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"We Used to Say Rats Fell from the Sky After a Flood": Temporary Recovery of Muskrat Following Ice Jams in the Peace-Athabasca Delta

Jason R. Straka,[1] Archie Antoine,[2] Rene Bruno,[2] David Campbell,[2,3] Ron Campbell,[2,3] Ross Campbell,[2]
John Cardinal,[2] Gerald Gibot,[2] Queenie Z. Gray,[3] Sharon Irwin,[3] Rhona Kindopp,[3] Ray Ladouceur,[2]
Walter Ladouceur,[2,4] Jessica Lankshear,[3] Bruce Maclean,[5] Stuart Macmillan,[3] Freddy Marcel,[2] George Marten,[2]
Larry Marten,[2] John McKinnon,[3] Lucy D. Patterson,[6] Charlie Voyageur,[2,4] Morgan Voyageur,[2]
George "Sloan" Whiteknife[2] and Leslie Wiltzen[2]

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ABSTRACT. Elders and Indigenous land users in the Peace-Athabasca Delta (PAD) have observed a dramatic decline in the relative abundance of muskrat in recent decades (~1935–2014). The main explanation for the decline has been reduction in suitable habitat as a result of decades with reduced frequency of ice-jam flooding on the Peace River. Under favourable conditions, ice jams can cause flooding of perched basins within the PAD that would otherwise receive no recharge from floodwaters. To examine whether abundance of muskrat in the PAD is driven by flooding, we tested the predictions that the density of muskrat (estimated by winter counts of houses) (1) was inversely related to the number of years since major ice-jam floods and (2) increased with water depth. An ongoing collaborative monitoring program initiated in 2011, combined with analysis of data from past surveys (1973–2015), allowed Indigenous land users and scientists to document a 10 to 100-fold increase in the density of muskrat houses in 24 basins, over the two years following ice-jam flood events in the PAD. During 1973–2015, in the periods between major floods, density of houses dropped by approximately 79% for every year after a significant flood. In 27 basins surveyed from 2011 to 2015, density of muskrat houses increased by two orders of magnitude in the two years following a flood in the spring of 2014. Density of muskrat houses had a non-linear relationship with estimated depth of water at the time of fall freeze-up; the highest densities of muskrat houses were in basins with about 60–250 cm of water at the time of freeze-up. The depth of snow at the time of surveys did not have a strong relationship with the density of muskrat houses. However, few houses were counted in basins with more than 20 cm of snow, likely because deeper snow made it more difficult to conduct surveys and spot houses. Factors other than an increase in the depth of water at fall freeze-up may provide the mechanisms by which flooding affects muskrat. Density of muskrat houses is clearly tied to ice-jam flooding in the PAD. However, the local mechanisms by which floods affect muskrat are best understood by Indigenous land users and remain poorly understood by Western science. Indigenous peoples continue to regard muskrat as an indicator of ecological and cultural health of the PAD. This study highlights the value of consistent ecological monitoring that includes Indigenous knowledge.

Key words: ecological monitoring; aquatic mammals; indicator species; wildlife management; climate change; hydro development; *Ondatra zibethicus*

RÉSUMÉ. Les aînés et les utilisateurs des terres autochtones du delta des rivières de la Paix et Athabasca ont observé une baisse draconienne de l'abondance du rat musqué au cours des dernières décennies (~1935-2014). La principale explication du déclin est la diminution d'abris convenables, et ce, en raison de plusieurs décennies marquées par la fréquence réduite d'inondations causées par des embâcles dans la rivière de la Paix. Dans des conditions favorables, les embâcles peuvent causer l'inondation des bassins perchés au sein du delta des rivières de la Paix et Athabasca qui autrement ne recevraient pas de recharge des eaux de crue. Afin d'examiner si l'abondance du rat musqué dans le delta des rivières de la Paix et Athabasca est favorisée par les inondations, nous avons testé des prévisions selon lesquelles la densité du rat musqué (estimée par le nombre d'abris en hiver) 1) était inversement liée au nombre d'années depuis les dernières importantes inondations causées par des embâcles et 2) augmentait avec la profondeur de l'eau. Un programme collaboratif de suivi continu lancé en 2011, combiné à l'analyse de données des relevés antérieurs (1973-2015), a permis aux utilisateurs des terres autochtones et aux scientifiques de multiplier de 10 à 100 fois la densité d'abris du rat musqué dans 24 bassins, au cours des deux années suivant des événements

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[1] Corresponding author: Parks Canada, Wood Buffalo National Park, Box 38, Fort Chipewyan, Alberta T0P 1B0, Canada; straka.jason@gmail.com
[2] General Delivery, Fort Chipewyan, Alberta
[3] Parks Canada, Wood Buffalo National Park, Fort Smith, Northwest Territories X0E 0P0, Canada
[4] Deceased
[5] Maclean Environmental Consulting, 812 Jubilee Avenue, Winnipeg, Manitoba R3L 1P9, Canada
[6] University of Ottawa, 30 Marie-Curie, Ottawa, Ontario K1N 6N5, Canada

