A historical perspective on the effects of trapping and controlling the muskrat (Ondatra zibethicus) in the Netherlands

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Abstract

BACKGROUND: The muskrat is considered to be a pest species in the Netherlands, and a year-round control programme is in effect. We aimed to evaluate the effectiveness of this programme using historical data on catch and effort collected at a provincial scale.

RESULTS: The development of the catch differed between provinces, depending on the year of colonisation by muskrat and the investment of effort (measured as field hours). The catch did not peak in the same year for the various provinces, and provinces that were colonised earlier in time took longer to attain the peak catch. Trapping resulted in declining populations, but only after a certain threshold of annual effort in trapping had been surpassed. On average, populations were observed to decline when the annual effort exceeded 1.4 field hours per km of waterway for several successive years. Having reached a phase of greater control, control organisations tended to reduce effort.

CONCLUSION: We conclude that control measures can make muskrat populations decline, provided that the effort is commensurate with the population size. Our study emphasises that experimentation is needed to confirm the causality of the findings, to establish the relation with damage or safety risk and to derive an optimal control strategy.

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Supporting information may be found in the online version of this article.

Keywords: historical data; muskrat; pest species; population dynamics; trapping intensity

1 INTRODUCTION

Ecology has a long history of investigating harvest, driven mainly by its importance to commercial fisheries.1 The true population of any harvested species is rarely known. It must be inferred from basic knowledge of population dynamics, the natural history of the harvested species and records of the catch and effort. In general, populations increase when the harvest effort is low and decline when effort is too high.2 The absolute number of animals captured in the long term is highest at intermediate levels of trapping effort,3 namely the point at which the absolute growth rate of the population is highest. This is a desirable aim for a fishery (‘maximum sustained yield’, or MSY), and over the past 70 years much effort has been devoted to determining the level of fishing that will generate MSY.

However, there are other situations in which MSY is not the goal,4,5 or in which other desirable outcomes (conserving biodiversity, reducing bycatch) conflict with MSY. In the case of slowly growing organisms, the long-term economic gain obtained from overharvesting and investing the proceeds can exceed that obtained from sustainable harvest. Clearly undesirable when applied to whales or old-growth forests, overharvesting to reduce populations and thus lowering expenditures in the long run can be desirable when applied to pest and invasive species.

The muskrat (Ondatra zibethicus L.) is native to North America and is considered an exotic species in Europe. It was first recorded in the Netherlands in 1941, evidently having spread from central Europe where it had been introduced as a furbearer. Basic reviews of its natural history and ecology are given by Perry,6 Boutin and Birkenholz7 and Heidecke and Seide.8 The history and result of muskrat introductions in Europe, as well as their dispersal rates and the impact of muskrat on biota and their habitats in north-western Europe, are discussed in Danell.9 Nowadays, muskrats are present...
everywhere in the lowlands of north-western Europe, and in some regions a control programme is in place. With how much conviction and by what strategy the control is implemented, however, vary greatly by region.

Muskrats have high reproductive potential. A pair produces on average three litters of approximately six young. Mortality is high, especially in fall and winter. Population trajectories show great seasonal fluctuations and there is also evidence for regular annual cycles on the North American continent. Muskrat populations are sensitive to extreme winter coldness and extreme variations in water levels (droughts and floods). Other factors influencing year-to-year variation in population levels include disease, predation and food abundance. In the absence of harvest by man, the densities may become high, with maxima varying by orders of magnitude between habitat and years. Although muskrats are generally site faithful, a varying proportion of young muskrats disperse from their natal site to settle at distances of several hundreds of metres or even multiple kilometres. Natal muskrats disperse from their natal site to settle at distances of several hundreds of metres or even multiple kilometres. Natal muskrats disperse from their natal site to settle at distances of several hundreds of metres or even multiple kilometres. Natal muskrats disperse from their natal site to settle at distances of several hundreds of metres or even multiple kilometres. Natal muskrats disperse from their natal site to settle at distances of several hundreds of metres or even multiple kilometres. Natal muskrats disperse from their natal site to settle at distances of several hundreds of metres or even multiple kilometres. Natal muskrats disperse from their natal site to settle at distances of several hundreds of metres or even multiple kilometres. Natal muskrats disperse from their natal site to settle at distances of several hundreds of metres or even multiple kilometres. 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The relation between relative change in catch and effort was assessed using a linear mixed-effects model with the effort predictor in addition to the random intercept per province; (3) a model with effort as predictor, but with both random intercept and random slope per province; (4) a model with both effort and winter coldness in addition to the random intercept per province. Models were assessed using their AICc values. All analyses were performed in R using the package lme4.43

### 3 RESULTS

#### 3.1 Initial invasion and growth of the control effort

The number of bounty hunters reached its maximum of 300 individuals in 1983, and declined to zero by 1992 as the national and provincial bounty systems were abolished (Fig. 1). Many former bounty hunters were later employed in the professional service operated by the State and the water authorities. In our interviews, bounty hunters reported that they did not change their trapping strategies under their new labour conditions. Catch and effort remained low until 1961, after which both increased rapidly from hundreds to thousands, and tens of thousands after 1966. At its peak in 1991, more than 430 000 catches were made by 431 trappers, a number that further increased to over 450 in 2004. The catch declined steeply after 2004, while effort remained approximately constant.

