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Epidemiological models to control the spread of information in marine mammals

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Socially transmitted wildlife behaviours that create human–wildlife conflict are an emerging problem for conservation efforts, but also provide a unique opportunity to apply principles of infectious disease control to wildlife management. As an example, California sea lions (*Zalophus californianus*) have learned to exploit concentrations of migratory adult salmonids below the fish ladders at Bonneville Dam, impeding endangered salmonid recovery. Proliferation of this foraging behaviour in the sea lion population has resulted in a controversial culling programme of individual sea lions at the dam, but the impact of such culling remains unclear. To evaluate the effectiveness of current and alternative culling strategies, we used network-based diffusion analysis on a long-term dataset to demonstrate that social transmission is implicated in the increase in dam-foraging behaviour and then studied different culling strategies within an epidemiological model of the behavioural transmission data. We show that current levels of lethal control have substantially reduced the rate of social transmission, but failed to effectively reduce overall sea lion recruitment. Earlier implementation of culling could have substantially reduced the extent of behavioural transmission and, ultimately, resulted in fewer animals being culled. Epidemiological analyses offer a promising tool to understand and control socially transmissible behaviours.

1. Introduction

Socially transmitted behaviours, ideas, or information can be contagious, spreading through populations like an infectious disease [1–3]. Interactions between individuals underlie transmission of both behaviours and diseases, creating similar patterns of spread across contact networks [3], and conservation biologists and wildlife managers increasingly need to control the spread of unwanted wildlife behaviours [4,5]. Human–wildlife conflict arises when specific behaviours increase exploitation of human resources [6], which may threaten human safety and economic livelihood and ultimately result in wildlife culling to eliminate the conflict [7]. Unfortunately, such culling strategies often have deleterious consequences for wildlife populations and raise technical, ethical, and scientific questions as to their scope and effectiveness. Understanding the transmission mechanisms that underlie the spread of detrimental behaviours may lead to science-based recommendations on culling strategies to limit the impact of these behaviours and potentially reduce absolute culling levels to a socially acceptable level.

Network-based diffusion analyses (NBDA) have proved valuable at testing the extent to which social transmission underlies the spread of behaviours through social groups [8–10]. NBDA works by relating observed contact
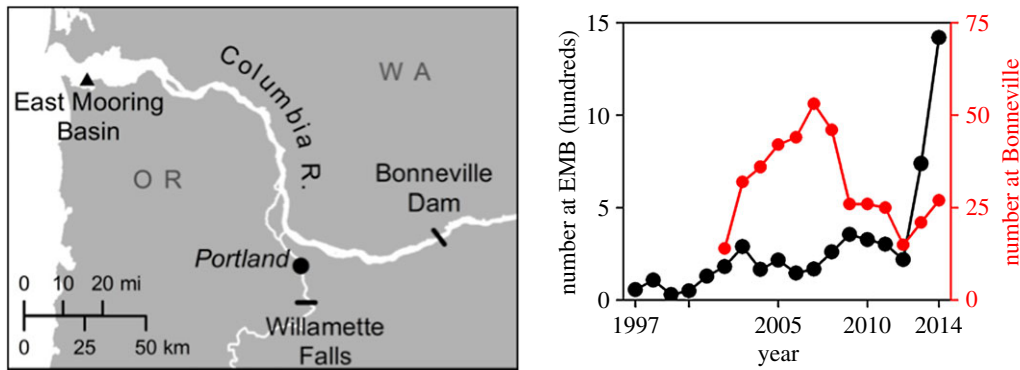
Figure 1. Columbia River and incidence of California sea lions at East Mooring Basin (EMB) and Bonneville Dam. The maximum California sea lions observed at EMB (black) and average daily number of Bonneville foragers in each year (red). (Online version in colour.)

networks to the order and/or timing in which individuals first demonstrate the behaviour [10]. Thus, NBDA currently functions as a means to quantify the current and past role of social learning. However, in guiding culling strategies, predictions about future impacts of culling or evaluations of how alternate past culling strategies would have changed the system are often desired. Without the ability to predict how observed contact networks will respond to the removal of individuals in the future or alternate individuals in the past, NBDA alone cannot currently be used to provide specific recommendations about alternate strategies to control the social transmission of detrimental wildlife behaviours. As such, new tools are needed to integrate the mechanistic insights from NBDA with the impacts of culling on unwanted wildlife behaviour.

