Research Article

Received: 16 October 2015 Revised: 13 February 2016 Accepted article published: 4 March 2016 Published online in Wiley Online Library:

(wileyonlinelibrary.com) DOI 10.1002/ps.4270

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

E Emiel van Loon,[a] Daan Bos,[b,c*] Caspara J van Hellenberg Hubar[d] and Ron C Ydenberg[d,e]

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.

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 Birkenholz[7] 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

* *Correspondence to: D Bos, Altenburg & Wymenga ecological consultants. P.O. Box 32, 9269 ZR Veenwouden, The Netherlands. E-mail: d.bos@altwym.nl*

a *Computational Geo-Ecology Group, University of Amsterdam, Amsterdam, The Netherlands*

b *Altenburg & Wymenga Ecological Consultants, Veenwouden, The Netherlands*

c *Community and Conservation Ecology – Centre for Ecological and Evolutionary Studies, University of Groningen, Groningen, The Netherlands*

d *Resource Ecology Group, Wageningen University, Wageningen, The Netherlands*

e *Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada*

everywhere in the lowlands of north-western Europe,[10,11] 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.[12] Mortality is high, especially in fall and winter. Population trajectories show great seasonal fluctuations,[13,14] and there is also evidence for regular annual cycles on the North American continent.[15−18] Muskrat populations are sensitive to extreme winter coldness and extreme variations in water levels (droughts and floods[13,19]). 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,[9,13,14] 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.[20−23] Natality, mortality and dispersal are all affected by population density and show strong seasonal variation.[13,14,24] However, these mechanisms are not necessarily straightforward: in some years, muskrats appear to tolerate much higher densities than in other years.[19]

Muskrats are semi-aquatic. The habitat available in the Netherlands is of high quality, as it offers a vast network of waterways, an ideal vegetation, a mild climate and carefully controlled water levels. Consequently, their populations can grow very quickly. Muskrats readily burrow into river banks, dykes and dams, so threatening the integrity of these structures, which in the Netherlands and other low-lying parts of north-western Europe are essential for public safety.

The arrival of the muskrat in the Netherlands (1941) was anticipated for more than a decade. Laws banning the ownership or transportation of muskrats were passed and control programmes organised, so that measures could begin immediately the first animals were recorded. The history of the control programme is described by Barends,[25] van Koersveld[26] and Doude van Troostwijk.[27] Run initially by the national Plant Disease Service, detailed records were kept from the very beginning on the amount of trapping effort (man hours) and the numbers of animals killed (control programmes utilised lethal traps only; no poison was used; details are described by Plug[28] and Barends[29]). Responsibility for the programme was later (1986) passed to the provinces, which in turn quickly passed its administration to the Dutch water authorities. These have divided the Netherlands into eight regions, each with its own muskrat control organisation.

The impetus for these control measures was to help maintain the physical integrity of the extensive system of dykes in the Netherlands. It is assumed that control measures lead to lower population size and less damage to the dyke system. Generally, population models predict that harvested populations have lower average densities than unharvested ones.[30] However, for the muskrat, no rigorous field studies have been conducted. Errington[19] studied fur refuges in the American state Iowa, and found that muskrat density within refuges is generally higher than outside. Parker and Maxwell[31] report on an experiment with controlled harvesting in different seasons and show that combined harvesting in spring and autumn leads to stronger effects on the muskrat population than harvesting in either autumn or spring alone. There are doubts about the effectiveness of muskrat control in Germany.[32]

In spite of this lack of evidence, many authors have expressed the view that the dangers of muskrat in the Netherlands are so obvious that the need for intensive trapping requires no discussion.[25−27,33−35] However, the control measures are expensive, large numbers of animals are killed and other species are killed as well, directly or indirectly, as side effects of the control measures. Hence, there is ongoing public debate within the Netherlands on the desirability and effectiveness of these control measures.[36] The American muskrat researcher Paul Errington introduced to ecology the notion of a 'doomed surplus',[37] which states that a (large) proportion of each year's production of young are doomed: those that predators do not catch die of starvation. Hence, it is possible that trapping effort would have no substantial population effects, because the animals are doomed in any case. Further, there may be alternatives to trapping that could mitigate or prevent damage. Finally, one can imagine scenarios in which an invasive population, such as that of the muskrat, would decline over time regardless of trapping effort, owing to changes in the predator community,[38] vegetation (cf. Danell[39]) or disease.[37] For all these reasons, a careful analysis of the control programme's effectiveness is warranted.