d'inondation causés par des embâcles dans le delta des rivières de la Paix et Athabasca. Entre 1973 et 2015, durant les périodes se situant entre les inondations importantes, la densité d'abris a diminué d'environ 79 % chaque année suivant une inondation importante. Dans 27 bassins sondés entre 2011 et 2015, la densité d'abris du rat musqué a augmenté de deux ordres de grandeur au cours des deux années ayant suivi une inondation survenue au printemps de 2014. La densité d'abris du rat musqué avait une relation non linéaire avec la profondeur de l'eau estimée au moment de la prise des glaces en automne; les plus fortes densités d'abris du rat musqué se trouvaient dans les bassins ayant de 60 à 250 cm d'eau au moment de la prise des glaces. La profondeur de la neige au moment des relevés n'avait pas de relation solide avec la densité d'abris du rat musqué. Cependant, nous avons compté peu d'abris dans les bassins comptant plus de 20 cm de neige, probablement parce qu'il était plus difficile d'effectuer des relevés et de trouver les abris dans la neige plus épaisse. Des facteurs autres que l'augmentation de la profondeur de l'eau au moment de la prise des glaces en automne pourraient fournir les mécanismes par lesquels les inondations se répercutent sur les rats musqués. La densité d'abris du rat musqué est manifestement liée aux inondations causées par des embâcles dans le delta des rivières de la Paix et Athabasca. Toutefois, les utilisateurs des terres autochtones comprennent mieux les mécanismes locaux par lesquels les inondations se répercutent sur les rats musqués, tandis qu'ils demeurent mal compris par la science occidentale. Les peuples autochtones continuent de considérer le rat musqué comme un indicateur de la santé écologique et culturelle du delta des rivières de la Paix et Athabasca. Cette étude fait ressortir la valeur d'un suivi écologique constant qui tient compte des connaissances autochtones.

Mots clés : suivi écologique; mammifères aquatiques; espèce indicatrice; gestion de la faune; changement climatique; aménagement hydroélectrique; *Ondatra zibethicus*

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INTRODUCTION

The Peace-Athabasca Delta (PAD) in northern Alberta, Canada, is one of the world's largest inland freshwater deltas (Timoney, 2013). Its dynamic system of channels, basins, marshes, and grasslands has been recognized as a Ramsar Wetland of International Significance within a UNESCO World Heritage site, in part because of its role as a boreal hotspot of biodiversity (Timoney, 2013) that has supported Indigenous peoples on a rich cultural landscape for generations. Ecosystems in the PAD are heavily influenced by availability of water (Timoney, 2013; Authors' pers. obs.). The PAD is considered to be vulnerable to existing and proposed hydroelectric dams on the Peace River (W.A.C. Bennett and Site C Dams; Peters and Prowse, 2001; Peters et al., 2006; Peters and Buttle, 2010; Carver, 2012; Beltaos, 2014); water withdrawals for oil sands, agriculture, and municipalities on the Athabasca River (Candler et al., 2010; Ohlson et al., 2010); and climate change throughout the watershed and in headwaters (Beltaos et al., 2006; Wolfe et al., 2008; Timoney, 2009). Proposed developments by industry and legal actions by Indigenous peoples have put the ecological integrity of the PAD in the international spotlight (e.g., Schindler and Donahue, 2006; Carver, 2012; Parks Canada, 2013; MCFN, 2014).

Indigenous knowledge (IK) holders and Western scientists working in the PAD have observed a drying trend in recent decades, but direct impacts to ecosystems and ways of life can be difficult to describe in terms that seem actionable or resonate with managers and decision makers (e.g., Candler et al., 2010; MCFN, 2014). Selecting appropriate ecological indicators for long-term monitoring is challenging for a deltaic system that constantly changes and can lack clear baselines (Timoney, 2002; Wolfe et al., 2012). IK holders and Western scientists agree that spring ice-jam floods are of paramount ecological importance to the PAD and that useful ecological indicators should be responsive to flooding (e.g., Peters and Prowse, 2001; Beltaos et al., 2006; Peters et al., 2006). Ice-jam floods occur in the PAD when conditions are appropriate for causing a "hydraulic dam" of ice, which backs up and raises water levels upstream of the ice jam (Peters and Prowse, 2001; Peters et al., 2006; Peters and Buttle, 2010). These floods are typically associated with high water levels that spill over the banks of major channels, flow in channels that are typically dry or disconnected from the main river system, replenishment of perched basins, and temporary reversal of the direction of flow (Peters and Prowse, 2001; Peters et al., 2006; Peters and Buttle, 2010).

Muskrat (*Ondatra zibethicus*) are considered an ecological and cultural keystone species in the PAD (Garibaldi and Turner, 2004; Garibaldi, 2009; P. Marcel, pers. comm. 2011). Muskrat may be an indicator of the health of wetlands because they are sensitive to changes in water levels (e.g., Fuller, 1949; Smith, 1983; Thorpe, 1986; J. Fraser, pers. comm. 2014). Muskrat rapidly and dramatically increase in abundance when habitat is improved (e.g., after flooding) (Poll, 1980; Kroll and Meeks, 1985; Wiacek and Westworth, 1999; WAE Ltd., 2005). Muskrat are also important members of ecosystems because they are prey for mink, foxes, marten, fishers, wolves, wolverines, and birds of prey, and they can alter circulation of waterways and patterns of vegetation (e.g., Westworth, 1974; Danell, 1979). To Indigenous people in the PAD, muskrat provide food, material for clothing, income, and a deep link to their culture, landscape, and ecosystem that cannot easily be expressed in Western terms (see Fuller; 1950; Tanner and Rigney, 2003; ACFN and MCFN, 2010; McCormack, 2011).

