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Original Article

A Large-Scale Experiment to Evaluate Control of Invasive Muskrats

DAAN BOS,[1,2] *Altenburg and Wymenga Ecological Consultants, Suderwei 2, 9269 TZ Feanwâlden, The Netherlands*
E. EMIEL VAN LOON, *Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94240, NL-1090 GE, Amsterdam, The Netherlands*
ERIK KLOP, *Altenburg and Wymenga Ecological Consultants, Suderwei 2, 9269 TZ Feanwâlden, The Netherlands*
RON YDENBERG, *Centre for Wildlife Ecology, Simon Fraser University, Burnaby, B.C. Canada V5A 1S6*

ABSTRACT The muskrat (*Ondatra zibethicus*) is an invasive species in Europe. The extensive waterways of the Netherlands provide ideal habitat for muskrats, and a large population established itself after arrival in 1941. A control program was put into effect immediately because muskrat burrowing can compromise the integrity of dikes and, hence, poses a significant public safety risk. The current (2015) annual catch of approximately 89,000 individuals is equivalent to approximately 0.30 muskrats/km of waterway, well above the national objective in spite of decades of effort. The control program is expensive (€35 M annually) and contested by animal rights groups. These factors created the need for a careful evaluation of the full range of control possibilities, from 'no control' to 'extermination.' As part of this, we experimentally evaluated the validity of a previously published correlation (based on historical data) between catch and effort. We raised or lowered removal effort (2013–2016) in a stratified random sample of 117 5-km × 5-km 'atlas squares' from the national grid. We found that catch-per-unit effort (CPUE) decreased after effort was increased, and rose after effort was decreased, by amounts slightly greater than expected based on the correlational data, though confidence intervals enclose zero. As anticipated, CPUE varied consistently and strongly between seasons. The biggest (and unanticipated) effects were those of the catch in the preceding 3 years ('history'), and surrounding area ('neighborhood'). Our experiment confirms estimates of intensity of control required to lower muskrat populations. These results will help with more effective allocation of control effort, and better-informed evaluation of the economic costs of various control options. © 2020 The Authors. *Wildlife Society Bulletin* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS catch-per-unit effort, management experiment, muskrat, *Ondatra zibethicus*, pest species, spatial context, The Netherlands, trapping.

The muskrat (*Ondatra zibethicus*), native to North America, was introduced to Europe as a furbearer early in the 20th Century (van den Bosch et al. 1992). Burrowing by muskrats can undermine the integrity of dikes, essential to public safety in parts of the continent (Barends 2002, Bayoumi and Meguid 2011). Significant resources are spent to control muskrat populations in The Netherlands (van Loon et al. 2017), Flanders (VMM 2010), and Germany (Pelz 1996). Although there was and still is broad support for muskrat control (Ritzema-Bos 1917, van Wijngaarden 1955, Doude van Troostwijk 1976), explicit doubts have been raised by animal welfare organizations (Zandberg et al. 2011) as well as by scientists (Pelz 1996) about the need for and effectiveness of these control programs.

Muskrats are aquatic and herbivorous, requiring bodies of water with good access to nutritious vegetation, and shorelines in which to excavate burrows (Boutin and Birkenholz 1987, Heidecke and Seide 1990). Reproduction and mortality (especially in winter) are both high (Errington 1963, Moens 1978). In their native range, muskrats show strong and irregular population fluctuations, attributed to high annual variation in predation, food abundance, disease, and the amount of habitat available as a result of strong variation in water level, which influences access to food resources and safety (Errington 1956, 1963; Messier et al. 1990; Clark and Kroeker 1993; Clark 1994; Virgl and Messier 2000). Muskrats are generally site-faithful and territorial (Errington 1963, Marinelli and Messier 1993, Virgl and Messier 1997), and dispersal is density-dependent (Simpson and Boutin 1989, Virgl and Messier 1996).

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[1]*E-mail: d.bos@altwym.nl*
[2]*Joint affiliation: Conservation Ecology Group—Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands*

Studies in Europe and North America have measured muskrat dispersal distances of hundreds of meters to several kilometers (Aldous 1947, Caley 1987, Adelberg 2008), taking place mostly between successive breeding seasons in autumn and spring (Mallach 1971, Verkaik 1987). Work by Simpson and Boutin (1989, c.f. Virgl and Messier 2000) supports predictions from source–sink theory (Pulliam 1988) that dispersal into trapped areas is a mechanism by which muskrat populations recover from high mortality rates induced by trapping. Dispersing animals are highly vulnerable to predators, and inspired the 'doomed surplus' hypothesis (Sinclair and Pech 1996, Boyce et al. 1999). This concept holds that compensatory mechanisms in the population dynamic system cause the mortality from one source to offset that from another. Hence, it is not at all inevitable that heightened harvest intensity lowers either the population or catch.

The extensive shallow, linear waterways bordered by abundant vegetation, the lack of many predators, carefully controlled water levels, and a mild climate make much of The Netherlands ideal muskrat habitat. Their number and distribution grew rapidly after their arrival in 1941. Although a control program was immediately initiated (Barends 2002), the annual numbers trapped climbed steadily for a half century, reaching a peak of 434,000 in 1991, representing a catch of approximately 1.5/kilometer waterway/year (#/km/yr). Thereafter, ongoing annual effort of 1.5–2.0 trapping-hours/kilometer waterway/year (hr/km/yr) have reduced the catch rate to approximately 0.30 km/year (~89,000 animals in 2015). This is (barely) within the range considered 'sufficiently under control' (see table 1 in van Loon et al. 2017), and well above the official national management objective of the Water Authorities of <0.15 km/year.

The actual population size of muskrats in The Netherlands is unknown. Population size and trend are inferred from measures of the number trapped and invested effort. The situation resembles many fisheries, with important differences in that trappers are generally not competitors, and especially that sustainable harvest is not the objective. Rather, the program aims to drive numbers down and maintain them at a low level, or even to exterminate this invasive species. Muskrat populations have been successfully eradicated or almost completely removed in other jurisdictions (Gosling and Baker 1989, VMM 2010).