The main aim of our analysis was a quantitative evaluation of how effective the control programme has been at reducing or reversing muskrat population growth. To achieve this, we have assembled data on the history of muskrat catch and control in the Netherlands from 1941 to 2013. The priority for and hence the budget allocated to control has varied over the years and between the various authorities, creating spatiotemporal variation in trapping effort, which allows for an evaluation of the relation between effort and catch. Our primary concern was therefore to establish whether the (relative) change in catches was dependent on effort. Secondary concerns related to the extent to which variation in catch could be attributed to differences among provinces, fluctuations in winter coldness or a regular population cycle, and whether the effort required to maintain control was lower that that required to gain control.

2 METHODS

2.1 Data collection

Data were assembled from annual reports published by the muskrat control organisations in the Netherlands. These reports detail the management organisation, the numbers of muskrats trapped and the effort (field hours) required to capture them. Data were available for the entire time series (1941–2013) for almost the entire country. Owing to the ongoing changes in organisation, the structure and detail available in the annual reports differed somewhat over the years. To help interpret these data, we interviewed past and present staff members, including trappers as well as the first coordinator of the national control programme. We aggregated data province by province, and used the 12 time series to investigate the effectiveness of the control programmes.

The data were incomplete and of variable quality. Some years had missing values for effort, because it could not be reliably estimated. For other years, assumptions had to be made to express effort in identical units. Prior to 1988, for example, field time was sometimes reported as the number of field staff. We converted this to field hours based on known values of field hours per staff member in other years within the same timeframe. Trapping was done both by professional trappers, enlisted by the organisations in charge of muskrat control, and by bounty hunters. The latter did not report their effort, so we assumed that the time required to capture an individual muskrat was on average equal to that of professional trappers. A detailed specification of assumptions is given in the supporting information.

Table 1. Practically defined 'phases of control' for muskrat management in the Netherlands

Situation		Muskrat trapped (n km^{-1} $year^{-1}$)
Before the peak	Pre-invasion	0
	Invasion to peak	>0
After the peak	No control	>0.35
	Sufficient control	0.15–0.35
	Full control	<0.15

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 given as the Hellman figure, the positive sum of all daily mean temperatures below 0 °C between 1 November and 31 March (http://www.knmi.nl).

2.2 Analyses

Trapping effort was expressed as field time per kilometre waterway per year (h km^{-1} $year^{-1}$), and catch as the number of muskrats caught per kilometre waterway per year (n km^{-1} $year^{-1}$). For each province, the time series was divided into five 'control phases', based on a classification developed by the Association of Regional Water Authorities (Table 1). This classification identifies two phases prior to the 'peak year' (defined as the year with the highest catch) and three post-peak phases, based on the catch (n km^{-1} $year^{-1}$). The phase preceding any catch at all is termed 'pre-invasion'. After 'invasion' the catch in all cases rose, eventually reaching a peak that in 11 of 12 provinces exceeded 1.0 n km^{-1} $year^{-1}$. Years with catch exceeding 0.35 n km^{-1} $year^{-1}$ were designated 'not under control', those with catch between 0.15 and 0.35 were deemed 'sufficiently under control' and those with catch less than 0.15 n km^{-1} $year^{-1}$ were deemed 'fully under control'. The practical management objective was to reach the latter situation.