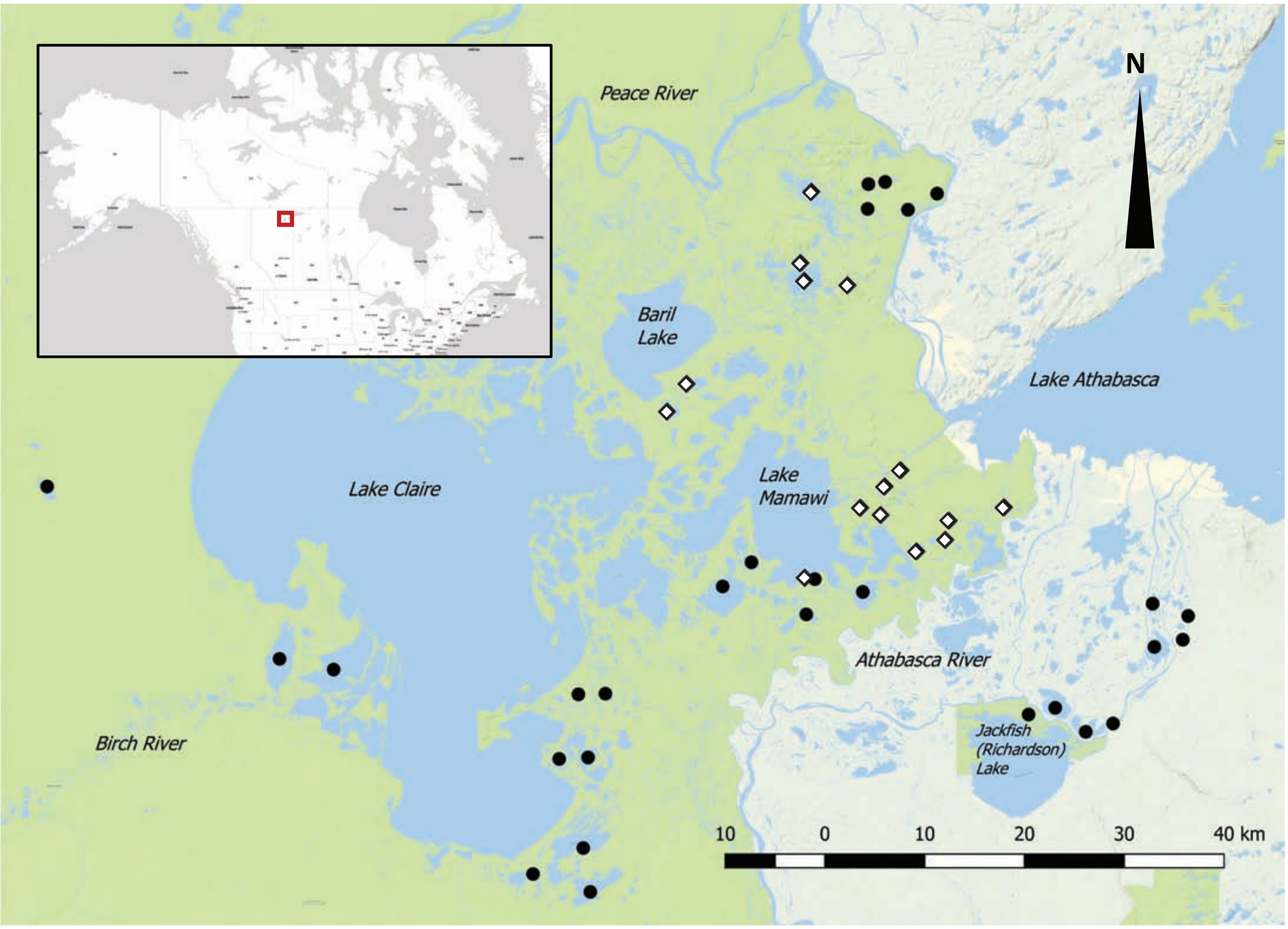

FIG. 1. Locations of basins in the Peace-Athabasca Delta where winter surveys for muskrat houses took place in 1973–2015 (diamonds) and 2011–15 (circles).

> Muskrat are like the bank for us. If you look back at fur prices you used to be able to go out and trap enough rats in one winter to get yourself a new boat and a motor by spring. Then you could fish for the summer to feed your family and your dog team. You could still do that today, if there were enough rats! In the old days we didn't worry about muskrat because we always knew they were there if we needed them. It was like money in the bank. We're only interested in muskrat now because they're suddenly gone, and it's just one indicator of the bigger picture of what's going on, and what's happening to our water.
>
> Ron Campbell: Mikisew Cree First Nation

Muskrat abundance in the PAD has been well below historical levels in recent decades (WAE Inc., 2005; Hood et al., 2009), and low abundance is also a recent concern in the Mackenzie Delta (Brietzke, 2015). The reliance of muskrat in a natural system on flooding, which provides adequate water and vegetation, is well known both to local trappers and elders and to experienced biologists (e.g., Bellrose and Brown, 1941; Elton and Nicholson, 1942; Fuller, 1949; Westworth, 1974). Depth of water under ice is relevant to whether muskrat can survive and feed on green vegetation under the ice throughout the winter (Westworth, 1974; Virgl and Messier, 1997), and depth of water before freeze-up affects their ability to access and select habitat in basins for building houses, overwintering (i.e., selection of habitat during fall dispersal), and feeding throughout the summer (Westworth, 1974). We hypothesized that (1) the abundance of muskrat in the PAD is driven by flooding and (2) the mechanism by which flooding affects muskrat is an increase in water depth. If the abundance of muskrat is driven by flooding, then abundance of muskrat will be inversely related to the number of years since the last major flood. If the mechanism by which flooding affects muskrat is an increase in water depth, then increased water depth will be associated with an increase in abundance of muskrat. To test the hypothesis that muskrat houses were more difficult to count in deeper snow, we also measured the depth of snow on the days we counted muskrat houses by snowmobile. From past experience, we predicted a negative relationship between depth of snow and abundance of muskrat.