Bos and Ydenberg (2011) used a stage-structured stochastic dynamic meta-population model to evaluate different strategies of control, and identify gaps in knowledge that hamper muskrat management. Their model compared year-round, time- and space-differentiated harvest strategies, at various levels of harvest intensity under a wide range of parameter values. They concluded that harvest intensity has a strong effect on population level, and year-round harvesting compares favorably to a time-differentiated strategy in which harvesting is restricted to part of the year, at least under the seasonal harvest proportions studied. This is because, with these proportions, the metapopulation is able to recover during the no-harvest seasons, and because the total annual effort is lower. However, harvesting animals in winter and spring was predicted to affect population viability more per animal harvested, than harvesting in summer and autumn. Thus, an allocation of effort toward winter and spring, while maintaining total annual effort, is predicted to result in relatively stronger effects on the population. More intense harvesting (the model compared scenarios with 10% and 25% of the population harvested per season) reduces the population size more quickly, and is also more effective at reducing the number of animals killed over the longer term. Although larger numbers are killed initially, numbers killed in later years are much reduced. Minimizing the total number of deaths (and associated suffering) of trapped animals, as well as considerations such as bycatch, are important elements of the broader social discussion in the Netherlands.

van Loon et al. (2017) analyzed catch and effort based on the extensive historical records. They found that relative to the preceding year, catch declined once trapping effort exceeded 1.4 hours/km/year. The relative catch fell by 0.295/hour of trapping effort. The *y*-intercept (i.e., the relative change in catch at zero trapping effort) had a value of 0.42 (95% CI = 0.33–0.51), suggesting that without trapping, the population would increase rapidly. However, these results are correlational and based on data aggregated on a large (provincial level) scale. More careful investigation, preferably including an experiment with manipulated effort levels, is required to evaluate causality in these relationships, assess how to lower costs, increase effectiveness, reduce the number of animals killed, and limit the risk to infrastructure.

Bioeconomic evaluation (Clark 2010) of the full range of control possibilities, from 'no control' to 'extermination' requires information on 1) population dynamics of muskrats (Bos and Ydenberg 2011), 2) the relation between catch and the amount of damage (Ydenberg et al. 2019), and 3) on the relation between effort and catch. We experimentally evaluated the relation between catch and effort, testing the validity of the previous correlational analysis (van Loon et al. 2017). This correlation predicts that catch-per-unit effort (CPUE) will fall after effort is increased, and rise after effort is decreased, changing by a factor of 0.295. We also anticipate, as described in the literature on muskrat natural history that there will be strong effects of season on the catch (Verkaik 1987). Finally, based on Bos and Ydenberg (2011), we predict that a seasonal concentration of trapping effort in winter and spring is more effective than year-round harvesting at the same total annual effort, resulting in stronger effects on the population over time.

STUDY AREA

The Netherlands (50–54°N, 3–8°E; 33,700 km^2) was characterized by flat topography, with nearly 26% of the land area below sea level. The low-lying western regions were characterized by peat and clay soils, while sandy soils predominated in the east and south. Peat extraction (mostly in the medieval period) lowered many areas to below sea level, and land reclamation projects have since the late 16th

Century created 'polders' by building elaborate drainage systems including dikes, canals, and pumping stations. The Netherlands had a dense human population of >17 M. It had a mild maritime climate, with average annual precipitation of approximately 780 mm. Intensive agriculture dominated land use, occupying >55% of the area. Muskrats were found throughout the country but numbers were especially high in low-lying regions with peat and clay soils (Fig. 1).

METHODS

We manipulated the trapping effort assigned to individual 'atlas squares' located across the Netherlands. Atlas squares are 5-km × 5-km areas fixed on a national reference grid (Vogelbescherming Nederland 2007; there are 2,202 atlas squares in the country). Use of atlas squares enabled direct reference to the national muskrat trapping database in which catch and effort are registered, and eased the considerable task of organizing the experiment. Atlas squares compare favorably in area with field studies of muskrats (e.g., Clark and Kroeker 1993), and exceed the size of muskrat home ranges reported in the literature (Caley 1987, Marinelli and Messier 1993).

In contrast to the largely isolated potholes and marshes in native muskrat habitat on North American prairies, aquatic habitats in the Netherlands are largely composed of highly connected linear landscape elements. The extent of muskrat habitat was estimated for each atlas square by the total length of waterways (km), calculated as the sum of 1) the length of linear waterways that carry water during