The catch and effort were summarised per province and per phase of control. Differences between provinces in the average annual effort in the various control phases after the peak were assessed using a linear mixed-effects model with the effort (response) as a function of catch (predictor), with province as a random effect. Effort was considered as a response variable in this case because it is a management decision to invest time in response to changing catches. Subsequently, possible relations between the duration of different phases of control were investigated. The degree of cyclicity in the time series was assessed using visual inspection of periodograms, and autocorrelation was evaluated via correlograms.[41]

The relative change in catch between successive years 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[42] 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 catch peaked 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 Drenthe (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,

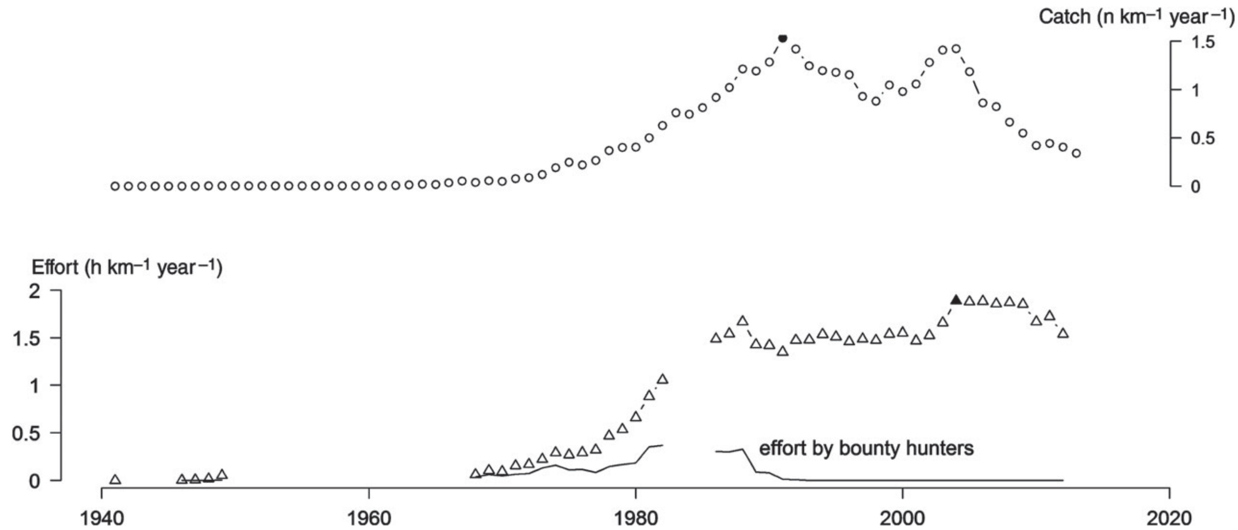

Figure 1. The number of muskrats trapped (dots, catches per km of waterway per year) and the effort (field hours per km per year) invested in the Netherlands as a whole, 1941–2013. Filled dots and triangles indicate the year with maximum values for the catch or the effort. Totals for each province are presented in the supporting information.