Given the parallels between social transmission of a behaviour and of a pathogen, models from disease ecology (e.g. susceptible–infected (SI) models) provide an ideal tool to extend NBDA outputs to explore alternate past and future culling strategies. In their most basic form, SI models assume that individuals contact each other randomly at specified rates [11]. Thus, changes in contact patterns can be represented by a simple change in the contact rate rather than attempting to predict how removal of particular individuals will alter the fine structure of the contact network. Here, we show how outputs from NBDA derived from detailed contact network data can be translated into an SI model framework to explore alternate culling strategies.

To demonstrate the application of such tools, we use foraging behaviour in California sea lions as a case study. In the early 2000s, California sea lions (*Zalophus californianus*) discovered concentrations of salmonids migrating upriver below the entrances to fish ladders at Bonneville Dam (located 235 km up the Columbia River, 45.6442° N, 121.9406° W). Increasing sea lion predation pressure impedes the recovery of the Columbia River's declining salmon and steelhead (*Oncorhynchus* spp.) runs, of which 13 evolutionarily significant units are federally listed under the US Endangered Species Act [12]. Near the mouth of the river is a major haulout for migratory male California sea lions with aggregations of tens to thousands of individuals (figure 1; [13]). Sea lions were observed sporadically at Bonneville Dam from when it was built in 1938 until the late 1990s [13,14], but the number of individuals foraging at the dam has increased sharply starting in 2002 (figure 1). The rapid increase in dam-foraging behaviour among a subgroup of the population is consistent with social transmission of learned exploitation of this novel food source, as opposed

to random asocial learning [15]. Sea lion foraging at the dam is a known source of mortality for the endangered salmonids. This impedes endangered salmonid recovery and has created local, regional, and national management conflicts because California sea lions are also federally protected under the US Marine Mammal Protection Act. Culling of sea lions preying on salmon at Bonneville Dam began in 2008, but was halted in 2011 during an injunction while being challenged in a lawsuit from the Humane Society of United States [16]. This highlights the challenges of culling charismatic predator species versus the threat of extinction of economically, culturally, and ecologically important salmon [17].

Here, we focus on three central aims. First, we used NBDA to estimate the social transmissibility of dam-foraging behaviour by sea lions in the Columbia River. Then, we show how the parameters derived from our NBDA can be translated into an SI model, where social transmission of behaviour was equivalent to transmission of disease through direct contact between individuals and asocial acquisition of behaviour mirrored constant background risk of infection (e.g. from an environmental reservoir). Finally, we used the resulting SI model to examine whether culling was necessary, as well as the effect of alternative culling strategies by analysing the impact of timing and level of culling on sea lion abundance at Bonneville.

2. Material and methods

(a) Data collection
Sight–resight data of branded individual California sea lions were collected at the main haulout near the mouth of the Columbia River; the East Mooring Basin of Astoria, OR, USA (river kilometre 25). Pacific States Marine Fisheries Commission and Oregon Department of Fish and Wildlife observers measured the number of individuals at each jetty/haulout from 1997 to 2014. Sampling occurred by performing counts of all individuals hauled out, followed by observing branded individuals at each haulout, and occasionally flushing all animals at specific haulouts and observing branded individuals during re-haulout. We used a 'gambit of the group' approach [18] with individuals considered associated if they were observed occupying the same dock or jetty. A simple-ratio association index was calculated in SOCPROG 2.4 [19], with association strengths ranging from 0 (never observed hauled out together) to 1 (always observed hauled out together). We estimated the association index for any individuals that were observed more than once (for alternate sighting threshold, see electronic supplementary material, figures S1 and S2).

Table 1. Comparisons of NBDA models with and without social transmission and with and without a change in learning parameters in 2008 using the change in sample-size corrected Akaike information criterion (ΔAICc; zero indicates the best model). Parameter estimates and their 95% CIs (in square brackets) for each model are given.

model	pre-2008 social learning coefficient[a]	pre-2008 asocial learning rate[b]	post-2008 social learning coefficient[a]	post-2008 asocial learning rate[b]	ΔAICc
social transmission + change in learning	11.23 [3.96, 19.02]	1.22×10^{-5} [4.07×10^{-6}, 2.42×10^{-5}]	1.05 [6.66×10^{-5}, 3.67]	2.57×10^{-5} [1.42×10^{-5}, 3.98×10^{-5}]	0
no social transmission + change in learning	—	4.42×10^{-5}	—	3.64×10^{-5}	31.4
social transmission + no change in learning	6.79 [3.35, 7.50][c]	7.70×10^{-6} [4.38×10^{-6}, 1.19×10^{-5}][c]	—	—	307.7
no social transmission + no change in learning	—	[2.18×10^{-5}][c]	—	—	357.8

[a]Unitless parameter.
[b]Daily rates.
[c]Estimates are for the entire period 2002–2014.