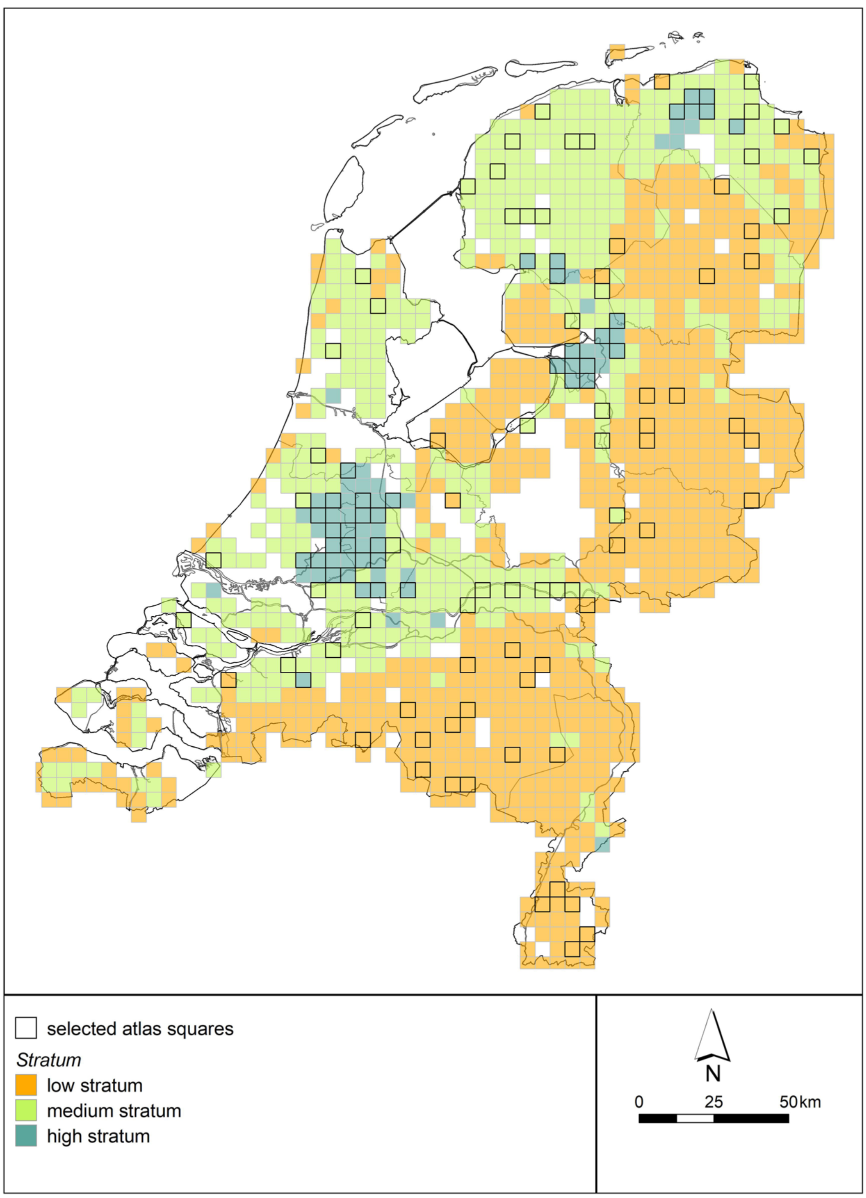

Figure 1. Location of experimental atlas squares (5 km × 5 km) in The Netherlands in which muskrat-trapping effort was manipulated from winter 2012/2013 to winter 2015/2016. The map also shows the 3 (high, medium, low muskrat density) strata within which atlas squares were stratified and randomly assigned to treatments.

>3 months of the year; 2) double the length of linear waterways wider than 6 m and deeper than 1 m; and 3) the circumference of lakes and ponds (unpublished data of the Dutch Muskrat Control Programme 2008). These 3 variables operationalize estimating the quantity of muskrat habitat based on the length of shoreline. We also classified each atlas square by the prevailing soil type (Alterra soil type map 2006).

We selected 117 atlas squares (from the total of 2,202 on the national grid) for the experiment, as follows. We first excluded 965 atlas squares dominated by water or urban areas, as well as those in which no muskrat had ever been trapped. We used the 2-step cluster algorithm in SPSS 20 (International Business Machines Corporation, Armonk, NY, USA) to classify the remaining 1,237 atlas squares into high ($n = 76$), medium ($n = 460$), or low ($n = 701$) strata, based on the mean annual muskrat catch and trapping effort over 3 years prior to the experiment (2009–2011) and the length of waterways, all of which co-vary strongly.

From each stratum, we randomly selected 39 atlas squares and assigned them to a combination of 'effort' and 'temporal' treatments (Fig. 1, Table 1). The even allocation to the 3 strata meant that the few high-stratum atlas squares, which we assume are most influential to the overall population, both in numbers and as source populations, are well-represented in the experiment. In the 'effort' treatments, we increased or decreased the allocated annual effort by 30%, relative to the level during the reference period, defined as the 12 months preceding the start of the experiment. In the 'temporal' treatments, trappers either adhered to their normal annual routine ('year-round'), or, in the 'seasonally-concentrated treatment', the hours expended during summer were limited to 20% of the total annual effort assigned to that atlas square. We conducted the experiment from December 2012 through January 2016. Trapping and the registration of catch and effort went on as usual in each of the atlas squares that were not included in the experiment.

Our aim was to estimate the effect of raising (or lowering) the quantity of the trapping effort invested, but not to alter the behavior of trappers. Hence, we made no prescriptions regarding the type of traps or trapping strategy. We instructed trappers to follow their normal routines, registering catch and effort following established standard procedures. We surveyed regional trapping team leaders after the conclusion of the experiment and asked them to score the quality of the trapping effort during the experiment, ranging from 1 (poor) to 10 (excellent).

Data Analysis

In the current data registration procedure (implemented 1987), each trapper records on a standard form the date, atlas square, number of muskrats trapped, as well as a record of time devoted to various task categories. The forms are processed centrally and entered into a database. For the purposes of our analysis, trapping effort includes the time spent in the field setting and checking traps, and the travel time between locations, but excludes holidays, administrative time, overhead, and time used in preparation and maintenance of equipment.

For each atlas square, we aggregated records by 'season,' defining seasons by the solar calendar. The experiment ran for 13 successive seasons, from winter 2012/2013 ('time' = 1) through winter 2015/2016 ('time' = 13). There were thus 1,521 observations (117 atlas squares in each of 13 seasons). We tabulated for each observation 'catch' and 'effort,' and calculated 'catch rate' (muskrats trapped per kilometer of waterway); CPUE (muskrats trapped per hour of trapping time); the 'historical CPUE' (average CPUE for the same season in that atlas square in the 3 years prior to the experiment 2010–2012); and 'neighboring CPUE' (the average CPUE for the same season in the 8 atlas squares surrounding each atlas square). Considering the 8 adjacent atlas squares enlarges the scale of the analysis from 5-km × 5-km (25 km^2) to 15-km × 15-km (225 km^2) and thus provides a step between the atlas-square scale analysis here and larger scale analysis of van Loon et al. (2017).