Our study could not have been done without the expert guidance of Indigenous people of Dene, Cree, and Metis heritage. We therefore seek to express our results in a way that respects and acknowledges the contributions of Indigenous peoples to understanding the relationship between muskrat and flooding in the PAD, now and in the future.

METHODS

Muskrat Surveys

Our data on abundance of muskrat were from (1) surveys conducted by the Canadian Wildlife Service (CWS) from 1973 to 1979 (Smith, 1976; Stelfox and McGillis, 1977; Poll and Stelfox, 1978; Poll, 1980), (2) surveys commissioned by BC Hydro and Parks Canada and led by D.A. Westworth and R. Wiacek from 1998 to 2004 (Wiacek and Westworth, 1999; WAE Inc., 2002, 2005), and (3) ongoing surveys initiated in 2011 by members of the Peace-Athabasca Delta Ecological Monitoring Program (PADEMP), including local trappers and IK holders, with staff from Wood Buffalo National Park. Several trappers and IK holders involved in the design of the ongoing PADEMP survey were also instrumental in completing earlier surveys for the CWS and BC Hydro. Basins surveyed in the PAD were selected on the basis of local IK of places that had historically been important for trapping muskrat and are still accessed by trappers today (Fig. 1).

Issues with Combining Data among Surveys

We identified two main challenges to comparing results among historical and contemporary surveys: first, the initial list of basins surveyed was not consistent among surveys, and second, the historical data lacked records of observer effort. We addressed these challenges by focusing our analysis on the subset of basins (24 basins) that were re-visited at least five times from 1973 to 2015. In inspecting the data, and in discussions with past and present surveyors, we found that variation in survey effort generally was not a major concern for two reasons. First, the magnitude of changes in muskrat abundance was very large, and most years had counts of zero. Second, the effective area in most basins that is suitable for muskrat is fairly well defined and can be accurately searched by experienced trappers, who know where to find muskrat in a specific basin and year through Indigenous knowledge generated over decades of revisiting basins, conversing with other trappers, and pre-survey reconnaissance.

House Counts and Indigenous Knowledge

Muskrat in the PAD build houses in the fall before freeze-up, and the number of houses remains consistent over the course of the winter until they deteriorate in the spring (Westworth, 1974). We counted houses by snowmobile between late November and early April. IK was invaluable both in accessing the basins and in determining where muskrat houses were likely to occur within basins. The cooperative nature of the surveys, over-night stays in trapping cabins, and multiple meetings including elders before and after surveys provided opportunities to share, exchange, and discuss knowledge about muskrat. To estimate the relative abundance of muskrat we used counts of muskrat houses, which is a commonly used index in highly seasonal environments such as the PAD where houses do not last more than one year (Proulx and Gilbert, 1984). We then calculated the number of muskrat houses per square kilometre by dividing the count of houses per basin by the surface area of the basin. We estimated surface area of each basin using the best available imagery to trace the outline of the basins on Google Earth Pro v.7.1.8.3036 and examined track logs of the hand-held GPS units that observers carried throughout the surveys to verify that search effort accurately reflected the size of the basins.

Water Levels and Snow

We determined years with major floods from historical records in Poll and Stelfox (1978), Peterson (1992), the Peace-Athabasca Delta Technical Studies report (PADTS Group, 1996), and unpublished data from Parks Canada (Parks Canada, unpubl. data. 2017). Between 1970 and 2015, significant spring floods occurred five times: in 1972, 1974, 1996, 1997, and 2014. We assumed that all basins surveyed were flooded during those years. In 2011–15, we drilled holes in four places across the widest part of each basin to measure ice thickness and water depth. We estimated the depth of water before fall freeze-up as depth of water + 0.92 (depth of ice) in order to account for the expansion of water as it freezes (D. Peters, pers. comm. 2017). We measured the depth of snow at each location where we measured water depth.

Analysis

All our statistics were done using R, version 3.3.3 (R Development Core Team, 2017). We ran two main analyses: one to determine whether density of muskrat decreased with the number of years since flooding and one to determine how density of muskrat was related to depth of water and snow. To determine whether the density of muskrat houses decreased with the number of years since flooding, we ran generalized linear mixed effects models (GLMMs) with a logit link function in the package lme4 (Bates et al., 2014). To determine whether flooding affects the abundance of muskrat, we included *years since flood* (number of years since a major flood) as a fixed effect. To determine whether the density of muskrat houses increased with water levels recorded during surveys in 2011–15, we ran a GLMM with *average depth of water in the fall* (the approximate amount of water present at freeze-up, when muskrat finish building their houses) and *average snow* as fixed effects. We tested whether there was evidence for an “optimal” depth of water in the fall by comparing the performance of two competing models: the first with *average depth of water in the fall* as a linear predictor of abundance of muskrat houses and the second with *average depth of water in the fall* as a non-linear, quadratic predictor of abundance of muskrat houses. In all our models, we included *basin* as a random effect to account for non-independence of repeated visits to basins over time. We were working with count data that were zero-inflated (many basins had no muskrat houses) and overdispersed, so we used a negative binomial distribution, which assumes that all data are positive and the variance around predicted values is greater than the predicted value (Zeileis et al., 2008). We calculated maximum likelihood (ML) estimates of parameters for our models using the Laplace approximation. We assessed the significance of fixed effects by using the Akaike Information Criterion corrected for small sample sizes (AICc) to compare models that included predictors of the density of muskrat houses on the landscape to a null model (a model including only basin as a random effect) to test whether adding predictors improved the model’s ability to describe the patterns we observed in the density of muskrat houses (Burnham and Anderson, 2002; Bolker et al., 2009). We calculated AICc using the function AICc in the package MuMIn (Bartoń, 2016). When selecting models for further examination, we chose the most parsimonious models (those with the lowest AICc score and the fewest parameters) (Table 1). We did not consider parameters to be useful predictors of the abundance of muskrat houses when adding them to a model either did not change ΔAICc values by more than 2 or had little or no effect on log-likelihood values (Arnold, 2010). To test how different ways of estimating muskrat abundance affected our results, we ran the same models with the raw number of houses per basin and the density of houses (calculated as the number of houses per basin, divided by the surface area of the basin). Both ways of estimating our response variable (abundance of muskrat) yielded similar results.