Seasonal observation effort at Bonneville Dam commenced each year with the first appearance of sea lions at the dam and continued until their absence. The timing of branded individuals foraging at the Bonneville Dam was collected by the US Army Corps of Engineers sea lion observers programme from 2002 to 2014. Observation effort methods are detailed elsewhere [14].

(b) Network-based diffusion analysis

We used NBDA on the association indices between individuals to assess social transmissibility of the dam-foraging behaviour. The time at which an individual first arrived at Bonneville was used as the marker for learning and was treated as a continuous variable in the NBDA. The rate of acquisition of a behaviour by individual i at time t, $\lambda_i(t)$, is defined by [10]:

$$\lambda_i(t) = \lambda_0(t)(1 - z_i(t))\left[s(t)\sum_{j=1}^{N} a_{i,j}z_j(t) + 1\right], \quad (2.1)$$

where, $\lambda_0(t)$ is the asocial learning rate at time t; $z_i(t)$ is an indicator function for whether individual i has learned the behaviour at time t ($z_i(t) = 1$) or not ($z_i(t) = 0$); $s(t)$ is the strength of social learning relative to asocial learning at time t; $a_{i,j}$ is association strength between individuals i and j; and N is the total number of individuals.

NBDAs were run to derive learning rates for two different models: (i) different social (as measured by $s(t)$) and asocial learning rates ($\lambda_0(t)$) prior to and after instituting culling in 2008, and (ii) constant social and asocial learning rates for the entire time series (2002–2014). Sample-size corrected Akaike information criterion (ΔAICc) was used to compare models, with a value of zero indicating the best model and values under two indicating preferred models [10].

(c) Discrete-time epidemiological model

To assess the impact of culling on sea lion foraging at Bonneville Dam, we translated the output of the NBDA into a discrete-time SI model that tracked the number of sea lions foraging at Bonneville, $Y(t)$, and the number of non-foragers at the mouth of the Columbia River, $X(t)$, over weekly time steps. Using equation (2.1), the weekly change in the number of foragers is defined as:

$$Y(t+1) = Y(t) + \sum_{i=1}^{N} \lambda_0(t)(1 - z_i(t))\left[s(t)\sum_{j=1}^{N} a_{i,j}z_j(t) + 1\right] - \mu Y(t) - \gamma(t)Y(t), \quad (2.2)$$

where μ is the natural removal rate of foraging individuals (i.e. natural mortality or dispersal to other foraging grounds), and $\gamma(t)$ is the time-varying rate at which foraging individuals are culled (which includes live capture and transfer to captivity in addition to culling).

Equation (2.2) requires individual-based data incorporating contact information from at least a sample of individuals in the population. However, if the association network is well connected (electronic supplementary material, figure S1a) and foragers do not occupy more central positions within the association network, as measured by the total number of associations (degree, electronic supplementary material, figure S1a) or the number of shortest paths between any two individuals in the association network that an individual sits on (betweenness, electronic supplementary material, figure S1b), then the specific network structure will not be as important in modelling the total number of foragers. Rather, only previous associations with foragers will be important in determining spread of the behaviour (electronic supplementary material, figure S1c). Thus, we assume that contacts between any two individuals in the population occur at random and at a constant strength (i.e. $a_{i,j} \approx c$, for all $i \neq j$), such that equation (2.2) simplifies to,

$$Y(t+1) = Y(t) + a\lambda_0(t)X(t) + a\lambda_0(t)s(t)cX(t)Y(t) - \mu Y(t) - \gamma(t)Y(t), \quad (2.3)$$

where a is a scaling factor that translates NBDA estimates obtained from a sample of the population into a final model of the total accumulation of foragers (see the electronic supplementary material for a full description of the NBDA translation).