To assess whether there may have been some bias in the selection of atlas squares for the experiment, we asked

Table 1. We experimentally evaluated the validity of a previously published correlation (based on historical data) between catch and effort in regard to effectiveness of muskrat control by trapping in The Netherlands. We assigned each of the 1,237 eligible atlas squares in The Netherlands to the Low, Medium, or High stratum of muskrat density[a]. We randomly selected 117 of the 1,237 and assigned them to the experiment, with the number of atlas squares assigned to each combination of the effort and temporal treatments given in the right portion of the table. 'yr' = 'year-round' treatment; 'sc' = 'seasonally concentrated' treatment.

					Effort manipulation[b]				
					Decrease		Control	Increase	
					Temporal manipulation[c]				
Stratum	*n*	Waterway (km)	Catch (*n*)	Effort (hr)	yr	sc	yr	yr	sc
Low	701	93	27	145	7	6	13	7	6
Medium	460	285	124	480	7	6	13	7	6
High	76	506	796	1,730	7	6	13	7	6

[a] Strata were based on the mean annual muskrat catch and trapping effort over 3 yr prior to the experiment (2009–2011) and the length of waterways, all of which co-vary strongly.
[b] In the 'effort' treatment, the allocated annual effort was increased or decreased by 30% or maintained (Control), relative to the level during the reference period, defined as the 12 months preceding the start of the experiment.
[c] In the 'temporal' treatment, the allocated trapping effort was adjusted so that more was expended in winter and spring and less in summer ('seasonally concentrated'), or else expended 'year-round', following the regular pattern.

whether the change in CPUE between the experiment (2013–2016) and 3 years preceding the experiment (2010–2012) differed between control atlas squares and nonexperimental atlas squares using a linear mixed-effects model (accounting for repeated measures over the 13 periods/atlas square). To evaluate effects of the effort and temporal treatments, we compared linear mixed models of CPUE. The null model contained 'atlas square' as a random factor and 'season' as a fixed factor. Other models included, in various combinations, the 'effort' and 'temporal' treatments, time, interaction of treatments and time, stratum (high, medium, low), predominant soil type, the Regional Water Authority responsible, neighboring CPUE, historical CPUE, and the quality of invested effort (from the postexperiment questionnaire; Table 2).

We assessed model performance using Akaike's Information Criterion, adjusted for small sample sizes (AIC_c). After fitting the models, residuals of the model(s) best supported by these data were checked for normality, and we inspected residuals of all variables. We tested for spatial autocorrelation in the residuals and slopes using semivariograms. We performed analyses in Program R (R Foundation for Statistical Computing; https://www.r-project.org/), using the package lme4 (Bates et al. 2015). We report parameter estimates from models with $\Delta AIC_c < 4.0$, using the value for 'autumn' as intercept. We did not model average because the 2 top models were similar.

We further investigated effects of neighborhood and history to assess the scale of these influences. We calculated the correlation coefficient of CPUE estimates between each possible pair of experimental atlas squares in relation to the distance between them. We also calculated the correlation coefficient between the CPUE measured during the experiment in each atlas square in relation to the temporal separation (no. of seasons) between the measures. We use correlograms to display these spatial and temporal autocorrelations.

RESULTS

The number of muskrats trapped annually in The Netherlands declined during the experiment, dropping by approximately 8%, from approximately 97,000 (2013) to 89,000 (2015). These numbers are the lowest in recent decades—total annual catch has been >100,000 since 1978, and (though fluctuating) has declined since the 1991 peak of 434,000. Matching this decline, mean CPUE in nonexperimental atlas squares fell by approximately 7.7% (equivalent to 0.021/hr; SE = 0.005). There were no indications that suggested a biased assignment of atlas squares to the experiment, Linear mixed-effects model indicated no difference between control atlas squares and nonexperimental atlas squares ($t_{1,438} = 1.18$, $P = 0.24$).

The overall average CPUE in the 117 atlas squares was 0.274 muskrats/hour (SE = 0.039). This was significantly greater than in nonexperimental atlas squares (0.147 muskrats/hr: $t_{1,438} = 3.25$, $P = 0.001$), which is almost entirely explicable by the overrepresentation of 'high stratum' atlas squares in the experiment relative to The Netherlands as a whole (39 of 117, or 33.3% in the experiment vs. 8% nationally; Table 1). The seasonal pattern was strongly evident, with CPUE peaking in spring and autumn and troughs in summer and winter (Fig. 2).

Implementation of Treatments

Effort in the reduced effort treatment was on average 16.7% ± 54.6 (SD) lower, and in the increased effort treatment 23.8% ± 24.5 (SD) larger, than the reference period (objectives were to raise or lower effort by 30%). Accordingly, we expected that the experimental decrease in effort would increase the annual CPUE by 0.295 × 16.7% = 4.9%, while the experimental increase in effort would decrease CPUE by 0.295 × 23.8% = 7.0%. The change in effort in control atlas squares relative to the reference period was a mere 1.7% ± 17.5 (SD).

The implementation of the 'seasonally concentrated' temporal treatment was as intended, with only 17.5% ± 5.0 (SD)

Table 2. Competition evaluating models of variation in muskrat-trapping catch-per-unit effort (CPUE; no./hr), in relation to season, time, neighborhood (Neighb; CPUE in the 8 neighboring atlas squares), history (Hist; CPUE in the 3 yr before the experiment for the same season), effort (EFF; increased or decreased), treatment (TEMP; year-round or seasonally concentrated), Regional Water Authority (RWA), and soil (predominant soil type), from winter 2012/2013 to winter 2015/2016 in The Netherlands. All models with any support (AIC_c weight >0) include a random slope per atlas square (Time|AS).