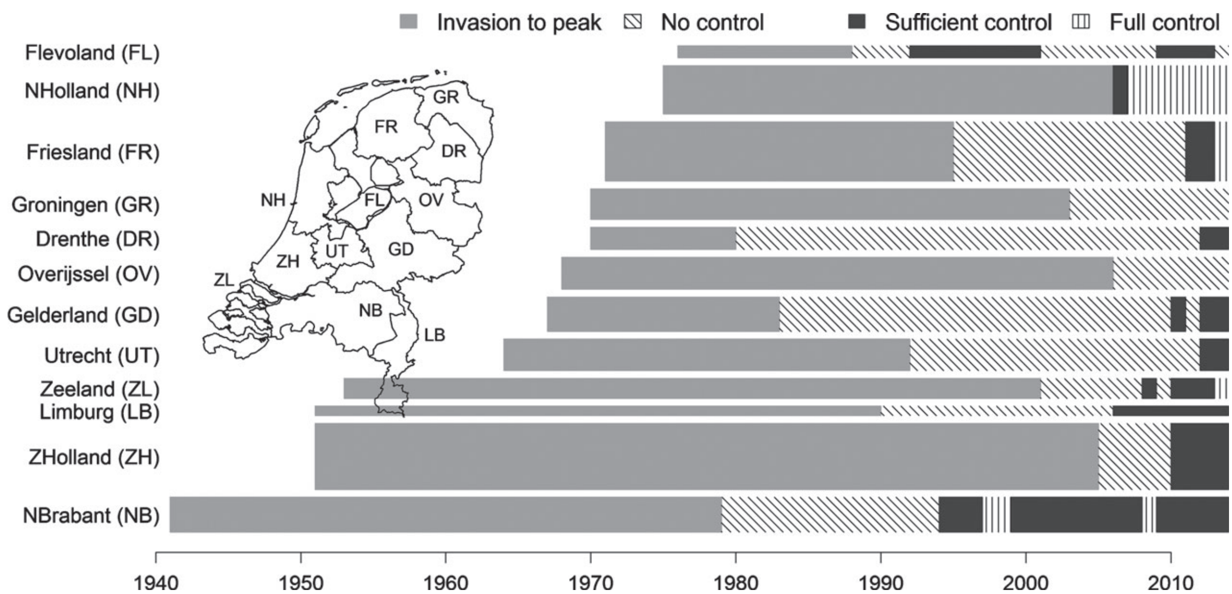

Figure 2. Timeline indicating the years when successive phases of muskrat control (defined in Table 1) were attained in each of the twelve provinces of the Netherlands. The height of each bar is proportional to the length of waterway in each province. Timelines begin with the year when muskrats were first registered ('invasion') in a province. The inset provides a map with the geographical boundaries per province.

$P < 0.0001$, conditional R^2 of 0.69; with random and normally distributed residuals).

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

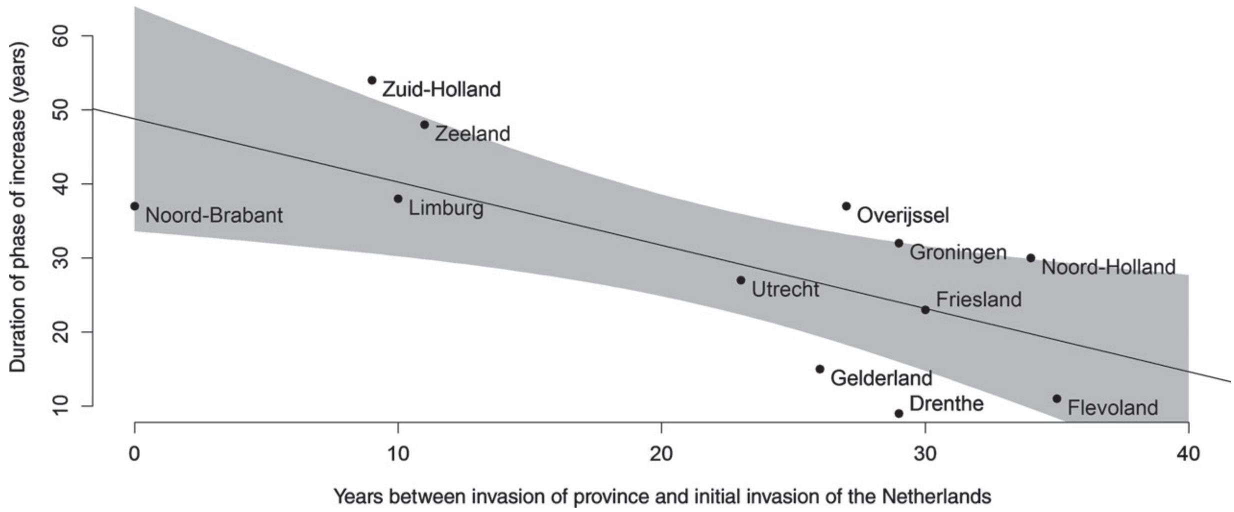

Figure 3. The relationship between the duration of the phase of increase ('invasion to peak' phase; years) and the numbers of years that had passed after the initial invasion of the Netherlands and the invasion of the province. The line $y = -0.85x + 48.8$ ($P = 0.01$, $R^2_{adj} = 0.43$) represents the linear regression model fitted. The grey area refers to the 95% confidence limits of this model.