Because equation (2.3) is translated from the NBDA (equation (2.1)), we used the parameter estimates from the NBDA (i.e. $\lambda_0(t)$ and $s(t)$; tables 1 and 2) directly in the SI model. In addition, the average contact strength, c, was calculated from the association

4

Table 2. Estimated parameters used in the epidemiological model. Parameters were estimated using observation thresholds of sea lions of 2, 10, and 20 sightings. All rates are weekly rates.

parameter	description	estimate using a 2 sight threshold	estimate using a 10 sight threshold	estimate using a 20 sight threshold
$\lambda_0(t) < 2008$	asocial learning rate before culling started in 2008	8.54×10^{-5}	2.59×10^{-4}	3.54×10^{-4}
$\lambda_0(t) > 2008$	asocial learning rate after culling started in 2008	1.80×10^{-4}	2.35×10^{-4}	2.33×10^{-4}
$s(t) < 2008$	social learning coefficient before culling started in 2008	11.23	2.62	1.49
$s(t) > 2008$	social learning coefficient after culling started in 2008	1.05	0	0
c	average association strength between two individuals	0.0122	0.0151	0.0175
μ	natural removal rate of foragers from Bonneville	0.0081	0.0077	0.0078
α	scaling factor	9.90	8.57	7.93
$X(0)$	initial number of foragers	12	0	0

Table 3. Yearly removals allowed for the actual culling employed as well as for strategies that removed the hiatus in 2011 and started before 2008.

year	culling strategy							
	Actual	Actual + 2011	Start 2007	Start 2006	Start 2005	Start 2004	Start 2003	Start 2002
2002	0	0	0	0	0	0	0	12
2003	0	0	0	0	0	0	12	12
2004	0	0	0	0	0	12	12	12
2005	0	0	0	0	12	12	12	12
2006	0	0	0	12	12	12	12	12
2007	0	0	12	12	12	12	12	12
2008	11	11	11	11	11	11	11	11
2009	15	15	15	15	15	15	15	15
2010	14	14	14	14	14	14	14	14
2011	1[a]	12	12	12	12	12	12	12
2012	13	13	13	13	13	13	13	13
2013	4	4	4	4	4	4	4	4
2014	15	15	15	15	15	15	15	15

[a]This one individual was removed after culling resumed the week of 17 May.

data included in the NBDA by taking the average association between temporally overlapping individuals (i.e. individuals observed within 1 year of each other, whether or not they were observed together; table 2). To estimate the rate at which individuals are naturally removed from Bonneville Dam, μ, we used the dates that foragers were first and last observed at Bonneville to estimate total observed foraging duration, the reciprocal of which gives us an estimate of the natural removal rate (table 2). However, because natural removals become confounded with human-initiated lethal removals after 2008, we only consider foraging durations for individuals who were last observed before 2008 in estimating μ.

For lethal removals via culling, $\gamma(t)$, we used the actual culling strategy implemented (table 3). Culling in the model began the week of 16 April, in line with the timing of actual removals [20]. A maximum of four individuals were removed each week to mimic actual culling efforts [20] (i.e. $\gamma(t) = 4$) until the total number of allowed removals during that year was reached (table 3).