Model[a]	K[b]	AIC_c[c]	ΔAIC_c[d]	Weight	Cum.Weight[e]
Season + Hist + Neighb + EFF + (Time|AS)	12	220	0.0	0.62	0.62
Season + Hist + Neighb + EFF × Time + (Time|AS)	12	223	2.2	0.20	0.82
Season + Hist + Neighb + (Time|AS)	10	224	4.1	0.08	0.90
Season + Hist + Neighb + TEMP × Time + (Time|AS)	13	225	4.2	0.08	0.98
Season + Hist + Neighb + Stratum + (Time|AS)	12	228	7.8	0.01	0.99
Season + Hist + Neighb + Soil + (Time|AS)	13	228	7.8	0.01	1.00
Season + Hist + Neighb + RWA + (Time|AS)	30	247	26.4	0.00	1.00
Season + Hist + Neighb + EFF + Time + (1|AS)	11	356	135.6	0.00	1.00
Season + Hist + Neighb + EFF × Time + (1|AS)	13	359	138.6	0.00	1.00
Season + Soil + RWA + (Time|AS)	31	460	239.3	0.00	1.00
Season + (1|AS)	6	617	397.1	0.00	1.00

[a] For the model best supported by the data, the marginal R^2 equals 0.40, while the conditional R^2 equals 0.59.
[b] K = no. of free parameters in the model.
[c] AIC_c = Akaike Information Criterion, adjusted for small sample sizes.
[d] ΔAIC_c = difference between model AICc and AICc value of the best model
[e] Cum.Weight = Cumulative weight.

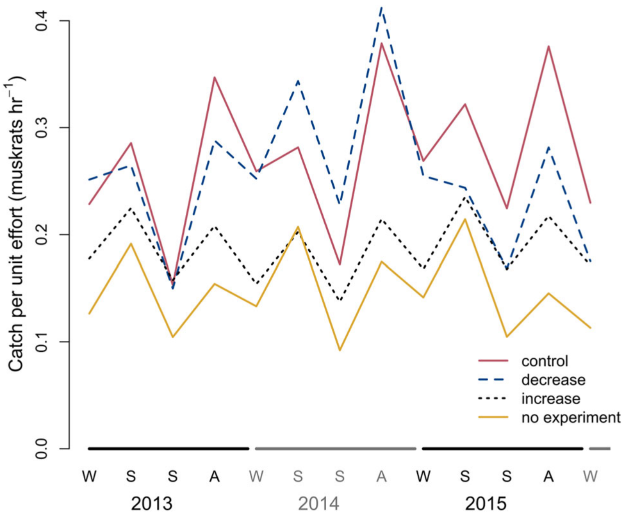

Figure 2. Basic experimental results, showing the catch-per-unit effort (CPUE; no./hr) over the successive 13 seasons (from winter 2012/2013 to winter 2015/2016) of the experiment in which muskrat-trapping effort was manipulated in The Netherlands. Portrayed is CPUE in the each of 3 experimental treatments, and in the nonexperimental atlas squares (yellow 'no-experiment' line). Note the strong seasonal variation: the peaks correspond to spring and autumn.

of the annual effort expended during summer (20% intended at maximum). However, the effort expended during summer in the 'year-round' treatment was only 21.6% ± 5.0 (SD). Considering this small difference in relation to the large variation among atlas squares, any effect of this treatment is in hindsight not expected to be detectable.

Experimental results

The best performing model includes the effort treatment, the variables season, historical CPUE, neighborhood CPUE, and contains a random slope of time per atlas square (Table 2). The model provides a good fit to the data (marginal $R^2 = 0.40$, conditional $R^2 = 0.59$). The residuals were normally distributed and showed no structural deviations in relation to the response variable, predictor variables, or length of waterway or stratum. The second-best model was nearly identical, differing only in that the effort treatment showed an interaction with time. Not included in either of the top models are the temporal treatment, the variables 'time', Regional Water Authority, soil type, the quality of invested effort, or the stratum.

Parameter estimates for the seasons range from −0.004 to −0.036 muskrats/hour (Table 3). Both top models indicate an effect of the effort treatment. As predicted, CPUE increased when effort was lowered (by 0.032/hr, or 11%; prediction 4.9%) and lowered when effort was raised (by 0.059/hr, or 21–26% in the top and second models; prediction 7.0%). These estimates are larger than predicted, but note that the confidence intervals for both include zero. Both top models assigned the largest parameter estimates to 'history' (~0.32 muskrats/hr) and 'neighborhood' (~0.63 muskrats/hr).

Neither of these large effects was anticipated, and we carried out a *post hoc* analysis to assess the scale of these influences in more detail (Fig. 3). These results show that the similarity of atlas squares extends, though in a diminishing fashion, to a distance of almost 40 km. Successive measures tend to be very similar (high values at temporal separation of 1–2 seasons), while the strong seasonality is evident by the peaks at 4 and 8 seasons (i.e., 1 and 2 yr).

DISCUSSION

We used an experiment manipulating trapping effort, carried out over 3 years in 117 5-km × 5-km 'atlas squares,' to test the correlation between trapping effort and muskrat catch identified by van Loon et al. (2017). As in their native range, muskrats in The Netherlands have low survival (Bos et al. 2019 estimate 0.26–0.34/half-year) but high reproductive potential (Clay and Clark 1985, Clark and Kroeker 1993, Virgl and Messier 2000). We thus had expected that population size, and hence the catch, would quickly change in response to a 30% change in trapping effort. The results were consistent with the correlational analysis of van Loon et al. (2017), in that CPUE changed by about the magnitude predicted, though we note that the confidence intervals around the parameter estimates enclosed zero. Nevertheless, the effect of the effort treatment

Table 3. Parameter estimates[a] with 95% confidence intervals (CI) in the 2 top-ranked models[b] of variation in muskrat-trapping effort, as measured from winter 2012/2013 to winter 2015/2016 in The Netherlands.