Table 2. Average annual effort (field hours per km per year) for the Netherlands and per province (acronym in brackets) for the successive phases of control after invasion by muskrat, and the peak catch (number per km per year). No entry in a cell indicates that a level of control was not attained. The inset in Fig. 2 provides a map with province boundaries

	Effort per control phase (h km^{-1} year^{-1})				
Province	Invasion to peak	No control	Sufficient control	Full control	Peak catch (n km^{-1} year^{-1})
The Netherlands	**0.6**	**1.6**			**1.5**
Drenthe (DR)	0.5	1.4	1.2		1.1
Flevoland (FL)[a]	1.1	1.7	1.5		2.0
Friesland (FR)	0.7	1.4	1.4	1.1	2.5
Gelderland (GD)	0.9	2.1	1.8		2.2
Groningen (GR)	1.4	2.0			2.3
Limburg (LB)	1.0	1.7	1.6		2.1
Noord-Brabant (NB)	0.7	2.0	1.7	1.7	1.7
Noord-Holland (NH)	0.5		1.2	1.0	0.2
Overijssel (OV)	1.4	1.9			1.4
Utrecht (UT)	0.7	2.3	1.8		4.2
Zeeland (ZL)	1.0	1.7	1.6	1.3	2.5
Zuid-Holland (ZH)	0.9	2.3	1.9		3.1

[a] Flevoland was established as a new province on land reclaimed between 1942 and 1968.

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 suggest 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.[44]

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

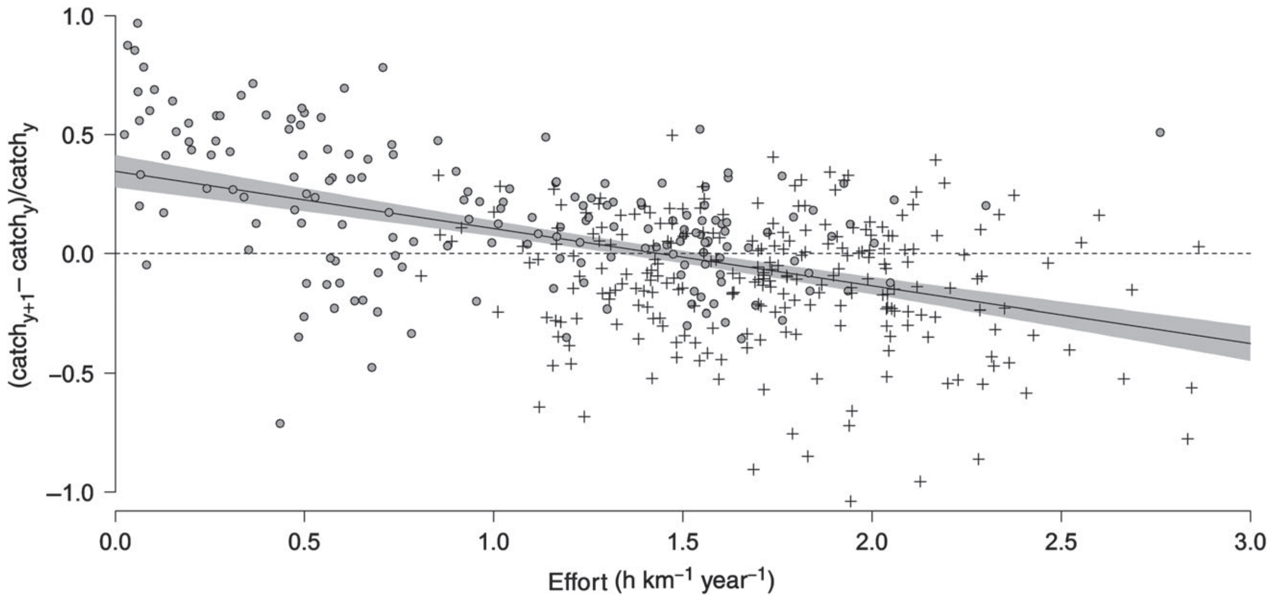

Figure 4. The relation between effort (*x*-axis, in field hours per km of waterway per year) and the proportional change in the number of muskrats caught. Each point represents a province–year combination ($n = 422$). Datapoints before (○) and after (+) the peak in a given province are indicated separately. 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

Model[a]	*K*[b]	AICc[c]	ΔAICc[d]	AICcWt[e]
effort	4	116.8	0.0	0.82
effort-rndslp	6	119.9	3.0	0.18
effort + cold	5	133.3	16.5	0.00
null	3	1157.7	1040.9	0.00

[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-rndslp) 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] ΔAICc = difference between model AICc and AICc value of the best model.
[e] AICcWt = AICc weights.

size or to make populations decline, in comparison with the other nine provinces. More effort was required in Utrecht and less in Zeeland and Noord-Holland. In addition, we have observed variation between provinces in the time of (initial) colonisation, the year of peak muskrat numbers and the year and size of peak catches.