When calculating the number of foragers using equation (2.3), we forced the number of non-foragers in the model, $X(t)$, using the count data on the number of sea lions hauled out in Astoria, OR, USA (electronic supplementary material, figure S2). We started simulations on 1 April 2001 with an initial
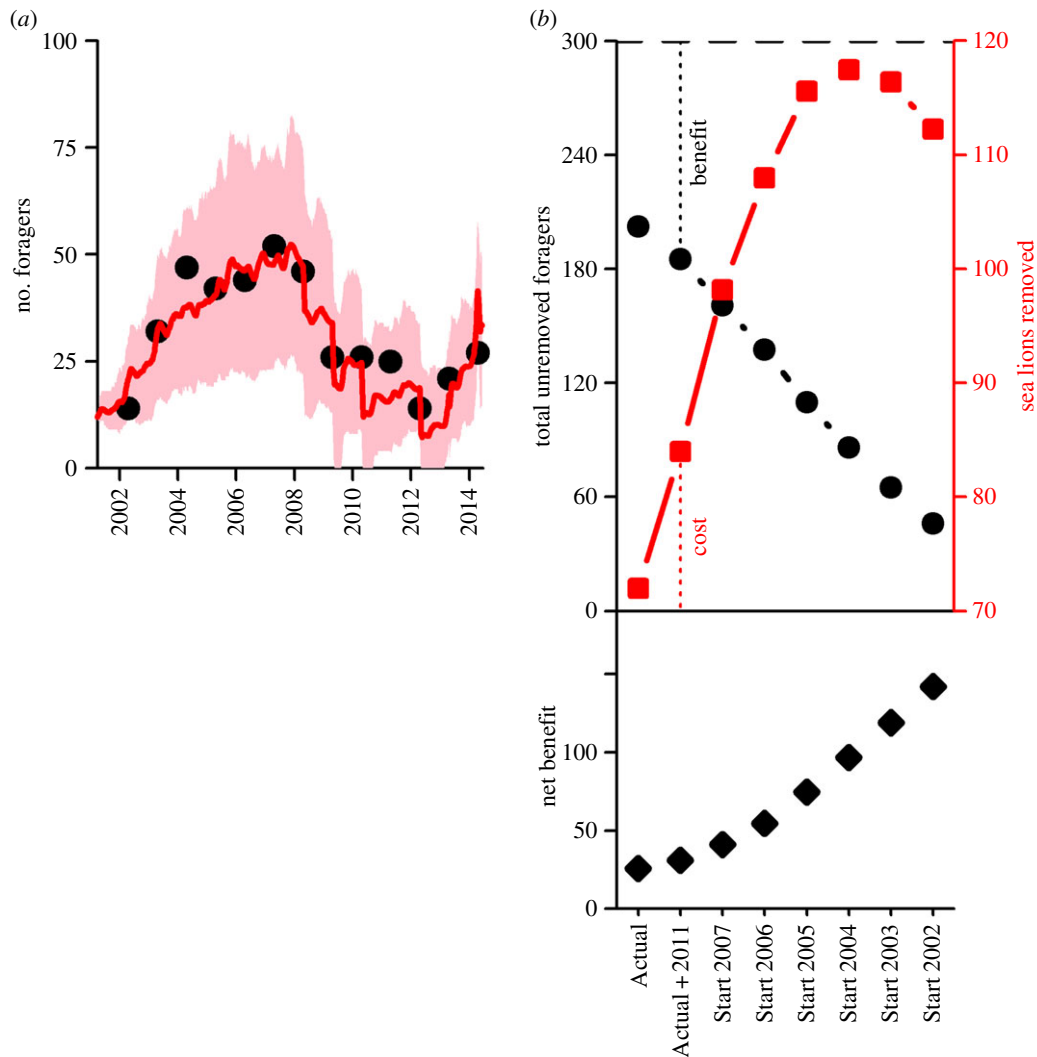
Figure 2. Total number of foragers at Bonneville Dam and the benefits of early implementation of culling. (a) Projected number of foragers through time for the model (solid red line) fit to the maximum daily number of foragers in each year (black circles). Light red shaded area is the 95% CI for model projections generated using Poisson errors. (b) The upper part of the graph depicts the total number of foragers to ever visit Bonneville Dam without culling (dashed, black line), the effect of different culling strategies (table 3) on the total number of unremoved foragers (black circles), and the number of sea lions removed (red squares). The lower part of the graph depicts the net benefits of these strategies (benefits minus the cost; black diamonds). The actual culling strategy used (Actual) began in 2008 with an injunction on culling in 2011. Alternate strategies included: (i) Actual + 2011—the actual strategy used but with the average number culled from 2008 to 2014 implemented in 2011 and (ii) Start 2002–2007—same as the Actual + 2011 strategy but with the average yearly cull from 2008 to 2014 implemented beginning in the year specified until 2008 (table 3). (Online version in colour.)

number of foragers, $Y(0)$. Because asocial learning allowed for accumulation of foragers in the absence of other foragers, we note that $Y(0) \geq 0$. We assumed an order of events within each week where new foragers arrived first, then were culled, and then were naturally removed, with all removals constrained so that the number of foragers was always greater than or equal to zero.

(d) Fitting the susceptible–infected model
Although other parameters were either observed (i.e. $\gamma(t)$), calculated directly from the NBDA (i.e. $\lambda_0(t)$ and $s(t)$), or calculated from data used in the NBDA (i.e. c and μ), the scaling parameter, a, and the initial number of foragers, $Y(0)$, were estimated by fitting the model with the actual culling strategy (table 3) to data. Because we did not explicitly model the arrival and departure of foragers at Bonneville Dam, we needed data on the total number of foragers through time that were not influenced by seasonal changes in abundance at the Dam. We used the maximum number of California sea lions counted on a single day during the spring at Bonneville Dam (F_{max_i}, $i = 2001, 2002, \ldots, 2014$) as representative of the total foraging population in each year [20] (results hold generally if maximum count represents greater

than 50% of the foraging population, see 'Sensitivity analysis' below and electronic supplementary material, figure S3). To calculate the likelihood of the model, we assumed that the observed maximum numbers of California sea lions each year were Poisson distributed with mean equal to the predicted number of foragers in the model during the week of 23 April for the year considered, to match the observed late April timing of the count data (i.e. $F_{max_i} \sim \text{Poisson}(Y(\text{April } 23, i))$). The likelihood for the model is then the product of the probabilities of each of the yearly observations given the number of foragers predicted by the model each spring. Maximum-likelihood estimates for the scaling parameter and the initial number of foragers were found by maximizing the likelihood using the 'optim' function in R v. 3.2.0 [21] (table 2).