RESULTS

Relationship between Density of Muskrat Houses and Flooding

Our data set encompassed four major fluctuations in abundance of muskrat, with estimated peaks around 1975, 1999, 2006, and 2015 (Fig. 2A). The average count of muskrat houses per km^2 varied from zero (in 2003 and 2011 surveys) up to 87 (in 1974) and was relatively high in the two years immediately following the ice-jam flood events of 1974, 1997, and 2014 (Fig. 2). The number of years elapsed since a major ice-jam flood in the PAD was a good predictor of the density of muskrat houses in basins from 1973 to 2015 (Fig. 2B); the GLMM including years since flood as a fixed effect was better than the null model including only basin as a random effect (ΔAICc = 69). The density of muskrat houses declined by 79% for every additional year following a significant flood event from 1973 to 2015 (GLMM: estimate = −1.58, SE = 0.16, $z = -9.88$, $p < 0.0001$; Table 2).

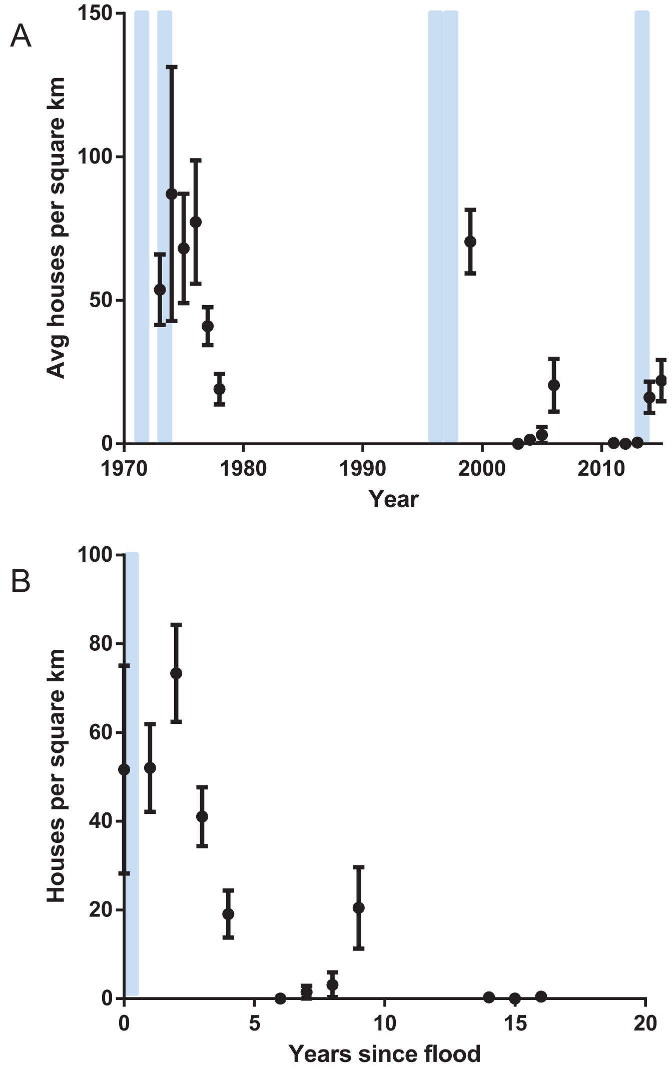

FIG. 2. Mean density (± SE) of muskrat houses in 24 basins in the Peace-Athabasca Delta surveyed at least five times from 1973 to 2015, shown (A) by year and (B) in relation to the number of years since the last significant flood. Shading indicates years with significant floods (1972, 1974, 1996, 1997, and 2014).

Density of Muskrat Houses in Relation to Water and Snow

For the 27 basins surveyed from 2011 to 2015, the number of years elapsed since a major ice-jam flood in the PAD remained the best predictor of the density of muskrat houses in basins (GLMM: estimate = −1.54, SE = 0.18, $z = -8.70$, $p < 0.0001$; Table 2). The estimated depth of water at the time of freeze-up was a good non-linear (negative, quadratic) predictor of the density of muskrat houses (Fig. 3A; GLMM: estimate = −0.46, SE = 0.17, $z = -2.67$, $p = 0.0077$). We found that muskrat houses were most dense in a specific range of depths of water in the fall; increasing

TABLE 1. Structure and parameter estimates for our best models used to predict density of muskrat in basins of the Peace-Athabasca Delta. Models 1 and 2 are for 24 basins, visited at least five times from 1973 to 2015. Models 3 and 4 are for 27 basins, visited from 2011 to 2015. Models were computed using maximum likelihood (ML) estimates; details are provided under *Analysis*.