The differences between provinces can be attributed to variation over time in the presence and population density of muskrats in neighbouring provinces and countries. We infer that this, in combination with geography, has greatly affected immigration rates over time. The province of Noord-Brabant was the first to be colonised by the muskrat,[25] because it was close to sources on the other side of the border with Belgium, where the muskrat had appeared earlier. The northern part of the province of Noord-Holland, on the other hand, has always been quite isolated and was colonised much later. Provinces also differed in habitat suitability for the muskrat. Some provinces had much more suitable habitat or greater quantities. Utrecht and Zuid-Holland had the greatest density of waterways. In addition, a waterway in the low-lying peat meadows or peat moors of Utrecht and Zuid-Holland may have supported a greater density of muskrats than other landscapes, consistent with previous findings by Bos *et al.*[45]

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.[4] 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. 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 vulpes* L.) have invaded the low-lying provinces,[46] and raptors 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 Ydenberg[3] 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 Poland[38] (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.[38] The catch and effort data presented in this paper were previously used by Hengeveld[51] 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 British[44] 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.[32,54,55] 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.

ACKNOWLEDGEMENTS

We greatly appreciate the input from two anonymous reviewers, Fred Barends, Jasja Dekker, Sjef Keustermans, Bob Litjens, Dolf Moerkens and Leo Wijlaars.

SUPPORTING INFORMATION

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

REFERENCES

1 Haddon M, *Modelling and Quantitative Methods in Fisheries*, 2nd edition. CRC Press, Boca Raton, FL (2011).
2 Begon M, Harper JL and Townsend CR, *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Oxford, UK (1986).
3 Bos D and Ydenberg R, Evaluation of alternative management strategies of muskrat *Ondatra zibethicus* population control using a population model. *Wildl Biol* **17**:143–155 (2011).
4 Clark CW, Optimal control theory in one dimension, in *Mathematical Bioeconomics: the Mathematics of Conservation*, ed. by Clark CW. John Wiley & Sons, Ltd, Hoboken, NJ, p. 368 (2010).
5 Robertson PA, Adriaens T, Lambin X, Mill A, Roy S, Shuttleworth CM *et al.*, The large-scale removal of mammalian invasive alien species in Northern Europe. *Pest Manag Sci* DOI: 10.1002/ps.4224 (2016).
6 Perry HR, Jr, Muskrats, in *Wild Mammals of North America*, ed. by Chapman JA and Feldhamer GA. The Johns Hopkins University Press, Baltimore, MD, pp. 282–325 (1982).
7 Boutin S and Birkenholz DE, Muskrat and round-tailed muskrat, in *Wild Furbearer Management and Conservation in North America*, ed. by Novak M, Baker JA, Obbard ME and Malloch B. Ontario Trappers Association, Toronto, Canada, pp. 315–325 (1987).
8 Heidecke D and Seide P, Bisamratte *Ondatra zibethicus* (L.), in *Buch der Hege Band 1 Haarwild*, ed. by Stubbe P. VEB Deutscher Landwirtschaftsverlag, Berlin, Germany (1990).
9 Danell K, Introductions of aquatic rodents: lessons of the muskrat *Ondatra zibethicus* invasion. *Wildl Biol* **2**:213–220 (1996).
10 Le Louarn H and Quéré J-P, *Les Rongeurs de France: Faunistique et Biologie*, 3rd edition. Editions Quae, Versailles, France (2011).