(e) Culling scenarios
The epidemiological model fit the observed data well, providing a good description of the total number of foragers present at Bonneville (figure 2a). This fit allowed us to assess the impact of culling by varying both the year of implementation as well as the number of animals removed each year.
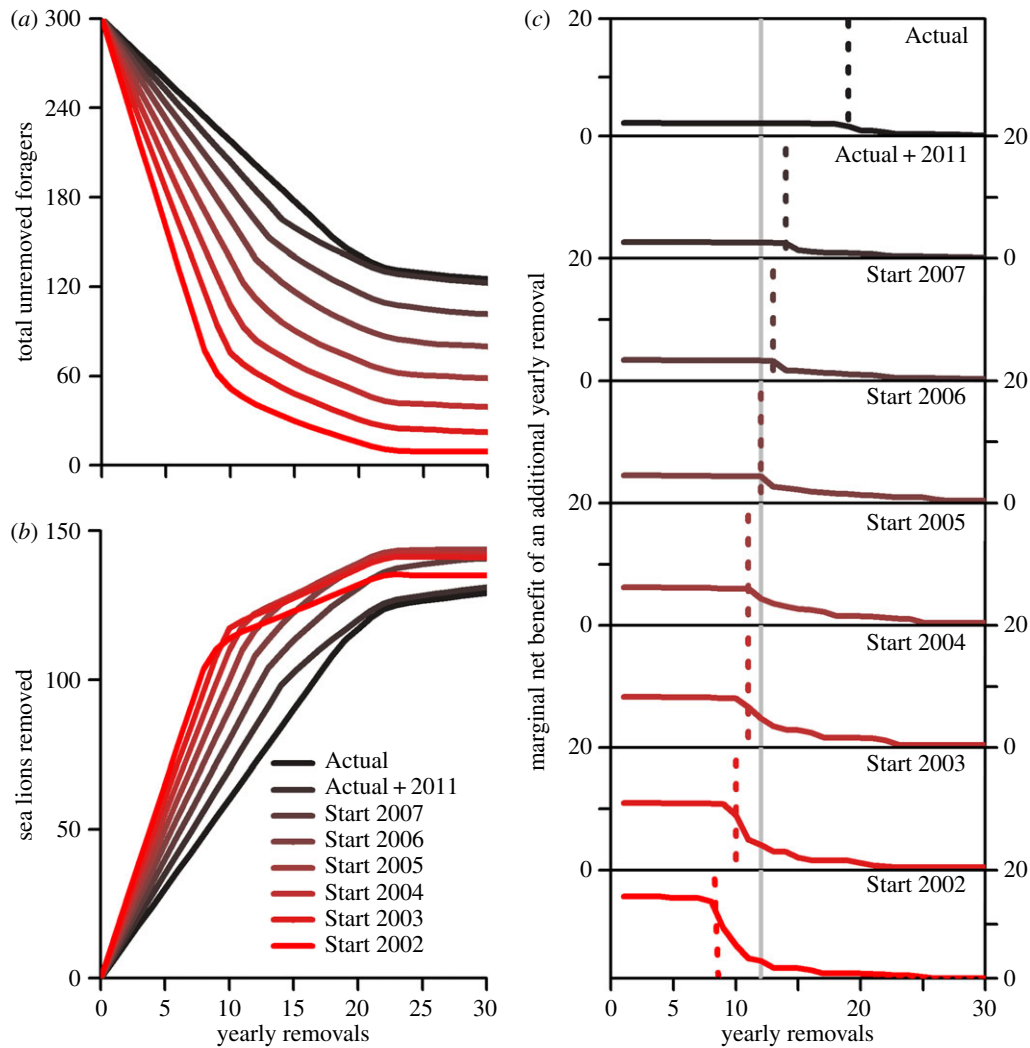
Figure 3. Target number of yearly removals. (*a*) The total number of unremoved foragers and (*b*) the number of sea lions removed across different numbers of yearly removals. The years during which removals occurred were the same as for the culling strategies in figure 2 and table 3 (ranging from Actual in black to Start 2002 in red). The number of removals in each year, however, was set equal and varied from 0 to 30. (*c*) The marginal net benefits of removing an additional sea lion a year (marginal benefit minus marginal cost). Dashed line denotes the target number of yearly removals that balances maintaining high benefits against the cost of an additional individual culled. Target strategies were chosen to minimize the derivative of the marginal net benefit, i.e. the culling level corresponding to the steepest decline in benefits when adding an additional yearly removal. The solid grey line indicates the average number of animals culled since 2008. (Online version in colour.)