Model	AICc	Log-likelihood	Residual deviance	Residual df
1: Years since flood (1973–2015): muskrat ~ yearssinceflood + (1 | basin)	1461.49	−726.6	1453.3	199
2: Null model (1973–2015): muskrat ~ (1 | basin)	1530.96	−762.4	1524.8	200
3: Full model (2011–15) muskrat ~ yearssinceflood + fall water + fall water^2 + (1 | basin)	519.95	−253.5	507.0	89
4: Null model (2011–15) muskrat ~ (1 | basin)	566.20	−280.1	560.2	92

water depth is positively associated with density of muskrat houses until about 150 cm of water, and negatively associated with water depth beyond 150 cm of water (Fig. 3A). Our model with average depth of water in the fall as a non-linear, quadratic predictor of density of muskrat houses was better than our model using average depth of water in the fall as a linear predictor of density of muskrat houses (ΔAICc = 4). For the 27 basins surveyed from 2011 to 2015, average depth of snow was not a good predictor of the density of muskrat houses. Including snow as a linear or non-linear predictor of density of muskrat houses resulted in slightly higher AICc values for the overall model, compared to models that did not include snow as a predictor (ΔAICc = 5 for linear, ΔAICc = 2 for non-linear). Snow was not statistically significant either as a linear predictor (GLMM: estimate = −0.28, SE = 0.26, $z = -1.08$, $p = 0.28$) or as a non-linear predictor (GLMM: estimate = −0.18, SE = 0.26, $z = -0.69$, $p = 0.49$).

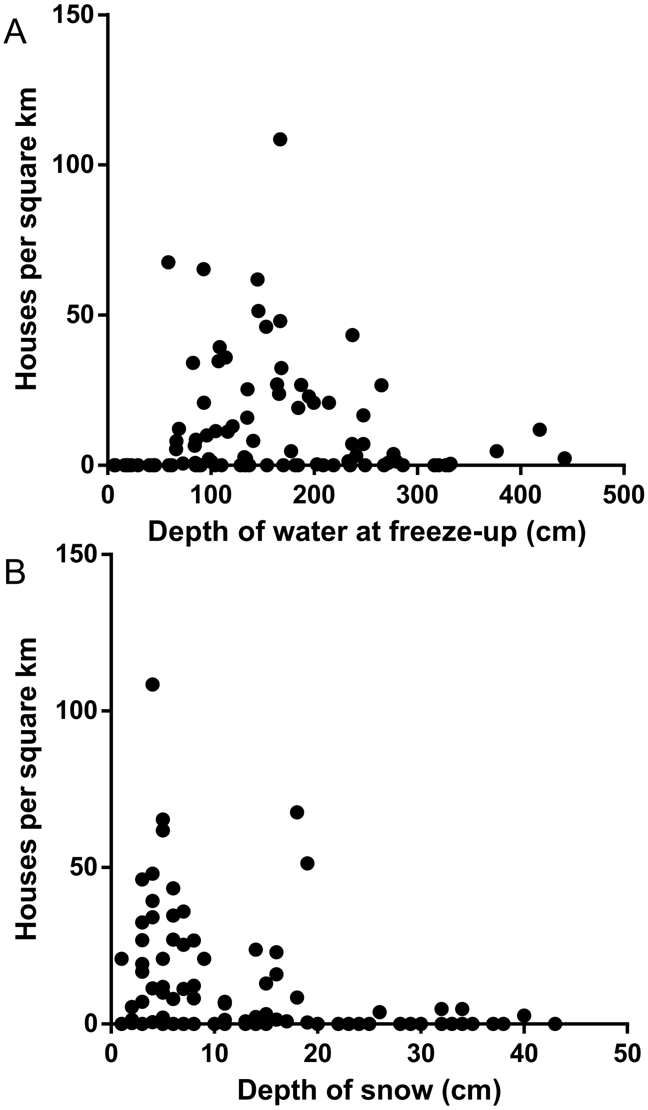

FIG. 3. Average density of muskrat houses in 27 basins in the Peace-Athabasca Delta from 2011 to 2015, in relation to depth of water at freeze-up, estimated (A) by the total depth of ice and water during winter surveys, and (B) in relation to the average depth of snow at the time of surveys.

DISCUSSION

As predicted, between 1973 and 2015 the density of muskrat houses generally declined over periods without flooding in the PAD. A decrease in density of muskrat houses associated with lack of flooding supported our hypothesis that abundance of muskrat is driven by flooding in the PAD. One nuance to the relationship between major floods and density of muskrat houses was a small peak in the density of muskrat houses around 2006, nine years after a major ice-jam flood in 1997 (Fig. 2A). This small peak followed a relatively small ice jam on the Athabasca River in 2003 (Wolfe et al., 2008) and an unusual summer flood event due to high rainfall in 2004 (D. Peters, pers. comm. 2016). The basins that showed an increase in muskrat abundance from 2003 to 2006 were mostly located in areas with hydrology that is influenced by both the Peace and the Athabasca Rivers. In keeping with our predictions, there was a clear association between water levels at the time of fall freeze-up and density of muskrat houses in the 2011–15 surveys. We found evidence for an "optimal" range of water depths, within which basins have higher abundance of muskrat houses. The highest densities of muskrat houses were in basins with 60–250 cm of water at the time of freeze-up (Fig. 3A). Notably, we found no muskrat houses in basins with an average estimated fall water depth of 50 cm or less (Fig. 3A). However, we are cautious about this result because although we counted houses throughout

TABLE 2. Predictors for fixed effects from our best models for density of muskrat houses in basins in the Peace-Athabasca Delta. Summary statistics of overall models are shown in Table 1. Details of model-selection are provided under *Analysis*.