11 Skyrienė G, Distribution of invasive muskrats (*Ondatra zibethicus*) and impact on ecosystem. *Ekologija* **58**:357–367 (2012).
12 Moens R, Étude bio-écologique du Rat musqué en Belgique. *Parasitica* **34**:57–121 (1978).
13 Errington PL, On the hazards of overemphasizing numerical fluctuations in studies of cyclic phenomena in muskrat populations. *J Wildl Manag* **18**:66–90 (1954).
14 Clark WR and Kroeker DW, Population-dynamics of muskrats in experimental marshes at Delta, Manitoba. *Can J Zool* **71**:1620–1628 (1993).
15 Erb JD, Stenseth N and Boyce MS, Geographic variation in population cycles of Canadian muskrats (*Ondatra zibethicus*). *Can J Zool* **78**:1009–1016 (2000).
16 Erb JD, Boyce MS and Stenseth NC, Spatial variation in mink and muskrat interactions in Canada. *Oikos* **93**:365–375 (2001).
17 Haydon DT, Stenseth NC, Boyce MS and Greenwood PE, Phase coupling and synchrony in the spatiotemporal dynamics of muskrat and mink populations across Canada. *Proc Natl Acad Sci USA* **98**:13 149–13 154 (2001).
18 Estay SA, Albornoz AA, Lima M, Boyce MS and Stenseth NC, A simultaneous test of synchrony causal factors in muskrat and mink fur returns at different scales across Canada. *PLoS ONE* **6**:1–8 (2011).
19 Errington PL, *Muskrat Populations*. Iowa State University Press, Ames, IA (1963).
20 Aldous SE, Muskrat trapping on Sand Lake national wildlife refuge, South Dakota. *J Wildl Manag* **11**:77–90 (1947).
21 Mallach N, Markierungsversuche zur Analyse des Aktionraums und der Ortsbewegungen des Bisams (*Ondatra zibethica* L.). *Anz Schadlingskde Pflanzenschutz Umweltschutz* **9**:129–136 (1971).
22 Caley MJ, Dispersal and inbreeding avoidance in muskrats. *Anim Behav* **35**:1225–1233 (1987).
23 Adelberg D, Ausbreitungsstrategien des Bisams *Ondatra zibethicus* (L. 1766) im Tal der unteren Hasen. Emsland, Universität Osnabrück, Osnabrück (2008).
24 Simpson MR and Boutin S, Muskrat, *Ondatra zibethicus*, population responses to harvest on the Old Crow Flats, Yukon-Territory. *Can Field Nat* **103**:420–422 (1989).
25 Barends F, The muskrat (*Ondatra zibethicus*): expansion and control in the Netherlands. *Lutra* **45**:97–104 (2002).
26 van Koersveld E, De Muskusrat, *Ondatra zibethica* L., in Nederland en zijn bestrijding. Plantenziektekundige Dienst, Wageningen, The Netherlands (1953).
27 Doude van Troostwijk WJ, The musk-rat (*Ondatra zibethicus* L.) in the Netherlands, its ecological aspects and their consequences for man. Rijksuniversiteit Leiden, Leiden, The Netherlands (1976).
28 Plug K, *Handboek* Muskusrattenbestrijding. Min LNV, The Hague, The Netherlands (1988).
29 Barends F, *Bestrijding van Muskusrat en Beverrat*. LCCM and TCM, The Hague, The Netherlands (2007).
30 Boyce MS, Sinclair ARE and White GC, Seasonal compensation of predation and harvesting. *Oikos* **87**:419–426 (1999).
31 Parker GR and Maxwell JW, An evaluation of spring and autumn trapping seasons for muskrats, *Ondatra-Zibethicus*, in Eastern Canada. *Can Field Nat* **98**:293–304 (1984).
32 Pelz HJ, Zur Geschichte der Bisambekämpfung Deutschland. *Mitt Biol Bundesanst Land-Forstwirtsch* **317**:219–234 (1996).
33 Kluyver HN, De bisamrat. *Versl Meded Plantenziektekundige Dienst Wageningen* **85**:1–32 (1937).
34 Ritzema-Bos J, De muskusrat, bisamrat of *Ondatra* (*Fiber zibethicus* L.). *Tijdschr Plantenziekten* **23**:1–79 (1917).