(i) Year of implementation

We assessed eight different culling strategies relative to the timing of implementation (table 3). The first was the actual culling strategy employed, which began in 2008 with a court-mandated break in 2011. We then assessed the impact of this one-year break by allowing for the mean number of animals removed in 2008–2010 and 2012–2014 to be removed in 2011 (i.e. [12]; table 3). Finally, we allowed for earlier removals beginning in 2007 and progressing back to 2002, again using the mean number of animals removed yearly under the actual culling strategy (table 3). We calculated the total number of foragers across all years as well as the total number of animals culled. We also calculated the predicted total number of foragers if there had been no culling to determine the reduction in foragers achieved by each culling strategy (dashed, black line in figure 2*b*). From these, we calculated the net benefit (i.e. the reduction in foragers minus the total number culled) to determine the effect of each strategy over current management timescales (figure 2*b*).

(ii) Identifying a culling strategy that balances ethical concerns of culling

Given the ethical concerns of culling native predators [17], we set out to identify the amount of culling necessary to yield benefits without having to cull excess individuals. As a way to evaluate this, we started with the case where there was no culling. Then, for each year when culling occurred in each of the eight culling strategies (table 3), we removed one animal and calculated the benefit of removing one sea lion per year (e.g. net benefit of one removal per year minus the net benefit of no removals per year). We continued to calculate the marginal net benefit of removing an additional sea lion per year until 30 animals per year were being removed (e.g. net benefit of 30 removals per year minus the net benefit of 29 removals per year). Minimizing the derivative of marginal net benefit provided the point at which an additional yearly removal begins to yield smaller reductions in the foraging population, an ad hoc target culling strategy that balanced the need to reduce the number of foragers with the need to keep culls to a minimum (i.e. does the potential reduction in foragers warrant the removal of an additional sea lion; figure 3*c*).

3. Results

The dataset spanned 17 years (1997–2014) with 64 900 sighting records of 1 439 unique, branded individuals. There was strong support for models with social transmission of the dam-foraging behaviour compared with those without (table 1). In

addition, the start of culling appeared to coincide with a change in the learning process for dam-foraging behaviour, because models that allowed for different learning rates before and after 1 January 2008 were strongly favoured (table 1). This change in learning patterns led to a 91% decrease in the estimated social transmission effect after culling (i.e. 11.23 before and 1.05 after; table 1). Thus, in addition to reducing the absolute number of foragers socially transmitting the behaviour, culling may also alter contact patterns to reduce the relative rate of transmission.

The current culling policy has reduced the transmission rate (table 1) and has yielded positive net benefits when comparing the number of lethal removals to the reduction in overall foragers (figure 2b). Had culling taken place during the 2011 injunction (figure 2b labelled 'Actual + 2011'), it would have yielded little additional reduction in the total number of foragers (figure 2b). By contrast, beginning removal policies in years prior to 2008 caused more substantial reductions in the total number of foragers compared with the actual policy but with increasing costs in terms of the total number of animals removed (figure 2b). However, culling implemented before 2004 showed increased benefits but with decreased numbers of lethal removals relative to strategies implemented in 2004 or later, despite the longer duration of control (figure 2b). The tremendous benefits of early interventions is a well-known principle in infectious disease control [22,23], and this result was robust to model assumptions and uncertainties, including parameter uncertainty and imperfect detection of foragers at Bonneville (see electronic supplementary material, figures S3–S9). These results show that earlier initiation of culling can lead to markedly fewer overall foragers than delayed implementation.

Even though early culling consistently yielded positive benefits, it is important to consider whether current culling levels sufficiently balance reductions in foragers with the ethical costs of lethal removals. Here, increasing the number of yearly removals from a baseline of zero continued to reduce the number of foragers, to a point, but then additional culling produced rapidly diminishing returns (figure 3). We defined the target yearly removal strategies as the point of diminishing returns that balances reduction of foragers versus overall culling (figure 3a,b). Current culling levels appear to be below this target strategy for the actual policy timeframe (figure 3c). This target strategy represents a 57% increase in the total number of removals over the current strategy during this timeframe and would have only reduced overall foragers by 28% (figure 3a,b). Full implementation of the target strategy in 2002 would have resulted in a 63% reduction in foragers with only a 43% increase in lethal removals over the current strategy (figure 3a,b). Similarly, if removals were implemented in 2005 or before, target strategies would have required fewer annual removals than currently employed (figure 3c).