#### 3.2 Differences in developments between provinces

The southern provinces were colonised first (Fig. 2). After initial invasion, muskrat populations expanded rapidly in the different provinces, and the control status went through successive phases (classified in Table 1). However, the progression showed great variation between provinces. For example, the province Noord-Brabant reached its peak in 1978, but Overijssel and Noord-Holland did not until 2005. The structure that became apparent in the data was a relation between time of invasion and time to reach peak catch per province: provinces that were invaded earlier took longer to reach their peak catch (Fig. 3). The peak catch at an average level of 2.1 n km⁻¹ year⁻¹ (SD = 0.98, n = 12), but was higher in Zuid-Holland and Utrecht and lower in Noord-Holland, Overijssel, Noord-Brabant and Drente (Table 2).

There were no significant correlations between the year of invasion, peak year or the year in which sufficient control was attained. Neither was there any apparent spatial pattern in timing of the peak and the timing of attaining sufficient control that suggested the operation of some common external factor. For example, the province Friesland showed a strong decline in catch after 1994, while in the neighbouring province of Groningen the catch fluctuated around a high level until 2012 (see the supporting information). At neither the provincial nor the national level was there any sign of a dominant frequency in the periodograms or cyclicity in the autocorrelation that pointed to the presence of a regular population cycle.

Only four of the provinces attained the practical management objective of ‘fully under control’ (<0.15 n km⁻¹ year⁻¹) by 2013. The duration between the peak year and a situation of ‘sufficient control’ (0.15 < n km⁻¹ year⁻¹ < 0.35) was on average 16.9 years (SD = 10, n = 9), and also differed greatly between provinces. Fluctuations in the catch were prominent in some provinces but not in others (see the supporting information for more details). In all provinces, the control phases following the peak year were characterised by higher average annual effort (Table 2) than before the peak. The control organisations tended to invest less effort with a declining catch (fixed-effects part: effort = 0.63 + 0.12 catch, -0.20 catch²).

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**Table 1.** Practically defined ‘phases of control’ for muskrat management in the Netherlands

<table>
<thead>
<tr>
<th>Situation</th>
<th>Muskrat trapped (n km⁻¹ year⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Before the peak</td>
<td>Pre-invasion: 0</td>
</tr>
<tr>
<td></td>
<td>Invasion to peak: &gt;0</td>
</tr>
<tr>
<td></td>
<td>No control: &gt;0.35</td>
</tr>
<tr>
<td></td>
<td>Sufficient control: 0.15–0.35</td>
</tr>
<tr>
<td></td>
<td>Full control: &lt;0.15</td>
</tr>
<tr>
<td>After the peak</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
</tbody>
</table>

For each province, the amount of muskrat habitat was expressed as kilometres of waterway, estimated for each province as the sum of 1 the length of linear waterways that carry water during more than 3 months of the year, 2 double the length of linear waterways that are wider than 6 m, and that cannot be crossed on foot (deeper than 1 m), and 3 the circumference of lakes and ponds.

The data were derived using Geographical Information System (GIS) maps for each province.40 Winter coldness in each year was calculated by subtracting the catch in year i from that in the following year (i + 1) and then dividing by the catch in year i. The relation between relative change in catch and effort was evaluated in a series of linear mixed-effect models, considering winter coldness as a possible covariate and province as a random factor. In total, we evaluated four models: (1) a null model, with only province as a random intercept; (2) a model with effort as predictor in addition to the random intercept per province; (3) a model with effort as predictor, but with both random intercept and random slope per province; (4) a model with both effort and winter coldness in addition to the random intercept per province. Models were assessed using their AICc values. All analyses were performed in R using the package lme4.43
3.3 Catch and effort

Trapping effort significantly affected the relative change in catch (Fig. 4). The model involving only effort as a predictor and province as a random effect was best supported by the data (Table 3), with a marginal $R^2$ of 0.29 and a conditional $R^2$ of 0.36. Also, the residuals for this model appeared to be random and normally distributed. Overall, the relative change in catch decreased with $-0.295$ (95% CI: $-0.34$ to $-0.24$) per hour increase in effort ($P < 0.000$, with a marginal $R^2$ of 0.29 and a conditional $R^2$ of 0.36). On average, the catch was observed to decline when the annual effort exceeded $1.4$ h km$^{-1}$ year$^{-1}$. The $y$-intercept (i.e. the relative change at zero trapping effort) had a value of 0.42 (95% CI: 0.33 – 0.51), indicating the net population change without trapping. Three provinces had intercepts that were significantly different from this overall mean value ($P < 0.05$): Zeeland and Noord-Holland had lower intercepts ($-0.13$ and $-0.12$ respectively), while the intercept for Utrecht was higher (+0.10).