Predictor	Estimate	Standard error	z	p
Years since flood (1973 – 2015)	−1.5845	0.1603	−9.882	< 0.0001
Years since flood (2011 – 15)	−1.5433	0.1774	−8.702	< 0.0001
Fall water (linear) (2011 – 15)	0.7705	0.2848	2.706	0.00681
Fall water (quadratic) (2011 – 15)	−0.4646	0.1743	−2.666	0.00768

each basin, we measured the depth of water at only four locations in each basin. To determine whether muskrat have a preferred depth of water at freeze-up in the PAD, a more effective approach would be to measure the depth of water at each individual muskrat house. IK holders have a much more intimate understanding of the water depths that muskrat prefer, as they are familiar with the preferences of muskrat within basins.

The mechanism by which flooding affects abundance of muskrat is more complex than an increase in depth of water at the time of fall freeze-up. Elders and trappers provided several potential explanations for why muskrat might prefer habitat with an "ideal" range of water depths and may not use basins if water is too deep or too shallow. Basins that are too deep tend to have less vegetation available for muskrat food, while basins that are too shallow freeze completely to the bottom, which makes it difficult for muskrat to feed in the winter. IK holders further noted that muskrat respond to diminishing water levels by retracting ranges to secondary habitat on banks of rivers or channels, persisting as "bank rats." These "bank rats" can then rapidly disperse and multiply during flood events, moving back to preferred habitat in shallow basins (Messier and Virgl, 1992). Factors such as dispersal of muskrat and connectivity of basins are likely important in determining the density of muskrat houses in a particular basin. We have recently begun collecting genetic data to investigate the historical links between floods and dispersal events for muskrat in the PAD.

As predicted, there was a negative relationship between density of houses and depth of snow at the time of surveys. It is likely that this relationship existed because it is more difficult to count houses by snowmobile when snow is deep and is not a true reflection of the abundance of muskrat. The influence of snow on estimates of muskrat abundance was likely affected by the way snow accumulates in basins in the PAD. Several centimetres of snow at the centre of a basin can accumulate as large drifts at the margins of basins, and on top of muskrat houses themselves, thereby hiding houses from view. Our results suggest that we might be concerned about the accuracy of house counts done when snow measured at the middle of basins is more than 20 cm deep; observers tended to count very few muskrat houses when snow was more than 20 cm (Fig. 3A). In the course of designing this study, conducting the fieldwork, and discussing our results, experienced trappers shared extensive and detailed IK regarding the ecology of muskrat. Acknowledging that a scientific journal article describing an observational experiment is not the best venue to share most of these observations, we present a few main points that informed our interpretation of results and could inform plans for future studies.

Houses as a Measure of Abundance

Counting houses provides only a rough estimate of muskrat abundance, as multiple muskrat can occupy a single house (see Proulx and Gilbert, 1984; Engeman and Whisson, 2003). An alternative to counting houses is counting push-ups, which are small holes in the ice with piles of mud and vegetation that muskrat use for feeding (Westworth, 1974). Counting push-ups is not more effective because a single muskrat (or multiple muskrat) can use multiple push-ups, and push-ups are more difficult to count accurately by snowmobile. In years that are exceptionally cold or have low water, muskrat can abandon houses, thereby allowing them to freeze, and burrow into the mud of basins or riverbanks to survive the winter (Messier and Virgl, 1992). No known studies have explicitly compared counts of houses to a census of muskrat in the PAD. However, local trappers and elders agree that more houses are built in years when there are more muskrat, and more muskrat can be trapped (even within individual houses) in years with more muskrat houses. The information above suggests that counts of muskrat houses may be a conservative estimate of muskrat abundance.

What Else Affects Abundance of Muskrat?

The presence of water following spring ice-jam floods is the main driver of muskrat abundance in the PAD. However, trappers note that responses of muskrat abundance to water levels or ice-jam flooding is likely mediated by responses of vegetation to flooding, frequency of flooding, hydrology of basins (e.g., connectivity to other basins, flow, and depth), disease, water quality, and abundance of predators. These factors are summarized in Table 3 as a series of questions for future investigation.

The influence of water levels on shoreline vegetation seems to be a major factor in determining populations of muskrat (Nadeau et al., 1995; Virgl, 1997). Water increases the availability of shoreline vegetation, which provides food that increases the survival of young, as well as room to forage under ice in the winter (Virgl, 1997). Attempts to manage muskrat populations by influencing water levels should consider not only how water levels

TABLE 3. Summary of questions for future investigation regarding factors that drive abundance of muskrat in the Peace-Athabasca Delta. These questions were identified by experienced trappers and Indigenous knowledge-holders as high priorities.