4. Discussion

Taken together, our results suggest that immediate implementation of culling during the period of sharp increase in sea lions foraging at the dam could have reduced the extent of behavioural transmission and recruitment to the dam. Rapid proliferation of dam-foraging behaviour through social transmission leads to more salmonid predation and ultimately requires more sea lions to be removed annually than when removal actions are delayed. We note, however, that our model does not address impacts on the endangered salmonid population. Future analyses should incorporate a consumer-resource component to determine how the lethal removal of sea lions relates to salmonid conservation. However, our current results highlight the necessity for early culling efforts from both a conservation and management perspective to prevent the spread of a detrimental behaviour and to minimize the total number of animals removed.

Our results also highlight the potential of culling activities to decrease the numbers of foragers not only through physical removal but also by slowing the rate of social learning in the population (table 1). Although the potential number of dyads increased in later years as the number of animals arriving at the mouth of the Columbia River increased, observed association strengths increased after 2008 leading to higher contact rates after culling was implemented (see the electronic supplementary material). Thus, the reduction in social transmission revealed by our analysis appears not to be due to an overall decrease in association strengths. Instead, we postulate that culling has altered the nature of the associations between foragers and the rest of the population. The structure of the interaction matrix may have become more assortative with increased clustering among foragers and non-foragers. These changes in network heterogeneity could serve to reduce the spread of the behaviour to non-foragers [24], particularly if Bonneville foragers grow more connected to each other while simultaneously disconnected from non-Bonneville foragers. However, follow-up analyses are needed to determine how culling interacts with other factors such as density to drive changes in network structure and transmission in the population. The consequences of culling on transmission can be complicated; in an infamous example, localized badger culling was actually found to increase tuberculosis transmission [25], putatively through social disruption which created increased mixing in the populations [26].

Although the conclusion that earlier implementation of culling leads to fewer removals is based on a simple model framework, this management strategy is robust to model assumptions and uncertainties. First, imperfect detection of sea lion foragers at Bonneville Dam is likely to lead to underestimates in the number of removals necessary to curb the spread of the behaviour. However, target strategies changed little as long as more than half of foragers were observed. Below this threshold, the qualitative pattern still held generally, but the target number of yearly removals increased to compensate for the greater number of foragers (electronic supplementary material, figure S3). Similarly, when assessing the impact of parameter uncertainty, we found that parameter combinations that generated greater numbers of foragers resulted in higher target numbers of yearly removals (electronic supplementary material, figures S4–S10). This result highlights the importance of developing accurate estimates of the total number of foragers at Bonneville Dam to minimize culling (electronic supplementary material, figures S3 and S10).

Our results also have broader policy implications for the region. Recently, Steller sea lions (Eumetopias jubatus), a larger competitor of California sea lions, have begun to forage at Bonneville Dam. Also, California sea lions are increasing their presence at other dams, such as Willamette Falls, to forage on salmonids in the lower Columbia River. For both species, we suggest that when socially transmitted

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8

foraging is expected, a shift in policy from delayed culling after assessment to early culling, with a hiatus if needed to assess efficacy, will ultimately result in fewer animals being culled. Our goal for this Bonneville Dam case study is to illuminate what could happen when culling is implemented in this and other systems rather than present a post hoc conclusion of what should have been done. In emergent scenarios, managers must make policy decisions based on the available data at the time, but these results can provide general guidance on management strategies that can be re-evaluated as further data becomes available. Culling protected predators to recover threatened and endangered salmonids stirs public emotions while raising legal and political concerns. Early application of lethal removal, while potentially controversial, is the most effective of the culling strategies we evaluated to control socially mediated transmission.

5. Conclusion

New techniques are required to facilitate human–wildlife coexistence in a world where wildlife and human interactions are increasing. Models from disease ecology offer a promising tool to understand behavioural transmission and can inform management policy for controlling human–wildlife conflicts. We developed a novel procedure for translating the output of a social network-based diffusion analysis into an epidemiological model. This novel synthesis provides a flexible framework that can be applied across a diversity of animal and human systems in order to test alternative management strategies in the containment of undesirable behaviours. We show that

epidemiological models can reduce the spread of unwanted behaviours in wildlife because they can help predict the risk factors for potential outbreaks, estimate the future prevalence of infection/behaviour in the population, and test the efficacy of interventions such as culling (i.e. lethal removal of specific individuals). Social transmission rapidly spreads behaviours through populations like an infectious disease. And, like an infectious disease, socially transmitted behaviours require early action to reduce their spread.

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9