	Top model (weight = 0.62)			Second model (weight = 0.20)		
Coeff.	**Estimate**	**2.5% CI**	**97.5% CI**	**Estimate**	**2.5% CI**	**97.5% CI**
(Intercept)	0.033	−0.021	0.090	0.054	−0.008	0.118
Winter	−0.004	−0.037	0.029	−0.002	−0.035	0.031
Spring	−0.036	−0.071	−0.001	−0.032	−0.067	0.002
Summer	−0.024	−0.060	0.012	−0.023	−0.059	0.013
Historical	0.322	0.243	0.401	0.320	0.241	0.399
Neighborhood	0.633	0.534	0.732	0.637	0.538	0.736
Decreased effort	0.032	−0.031	0.094	0.030	−0.047	0.106
Increased effort	−0.059	−0.122	0.003	−0.073	−0.150	0.004
Time				0.026	−0.010	0.062
Interactions						
Decreased effort × time				−0.003	−0.053	0.048
Increased effort × time				−0.015	−0.066	0.035

[a] Parameter estimates are given with respect to the control treatment in autumn.
[b] Model specification given in Table 2. The second model contains the interaction terms.

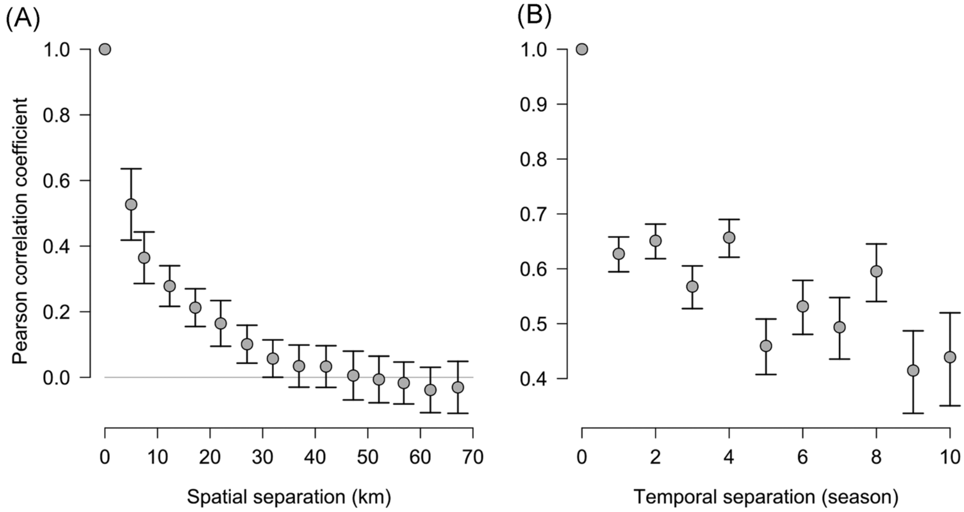

Figure 3. Correlograms showing spatial and temporal autocorrelation in muskrat CPUE (catch-per-unit effort; no./hr, with standard errors) in 117 experimental atlas squares over 13 successive seasons (from winter 2012/2013 to winter 2015/2016) of the experiment in which muskrat-trapping effort was manipulated in The Netherlands. The left panel A) displays the correlation between CPUE in pairs of atlas squares in relation to the distance between their centers. The right panel B) displays the correlation between CPUE measures in each atlas square, in relation to the number of seasons between the measures.

on CPUE was small compared with that of the factors ‘neighborhood’ and ‘history’ (0.633 and 0.322 muskrats/hr, respectively). These parameters had the largest effects on the experimental outcome, and show that the scale of an atlas square, though convenient for the experimental procedure and data registration, is relatively small for trapping effort to have a large effect as long as neighboring squares are not managed in the same way. Our findings illustrate at what scale a control program needs to be organized to be more effective. The dispersal into trapped areas is a powerful mechanism by which muskrat populations recover from high mortality rates induced by trapping over multiple kilometers (Mallach 1971, Simpson and Boutin 1989), in spite of the fact that muskrats are generally site-faithful, territorial (Errington 1963) and dispersal distances may on average be only hundreds of meters (Caley 1987). Indeed, van den Bosch et al. (1992) estimated the velocity of population expansion for muskrats to be 10.9 and 5.1 km/year, respectively, for 2 phases of population expansion in Europe, before and after the start of large-scale trapping programs around 1925–1930. The correlational analysis of van Loon et al. (2017) was based on data aggregated by province (12 in all), on average approximately 100 times larger than the individual atlas squares on which the experiment was based. Thus, it was perhaps not surprising that experimental effects were noisy and difficult to detect. The expected seasonal pattern is strongly evident, however, with relatively high CPUE in spring and autumn, when there is more movement of animals (due to mating and dispersal; Errington 1963, Verkaik 1987).

We were unable to evaluate the prediction of Bos and Ydenberg (2011) that a time-differentiated strategy with ‘seasonally concentrated’ trapping is more effective than year-round harvesting. The temporal treatment was not included in either of the top-ranked models; thus, without evidence suggesting an influence on CPUE. We propose this is likely because the ‘temporal’ treatments intended to test this idea were not sufficiently contrasting.

The historical variation in control effort has been considerable over the 8 decades that muskrats have been present in The Netherlands, ranging from almost zero in some places to >4 hours/km in several locales over shorter periods. Part of that variation is logically related to differences in history (time since local muskrat invasion; van Loon et al. 2017) and landscape. But much has been unguided by quantitative evaluation of the effect of trapping on muskrat populations. The general management strategy has been to increase the effort allocated where the catch rate rose, on the reasonable premise that this indicates the muskrat population is increasing. Our study makes clear that the catch rate changes in relation to several factors, which implies that the recent history in any atlas square should be seen only as an approximate guide for what is required to maintain control. The true required effort could deviate strongly from this estimate as a result of recent history, or the neighborhood. For example, if the effort allocated during the reference period drove numbers down, it likely overestimates that required to maintain control (or *vice versa*). The strong effect of history may be due partially to such effects.

