out by spring-embedding using Netdraw (25) software.

Table 2. Individual-level effects. Summed Akaike weights (ω_i), model-averaged parameter estimates, and maximum-likelihood effect sizes for individual-level variables from multiplicative OADA models. Effect sizes are only interpreted where there is more support for a variable than against ($\omega_i > 0.5$).

Variable	$\Sigma\omega_i$	Estimate	95% CI	Effect size	Interpretation
Age	0.713	-0.109	-0.34–0.03	0.9827	Learning rate decreases by factor of 0.98 per year of age.
Number of sightings	0.626	0.058	-0.05–0.23	1.0003	Apparent learning rate increases by factor of 1.0003 per sighting (e.g., by 1.03 or 3% for median number of sightings).
Stellwagen residency	0.616	0.616	-0.37–2.48	1.8514	Individual seen exclusively on the bank has a learning rate increased by 80% as compared to one never seen on the bank.
Sex	0.460	-0.040	-0.25–0.09	0.9222	Little support for gender effect
Lobtail-feeding mother	0.353	-0.034	-0.37–0.14	0.9352	Little support; not consistent with major genetic influence

of times that individual was sighted within the Stellwagen Bank sanctuary area (Table 2). We interpret this as indicating a role for ecological factors in promoting the acquisition of the feeding technique, but the effect size (an 80% increase in learning rate for an individual sighted exclusively within the sanctuary) does not approach the estimated effect of social transmission. In the TADA analysis, we were able to include annual sand lance biomass estimates as a predictor of learning rates, and it received strong support [summed Akaike weights ($\Sigma\omega_i$) = 0.998], with a positive effect on asocial learning rates (a 40% increase per kilogram of increase in mean annual sand lance weight in research trawls, table S1), providing direct evidence of a link between lobtail feeding and sand lance. The OADA analysis indicated that having an informed mother has virtually no effect on learning rates (Table 2), whereas in the TADA analysis, having an informed mother was well supported as a predictor, but its effect was estimated as negative (table S1). Both of these results are inconsistent with a significant role for genetic factors or vertical social learning in the acquisition of lobtail feeding, showing that horizontal cultural transmission is largely responsible for the spread of the behavior. Most learning

of this behavior occurred after weaning—just 2% of the 241 informed individuals of known age were first seen lobtail feeding when less than 2 years old—and mothers do not preferentially associate with their offspring after weaning (14), which helps explain the lack of maternal influence.

A powerful advantage of the NBDA approach is that it allows the simultaneous consideration of ecological, social, and genetic factors as predictors of individual learning rates, thus moving away from sterile arguments about excluding such factors in the development of behavior and instead reflecting the reality that all behavior develops as an interaction of multiple factors (1). Thus, in the present study we are able to describe the roles of both ecology and social transmission in the spread of a feeding innovation, reflecting the notion that social learning allows dynamic adaptation to changing ecological circumstances. Lobtail feeding first appeared in this population during a rapid rise in the abundance of sand lance, which gather in high densities to spawn on Stellwagen Bank, after a crash in another important prey, herring (18). Although the purpose of adding a lobtail to the beginning of a bubble-feeding dive sequence is unknown, the link with contemporaneous prey dynamics suggests some function specific to foraging on sand lance, perhaps provoking a tightening of the prey school before bubble entrapment. Our results show that social transmission played a crucial role in the spread of lobtail feeding behavior, which has now persisted over 27 years and multiple generations (14). Lobtail feeding can therefore be considered a tradition (26), and because humpback populations are known to also carry vocal traditions in

the form of song (10, 11), this population can be considered to carry multiple traditions.

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Supplementary Materials

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Materials and Methods
Table S1
References (28–30)
Database S1

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Population Growth in a Wild Bird Is Buffered Against Phenological Mismatch

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Broad-scale environmental changes are altering patterns of natural selection in the wild, but few empirical studies have quantified the demographic cost of sustained directional selection in response to these changes. We tested whether population growth in a wild bird is negatively affected by climate change–induced phenological mismatch, using almost four decades of individual-level life-history data from a great tit population. In this population, warmer springs have generated a mismatch between the annual breeding time and the seasonal food peak, intensifying directional selection for earlier laying dates. Interannual variation in population mismatch has not, however, affected population growth. We demonstrated a mechanism contributing to this uncoupling, whereby fitness losses associated with mismatch are counteracted by fitness gains due to relaxed competition. These findings imply that natural populations may be able to tolerate considerable maladaptation driven by shifting climatic conditions without undergoing immediate declines.

When environments change over time, individuals with extreme trait values can have higher fitness in the new environment, and thus directional selection toward that end of the phenotype distribution will occur

(1). Given a heritable basis to trait variation, evolutionary responses may ensue (2), but a major concern is that the rate of environmental change might outstrip the pace of evolutionary adaptation, thereby threatening the persistence of popu-

lations and species (3, 4). Theoretical models have explored this problem by framing the issue in terms of fitness landscapes, where environmental change causes the fitness optimum to shift through trait space (4–8), rendering the population less well-adapted to its environment as compared to the situation before the change. As the lag between mean phenotype and optimum phenotype increases, the strength of directional selection toward the optimum intensifies, but the population is also expected to accrue an increasing “lag load,” or demographic cost, in terms of reduced mean fitness (5–10). Despite the central importance of these concepts in evolutionary theory and conservation biology (7, 11, 12), empirical studies quantifying the demographic cost of selection in wild populations are lacking [but see (13)].

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