4 DISCUSSION

4.1 Trapping affects the population size

Our main result is that the relative change in muskrat catch is significantly reduced with increased trapping effort, strongly suggesting that trapping affects population size. Prior to the peak year, all the provinces showed increasing catches, in some cases lasting decades, in spite of generally increasing effort. Our interpretation is that, under these circumstances, field time limited...
the catch, and effort was not intensive enough to cause a decline. After the peak, catch was limited by muskrat population size, and extra effort further depressed the population, reducing the catch in the following year. Currently, from approximately 2004 to 2013, there was a considerable decline, and low catches in spite of high trapping effort generally point to low population sizes in the Netherlands. Experience from abroad and from within the country suggests that further decline is possible. In Friesland, the catch diminished from 2.4 to 0.1 n km\(^{-1}\) year\(^{-1}\), which is less than half the Dutch average in 2013. In Flanders (Belgium), the catch also declined almost certainly owing to trapping, from well over 42,000 in 2001 (>1.9 n km\(^{-1}\) year\(^{-1}\), even without including data from catches by other parties) to 730 in 2013 (0.03 n km\(^{-1}\) year\(^{-1}\); Van der Weeën M, Vlaamse Milieumaatschappij, private communication). In the United Kingdom, an entire feral muskrat population was eradicated in a campaign in the 1930s, after killing at least 4388 muskrats.\(^4\)

The data have a few shortcomings that should be recognised. The level of effort inferred from the data is not always exact, given changing interpretations of the concept of ‘field time’, and the trapping result (catch) is prone to reporting error. These inaccuracies are, however, assumed to be of minor importance relative to the large differences reported in space and time for both variables. From our interviews it appears that the dataset as a whole and our conclusions are sufficiently robust with respect to these sources of error.

### 4.2 Differences between provinces and other sources of variation

The slope of the relation between relative catch and effort did not vary between the provinces. In three provinces, different levels of effort were required to maintain a stable population.
The relation between effort (x-axis, in field hours per km of waterway per year) and the proportional change in the number of muskrats caught. Each point represents a province–year combination (n = 422). Datapoints before (-) and after (+) the peak in a given province are indicated separately. The line $y = -0.295x + 0.42$ ($P < 0.000$, marginal $R^2 = 0.36$) represents the fixed part of the linear mixed-effects model (i.e. not taking the random intercept per province into account), with the grey area showing the 95% confidence limits.

Table 3. Ranking of models for the relative change in catch that were evaluated according to AICc values

<table>
<thead>
<tr>
<th>Modela</th>
<th>$K^b$</th>
<th>AICc$^c$</th>
<th>$\Delta$AICc$^d$</th>
<th>AICcWte$^e$</th>
</tr>
</thead>
<tbody>
<tr>
<td>effort</td>
<td>4</td>
<td>116.8</td>
<td>0.0</td>
<td>0.82</td>
</tr>
<tr>
<td>effort-rnds</td>
<td>6</td>
<td>119.9</td>
<td>3.0</td>
<td>0.18</td>
</tr>
<tr>
<td>effort + cold</td>
<td>5</td>
<td>133.3</td>
<td>16.5</td>
<td>0.00</td>
</tr>
<tr>
<td>null</td>
<td>3</td>
<td>1157.7</td>
<td>1040.9</td>
<td>0.00</td>
</tr>
</tbody>
</table>

a The model set comprised a null model with only province as a random intercept (null), a model with effort as predictor in addition to the random effect of province (effort), a model with effort as predictor but with both random intercept and random slope per province (effort-rnds), and a model with both effort and winter coldness in addition to the random effect of province (effort + cold).

b $K$ = number of free parameters in the model.

c AICc = Akaike information criterion.

d $\Delta$AICc = difference between model AICc and AICc value of the best model.

e AICcWt = AICc weights.

Further variation may be due to density-dependent factors. For example, both the ease with which animals can be captured (i.e. catch per unit effort) and the population growth rate likely vary with population density, perhaps non-linearly. The exact nature of the relationship is highly relevant from an economic point of view and deserves further elucidation. It seems to be progressively cheaper to maintain control at lower population density. This is corroborated by our finding that, in practice, lower investments were made as each new phase of control was attained. Knowledge of the relationship between costs and population size is a prerequisite for the proper calculation of an optimal control strategy. This will require experimentation.