The experimental design fixed the total annual effort assigned to each atlas square, but each trapper retained other means to exert control over their effort (e.g., by shifting the timing of their field work). Trappers often related that their effectiveness varies greatly with environmental circumstances. For example, it is greater after mowing of shoreline vegetation, when the water table is lower, or during weather such as frost; and trappers were clear that they routinely adjust their schedules to take advantage of such conditions. Trappers are professional and highly dedicated, and many were reluctant participants in the experiment. By randomly assigning atlas squares to treatments, the imposed experimental design drove the allocation of effort away from that what would have chosen based on the usual procedure. Many trappers felt this created an unwarranted hazard and to some extent, trappers may have felt a necessity to make adjustments to hedge against muskrat outbreaks (e.g., by timing visits to the atlas square concerned under ideal field circumstances). This would result in reduced contrast among treatment effects. Any effect on our results is difficult to quantify, but it is noteworthy that CPUE in the nonexperimental atlas squares declined during the experiment (by 0.021 muskrats/hr, continuing the national trend of the previous decade), whereas CPUE in the experimental atlas squares rose (by 0.026 muskrats/hr).

Concerns about liability related to muskrat outbreaks have long kept the responsible authorities very averse to field experiments. But in this case, the Dutch Water Authorities were persuaded to permit experimental variation in trapping effort, the parameter considered most influential in affecting muskrat population development. Fortunately, only a few situations (<5—about the usual rate) with 'large' damage (defined as repair costs exceeding €10,000, or compromising public safety) occurred during the experiment. Now, having finished the experiment and the associated studies (van Loon et al. 2017, Bos et al. 2019, Ydenberg et al. 2019), the authorities have greatly enhanced the evidence-base to support future management decisions.

MANAGEMENT IMPLICATIONS

Control of muskrat numbers is a means to reduce the risk that their burrowing activities pose to dikes and other water control infrastructure. However, it is also expensive (currently requiring €35 M annually in The Netherlands). Ultimately, the total national investment in muskrat control is a political decision, influenced by the acceptable level of safety risk (Doude van Troostwijk 1976), economic costs and benefits (Clark 2010), availability of other methods to prevent damage, ethical considerations (Warren 2007, Zandberg et al. 2011), effects on biodiversity (Danell 1979, Vermaat et al. 2016), and potential for transfer of disease (Ulrich et al. 2009). These aspects almost certainly vary among landscapes in northwest Europe. For the low-lying landscapes of The Netherlands, vulnerable to flooding, we have strong indications that large muskrat populations compromise public safety (Ydenberg et al. 2019). Thus, we strongly recommend continuing the control program until the risks, costs, and other considerations have been substantiated and debated. This is in line with recommendations of the global Convention on Biological Diversity (Aichi Target 9; https://www.cbd.int/sp/targets/), scientific sources (Genovesi 2005, Lambertini et al. 2011, Luque et al. 2014), and recent European legislation (Regulation (Eu) no 1143/2014 of the European Parliament and The Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species). Our results confirm estimates of the intensity of control required to lower muskrat populations. These experimental results will support more effective allocation of control effort, given the emphasis on spatial scale of implementation. In combination with other information (e.g., on the relation between damage to infrastructure and muskrat numbers; Ydenberg et al. 2019), a careful bioeconomic analysis of control strategies is now possible.

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LITERATURE CITED

Adelberg, D. 2008. Ausbreitungsstrategien des Bisams *Ondatra zibethicus* (L. 1766) im Tal der Unteren Hasen/Emsland. Thesis, Universität Osnabrück, Osnabrück, Germany. [In German.]

Aldous, S. E. 1947. Muskrat trapping on Sand Lake National Wildlife Refuge, South Dakota. Journal of Wildlife Management 11:77–90.

Barends, F. 2002. The muskrat (*Ondatra zibethicus*): expansion and control in The Netherlands. Lutra 45:97–104.

Bates, D., M. Maechler, M. Bolker, and S. Walker. 2015. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-9. <https://CRAN.R-project.org/package=lme4> Accessed 6 Jun 2016.

Bayoumi, A., and M. A. Meguid. 2011. Wildlife and safety of earthen structures: a review. Journal of Failure Analysis and Prevention 11:295–319.

Bos, D., R. Kentie, M. La Haye, and R. C. Ydenberg. 2019. Evidence for the effectiveness of controlling muskrat (*Ondatra zibethicus* L.) populations by trapping. European Journal of Wildlife Research 65:45.

Bos, D., and R. Ydenberg. 2011. Evaluation of alternative management strategies of muskrat *Ondatra zibethicus* population control using a population model. Wildlife Biology 17:143–155.

Boutin, S., and D. E. Birkenholz. 1987. Muskrat and round-tailed muskrat. Pages 315–325 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Trappers Association, Toronto, Canada.

Boyce, M. S., A. R. E. Sinclair, and G. C. White. 1999. Seasonal compensation of predation and harvesting. Oikos 87:419–426.

Caley, M. J. 1987. Dispersal and inbreeding avoidance in muskrats. Animal Behaviour 35:1225–1233.

Clark, C. W., editor. 2010. Optimal control theory in one dimension. Pages 62–74 *in* Mathematical bioeconomics: the mathematics of conservation. Third edition. John Wiley and Sons, Hoboken, New Jersey, USA.

Clark, W. R. 1994. Habitat selection by muskrats in experimental marshes undergoing succession. Canadian Journal of Zoology-Revue Canadienne de Zoologie 72:675–680.

Clark, W. R., and D. W. Kroeker. 1993. Population-dynamics of muskrats in experimental marshes at Delta, Manitoba. Canadian Journal of Zoology 71:1620–1628.

Clay, R. T., and W. R. Clark. 1985. Demography of muskrats on the Upper Mississippi River. Journal of Wildlife Management 49:883–890.

Danell, K. 1979. Reduction of aquatic vegetation following the colonization of a northern Swedish lake by the muskrat, *Ondatra zibethica*. Oecologia 38:101–106.

Doude van Troostwijk, W. J. 1976. The musk-rat (*Ondatra zibethicus* L.) in The Netherlands, its ecological aspects and their consequences for man (RIN verhandeling 7). Thesis, Rijksuniversiteit Leiden, Leiden, The Netherlands.

Errington, P. L. 1956. Factors limiting higher vertebrate populations. Science 124:304–307.

Errington, P. L. 1963. Muskrat populations. Iowa State University Press, Ames, USA.