Question	Explanation	Suggested research methods
1) Are stable water levels or fluctuating water levels better for muskrat?	Muskrat occupy a wide geographical area. In some areas, water levels are stable. The PAD is a productive area for muskrat, but numbers have historically fluctuated widely over time.	• Genetic studies investigating inbreeding depression or evidence of population bottlenecks in populations with fluctuating water levels. • Standardized comparison of muskrat productivity over time between areas with stable vs. fluctuating water levels.
2) What is the mechanism for increased muskrat abundance following flooding? To what extent do the effects of floods lag behind flood events?	Mechanisms may include increased availability of habitat (food, water) via effects on vegetation, increased overwinter survival with deeper water in basins, and increased dispersal (“seed rats” moving from rivers into flooded areas) through access to new areas.	• Genetic/spatial analysis of muskrat populations through fluctuations in population, water levels, and range. • Study of population bottlenecks and dispersal range, comparing flood years to periods between floods (through genetics, or satellite tracking/telemetry).
3) How does hydrology of basins affect muskrat abundance?	Hydrological factors that may influence suitability of basins for muskrat over time may include connectivity (e.g., channels vs. perched basins), porosity of substrate (rate of drawdown), and rates of evaporation (due to climate or surface area-to-volume ratio).	• Hydrological assessment/description of basins surveyed for muskrat, combined with multivariate analysis to separate the influence of other co-varying factors affecting muskrat abundance.
4) How can knowledge of the link between flooding and muskrat be used to manage existing muskrat habitat, or to restore habitat that is no longer suitable for muskrat in the PAD?	Simulating floods or enhancing the ability of basins to retain water has increased muskrat abundance in some situations (e.g., Smith, 1985; Eng and Green, 1989; Toner et al., 2010). In the PAD, these measures require understanding of impacts of flood frequency and extent, lag effects on muskrat and vegetation, and longevity of effects on muskrat abundance.	• Improvement of predictive models linking hydrology and muskrat abundance. • Replicated and controlled experiments altering hydrology of basins by adding or removing water with pumps, human-caused ice jams, enhancing hydrological connectivity by opening channels (See e.g., Smith, 1985; Eng and Green, 1989).
5) What is the effect of water quality on muskrat abundance and health?	Muskrat seem tolerant of poor water quality (d’Entremont, 2014), but trappers are concerned about muskrat health and susceptibility to stress or disease as it relates to exposure to contaminants (e.g., presence of metals, nutrients, and hydrocarbons). Water quality likely interacts with rates of flow, flood events, and hydrology of basins, so it is difficult to address this factor on its own.	• Water sampling in basins with variation in muskrat abundance. • Assessment of health of muskrat across basins via sampling for contaminants in water, vegetation, and muskrat tissues and organs. • Multivariate analysis separating influence of other co-varying factors (e.g., vegetation and depth of water) that affect muskrat abundance.
6) How do high density and disease affect muskrat populations? Does lack of intense trapping at high densities lead to more dramatic declines in populations?	Trappers report that when there were many trappers on the land, they could regulate population crashes attributable to disease caused by high densities after floods. With fewer trappers on the land, this may no longer be the case, and perhaps population bottlenecks are exacerbated as a result.	• Requires improved understanding of the effects of density on disease outbreaks and the impacts of disease on muskrat populations. Controlled and replicated experiments with removal or trapping of muskrat at some basins (and not others, e.g., on occupied vs. unoccupied trap lines) could help.
7) How accurate are counts of muskrat houses or push-ups as estimates of abundance of muskrat?	Counting houses only provides a rough estimate of the abundance of muskrat; see section on “Houses as a Measure of Abundance.”	• Opening muskrat houses to count individuals per house, and/or interviewing trappers; comparing counts of houses and push-ups to estimates of population size from genetics or mark-recapture.

influence vegetation, but also how muskrat use different types of vegetation (e.g., Danell, 1978). Muskrat can persist through a range of conditions, including human-altered wetlands with invasive vegetation and water with high concentrations of contaminants (e.g., Clark, 1994; Cotner and Schooley, 2011; d’Entremont, 2014), but trappers point out that persistence does not mean that muskrat are healthy (see Halbrook et al., 1993). Instead, they emphasize the necessity of knowing much more about muskrat than an estimate of abundance. As stated by one Parks Canada staff member who was involved throughout the survey:

> In 2011, when we first came together to discuss, design, and then conduct a muskrat survey, one of the first meetings that I facilitated was focused on identifying which muskrat basins to include in the survey. In my mind, at the end of that meeting we had selected 15 basins that were relevant to members of the group and represented important muskrat habitat in the PAD. Alas, I was so naïve then, to think that elements of IK could simply be plucked from that body of knowledge. I’ve since learned that they will come to you, and they will come through the telling of a story—so you must be a good listener, which takes time. Unbeknownst to me back in 2011, the suite of basins that were identified represented only the beginning of the story that was going to be shared with me. We travelled to those basins, I was prepared to count houses, measure

> snow, ice and water depth, but when we got to many of them, we found ourselves standing in the middle of grasslands that were transitioning to willow stands! I was confused. The next year we met again and a new suite of basins was selected—again we surveyed—I collecting the all-important snow, ice and water depths, from the basins that had water, while listening to the local participants talk about present and past conditions and concerns for present and future conditions while they helped me. I believe now that my partners took me to those places early on in our endeavour to show me how much had changed, and that showing me those places was where they began their story.

CONCLUSIONS

The repeated fluctuations of muskrat abundance from 1973 to 2015 indicate a strong historical link between ice-jam flooding and relative abundance of muskrat in the PAD. Though many factors threaten to reduce the frequency and intensity of ice-jam floods in the PAD, the link between muskrat and flooding can be restored when conditions are appropriate. Management actions such as artificially induced flood events may be somewhat effective at restoring muskrat populations (e.g., Smith, 1983, 1985). Abundance of muskrat increases in response to ice-jam flooding in the PAD, but with many mitigating factors that remain poorly understood by Western scientists. A key first step is continued and consistent monitoring of water levels and abundance of muskrat in the PAD. Winter surveys not only provide useful data, but also enable Indigenous people and Western scientists to engage on the land. IK and Western science can and should continue to work together in productive, mutually supportive ways to identify the specific ways in which floods have a positive effect on muskrat and guide development in a way that ensures cultural and ecological sustainability in the PAD.

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