Our 12 time series showed that the catch changed markedly when responsibility for the control programme passed from one organisation to another. Such delegation of responsibility often involved a change in management procedures. We identified 24 such management changes, three of which apparently led to a situation of diminished control, while in ten of these cases there were clear indications that the change in management was directly followed by a situation of greater control. There was no change following 11 of these cases. The control status generally increased when the water authorities assumed responsibility, but this was in all cases confounded with ‘time since invasion’, and often involved greater trapping effort, making it impossible to unravel the relative importance of the quality of management and quantity of trapping effort. We noted great variation in skill and motivation between individual muskrat trappers, and feel that such differences may be partially attributable to details of the organisation and its management, such as the extent to which individual trappers were supported to arrive at a coherent control strategy.

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strategy. Further analysis of such differences in the quality of management and how these may have played a role in the Dutch muskrat control programme are beyond the scope of this paper.

Why did it take the provinces invaded first longer to reach peak muskrat density? This may to a certain extent be explained by the idea that the control organisations were able to slow down the invasion in the originally invaded provinces. Provinces invaded later had muskrats coming from multiple directions and in higher quantities, necessitating a quicker response in the investments of effort. They may also have learned from developments elsewhere in the country.

4.3 Possible confounding factors
The changes we have documented here have taken place over recent decades, but they are not the only changes that are potentially important to the population dynamics of muskrats. Although there are no indications of a general change in food availability, or the emergence of disease, the predator community has changed over the years studied. Foxes (Vulpes v. L.) have invaded the low-lying provinces.46 and rapscals have generally recovered from low numbers in the 1960s.47 White-tailed sea eagles (Haliaeetus albicilla L.) have settled in several nature areas.48,49 American mink (Neovison vison S.) are present, as they regularly escape from fur farms, though no viable population has established.50 Hence, it is in principle possible that this factor could explain the overall decline of the muskrat in the Netherlands over recent decades. However, some areas in the country still have high numbers of catches (e.g. the province of Groningen) or indications of high population size (the nature reserve Oostvaardersplassen), even in the presence of all or most of these predators, and Bos and Ydenberg3 argue that the role of predation in the population regulation of muskrat in the Netherlands is small in comparison with the effects of trapping. This is in contrast to findings in Poland58 (see below).

It seems that the intense control measures are most likely responsible for the population decline.

4.4 The value of hunting bag statistics and the need for experimentation
Catch statistics have often been used to make inferences about population development. Long-term time series from the North American continent provide evidence for regular cycles in the populations of muskrat, differing regionally in cycle length and amplitude.15–18 There, hunting or trapping may be intense on a local scale, but current management regimes prevent overharvesting. In Poland, an analysis of the decline in the hunting bags of muskrat identified American mink predation as one of the most important factors affecting muskrat numbers.48,51 The catch and effort data presented in this paper were previously used by Hengeveld51 and Matis et al.52,53 to describe the processes of biological invasion, and to explain models estimating population parameters such as birth and death rates. It would be extremely worthwhile to elaborate their quantitative population models. Belgian and British46 data support our findings that populations can strongly decline owing to trapping, while an analysis of the German catch data has led to doubt about the effectiveness of Muskrat control in that country.52,34,35 We recommend assembling the data for these countries to help assess the costs of trapping at different levels of intensity and the differences between strategies and landscapes.

Our data are consistent with the hypothesis that the control measures affect population density, but the findings are not detailed enough as yet to guide policy. As stressed in the Introduction, the Dutch control programmes originally arose owing to concern for the integrity of dykes. Hence, for policy purposes it is essential to establish the relationship between muskrat population density on the one hand and economical damage or safety risk on the other. It may also be helpful to quantify the publicly acceptable level of damage per region of interest. These gaps in knowledge hamper proper policy-making at the moment. As formulated before,3 the benefits that can be derived from guiding expensive control programmes like these with information derived from well-designed field experiments are likely to outweigh the costs of such research.

It is common to encounter situations with overharvesting in fisheries, or successful population reduction in pest management, but for muskrats in the Netherlands (and possibly Flanders) we have the unique situation that trapping effort is known and can be manipulated in the future. Such experimentation would lead to better insight into the causality of relationships and more precise models of optimal harvesting.

5 CONCLUSION
Control measures have an effect on muskrat populations, provided that the levels of investment are in adequate proportion to population size. The study emphasises the need for experimentation to confirm the causality of the findings, to establish the relation with damage or safety risk and to derive an optimal control strategy.

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SUPPORTING INFORMATION
Supporting information may be found in the online version of this article.

REFERENCES