35 Thijsse JP, De muskusrat. *Levende Nat* **41**:348–349 (1937).
36 Zandberg F, de Jong P and Kraaijeveld-Smit F, Muskusrat. Op alternatieve wijze schade voorkomen. Bont voor Dieren, De Faunabescherming, Nederlandse Vereniging tot Bescherming van Dieren, The Hague, The Netherlands (2011).
37 Errington PL, Factors limiting higher vertebrate populations. *Science* **124**:304–307 (1956).
38 Brzezinski M, Romanowski J, Zmihorski M and Karpowicz K, Muskrat (*Ondatra zibethicus*) decline after the expansion of American mink (*Neovison vison*) in Poland. *Eur J Wildl Res* **56**:341–348 (2010).
39 Danell K, Short-term plant successions following the colonization of a Northern Swedish lake by the muskrat, *Ondatra zibethica*. *J Appl Ecol* **14**:933–947 (1987).
40 Landelijk jaarverslag 2007 muskus- en beverrattenbestrijding. Landelijke Coördinatie Commissie Muskusrattenbestrijding (LCCM), Tiel, The Netherlands (2008).
41 Legendre P and Legendre L, *Numerical Ecology. Developments in Environmental Modelling, Vol. 24*, 3rd edition. Elsevier Science BV, Amsterdam, The Netherlands (2012).
42 *R: A Language and Environment for Statistical Computing.* [Online]. R Core Team, Vienna, Austria. Available: https://www.R-project.org/ [2 October 2015].
43 Bates D, Maechler M, Bolker M and Walker S, lme4: linear mixed-effects models using Eigen and S4. *R Package Version 1.1-9.* [Online]. Available: https://CRAN.R-project.org/package=lme4 [2 October 2015].
44 Gosling LM and Baker SJ, The eradication of muskrats and coypus from Britain. *Biol J Linn Soc* **38**:39–51 (1989).
45 Bos D, van Belle J, van Wieren S, Ydenberg RC and Goedhart PW, Naar objectieve schatting van aantallen Muskusratten in Nederland. *Levende Nat* **111**:94–99 (2010).
46 Mulder JL, Vos *Vulpes vulpes*, in *Atlas van de Nederlandse Zoogdieren. Natuur van Nederland 12*, ed. by Broekhuizen S, Spoelstra K, Thissen JBM, Canters KJ and Buys JC. Naturalis Biodiversity Centre, Leiden, The Netherlands, pp. 236–238 (2016).
47 Bijlsma RG, Hustings F and Camphuysen CJ, *Algemene en Schaarse Vogels van Nederland (Avifauna van Nederland 2)*. GMB Uitgeverij/KNNV Uitgeverij, Haarlem/Utrecht, The Netherlands (2001).
48 van Rijn S, Zijlstra M and Bijlsma RG, Wintering white-tailed eagles *Haliaeetus albicilla* in the Netherlands: aspects of habitat scale and quality. *Ardea* **98**:373–382 (2010).
49 Boele A, van Bruggen J, Hustings F, Koffijberg K, Vergeer J-W and van der Meij T, *Broedvogels in Nederland 2013*. Sovon Vogelonderzoek Nederland, Nijmegen, The Netherlands (2015).
50 Dekker JJA and Hofmeester TR, The status of the American mink (*Neovison vison*) in the Netherlands. *Lutra* **57**:5–15 (2014).
51 Hengeveld R, *Dynamics of Biological Invasions*. Chapman and Hall, London, UK (1989).
52 Matis JH and Kiffe TR, Effects of immigration on some stochastic logistic models: a cumulant truncation analysis. *Theor Popul Biol* **56**:139–161 (1999).
53 Matis JH, Kiffe TR and Hengeveld R, Estimating parameters for models from birth-death-migration abundance data: case of spatio-temporal muskrat spread in the Netherlands. *J Agric Biol Environ Statist* **1**:40–59 (1996).
54 Halle S and Pelz HJ, Zur Effizienz der Bekämpfung des Bisams (*Ondatra zibethicus*) anhand von Fangdaten aus dem Land Bremen. *Z Angew Zool* **77**:204–218 (1990).
55 Pelz HJ, Spread of the muskrat in the Federal Republic of Germany. *Bull OEPP* **14**:153–157 (1984).