Genovesi, P. 2005. Eradications of invasive alien species in Europe: a review. Biological Invasions 7:127–133.

Gosling, L. M., and S. J. Baker. 1989. The eradication of muskrats and coypus from Britain. Biological Journal of the Linnean Society 38:39–51.
Heidecke, D., and P. Seide. 1990. Bisamratte *Ondatra zibethicus* (L.). *in* H. Stubbe, editor. Buch der Hege Band 1 Haarwild. VEB Deutscher Landwirtschaftsverlag, Berlin, Germany. [In German.]
Lambertini, M., J. Leape, J. Marton-Lefevre, R. A. Mitter-Meier, M. Rose, J. G. Robinson, S. N. Stuart, B. Waldman, and P. Genovesi. 2011. Invasives: a major conservation threat. Science 333:404–405.
Luque, G. M., C. Bellard, C. Bertelsmeier, E. Bonnaud, P. Genovesi, D. Simberloff, and F. Courchamp. 2014. The 100th of the world's worst invasive alien species. Biological Invasions 16:981–985.
Mallach, N. 1971. Markierungsversuche zur Analyse des Aktionraums und der Ortsbewegungen des Bisams (*Ondatra zibethica* L.). Anzeiger Fur Schadlingskunde Pflanzenschutz Umweltschutz 9:129–136. [In German.]
Marinelli, L., and F. Messier. 1993. Space use and the social system of muskrats. Canadian Journal of Zoology-Revue Canadienne de Zoologie 71:869–875.
Messier, F., J. A. Virgl, and L. Marinelli. 1990. Density-dependent habitat selection in muskrats—a test of the ideal free distribution model. Oecologia 84:380–385.
Moens, R. 1978. Étude bio-écologique du rat musqué en Belgique. Parasitica 34:57–121. [In French.]
Pelz, H. J. 1996. Zur Geschichte der Bisambekämpfung Deutschland. Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft 317:219–234. [In German.]
Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.
Ritzema-Bos, J. 1917. De muskusrat, bisamrat of Ondatra (*Fiber zibethicus* L.). Tijdschr over Plantenziekten 23:1–79. [In Dutch.]
Simpson, M. R., and S. Boutin. 1989. Muskrat, *Ondatra-zibethicus*, population responses to harvest on the Old Crow Flats, Yukon-Territory. Canadian Field-Naturalist 103:420–422.
Sinclair, A. R. E., and R. P. Pech. 1996. Density dependence, stochasticity, compensation and predator regulation. Oikos 75:164–173.
Ulrich, R. G., G. Heckel, H.-J. Pelz, L. H. Wieler, M. Nordhoff, G. Dobler, J. Freise, F. R. Matuschka, J. Jacob, J. Schmidt-Chanasit, F. W. Gerstengarbe, T. Jäkel, J. Süss, B. Ehlers, A. Nitsche, R. Kallies, R. Johne, S. Günther, K. Henning, R. Grunow, M. Wenk, L. C. Maul, K. P. Hunfeld, R. Wölfel, G. Schares, H. C. Scholz, S. O. Brockmann, M. Pfeffer, and S. S. Essbauer. 2009. Nagetiere und nagetierassoziierte krankheitserreger. Bundesgesundheitsblatt—Gesundheitsforschung—Gesundheitsschutz 52:352–369. [In German.]
van den Bosch, F., R. Hengeveld, and J. A. J. Metz. 1992. Analyzing the velocity of animal range expansion. Journal of Biogeography 19:135–150.
van Loon, E. E., D. Bos, C. van Hellenberg Hubar, and R. C. Ydenberg. 2017. A historical perspective on the effects of trapping and controlling the muskrat (*Ondatra zibethicus*) in The Netherlands. Pest Management Science 73:305–312.
van Wijngaarden, A. 1955. De bestrijding van de muskusrat (*Ondatra zibelthica* L) in 1955—landelijk jaarverslag. Plantenziektenkundige Dienst, Wageningen. [In Dutch.]
Verkaik, A. J. 1987. The muskrat in The Netherlands. Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen Series C-Biological and Medical Sciences 90:67–72.
Vermaat, J. E., B. Bos, and P. van der Burg. 2016. Why do reed beds decline and fail to re-establish? A case study of Dutch peat lakes. Freshwater Biology 61:1580–1589.
Virgl, J. A., and F. Messier. 1996. Population structure, distribution, and demography of muskrats during the ice-free period under contrasting water fluctuations. Ecoscience 3:54–62.
Virgl, J. A., and F. Messier. 1997. Habitat suitability in muskrats: a test of the food limitation hypothesis. Journal of Zoology 243:237–253.
Virgl, J. A., and F. Messier. 2000. Assessment of source–sink theory for predicting demographic rates among habitats that exhibit temporal changes in quality. Canadian Journal of Zoology-Revue Canadienne de Zoologie 78:1483–1493.
Vlaamse Milieumaatschappij [VMM]. 2010. Ratten op Vlaamse wijze. Vlaamse Milieumaatschappij-VMM, Erembodegem, Belgium. [In Dutch.]
Vogelbescherming Nederland. 2007. Topografische inventarisatieatlas voor flora en fauna van Nederland. P. Huigen and R. Vogel, editors. Vogelbescherming Nederland, Zeist. [In Dutch.]
Warren, C. R. 2007. Perspectives on the 'alien' versus 'native' species debate: a critique of concepts, language and practice. Progress in Human Geography 31:427–446.
Ydenberg, R. C., E. E. van Loon, D. Bos, and H. van Hemert. 2019. Damage to dykes and levees in The Netherlands is extensive and increases with muskrat (*Ondatra zibethicus*) density. Lutra 62:39–53.
Zandberg, F., P. de Jong, and F. Kraaijeveld-Smit. 2011. Muskusrat. Op alternatieve wijze schade voorkomen. Bont voor Dieren, De Faunabescherming, Nederlandse Vereniging tot Bescherming van Dieren, Den Haag, The Netherlands. [In Dutch.]

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