diversity

Article

Trappings of Success: Predator Removal for Duck Nest Survival in Alberta Parklands

Emily M. Blythe * and Mark S. Boyce

Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada; boyce@ualberta.ca
* Correspondence: blythe@ualberta.ca

Received: 10 February 2020; Accepted: 15 March 2020; Published: 24 March 2020

Abstract: Nest survival is most limited by nest predation, which often is increased by anthropogenic causes including habitat fragmentation, mesopredator release and predator subsidies. In mallards and other upland-nesting duck species in the North American prairies, the rate of nest survival is the vital rate most influential to population dynamics, with 15%–20% survival required for maintenance of stable populations. Predator removal during the nesting season has increased duck nest survival on township-sized (9324 ha) areas of agricultural ecosystems in eastern locations of the prairie pothole region (PPR). However, predator removal has not been evaluated in western parkland habitats of the PPR where three-dimensional structure of vegetation is considerably greater. During 2015–2017, we evaluated nest survival on control and predator-removal plots at two study areas in the parklands of central Alberta, Canada. In the second year of the study, we transposed predator removal to control for habitat effects. Estimates of 34-day nest survival did not significantly differ between trapped ($\bar{x}$ = 20.9%, 95% CI = 13.2%–33.7%) and control ($\bar{x}$ = 17.8%, 95% CI = 10.5%–30.0%) plots in any year. We do not recommend predator removal be continued in Alberta parklands due to its ineffectiveness at improving duck nest survival at the local scale.

Keywords: *Anas* spp.; nest survival; nest predation; predator removal; prairie pothole region; compensatory predation

---

1. Introduction

In mallards (*Anas platyrhynchos*) and presumably other duck species, nest survival is the most important vital rate influencing population dynamics in the Prairie Pothole Region (PPR) [1]. Maintenance of stable dabbling duck (*Anas* spp.) populations requires ~15%–20% annual nest survival [2–4]; success herein defined as the hatching of at least one duckling. Low nesting success is usually attributed to degradation of breeding habitat, including the loss of nesting cover and wetlands resulting from agricultural, industrial and residential land use [5,6]. Anthropogenic habitat alteration also has led to increased nest predation [4,5,7].

Nest predation is the strongest limiting factor of nest survival in ducks [8], and indeed most bird species [9]. Mesopredator release, resulting from the loss of regulatory influence by apex predators, can contribute to enhanced richness and abundance of mid-trophic level predators [10,11]. Anthropogenic resource subsidies, provided unintentionally as food or shelter, is another phenomenon that can benefit generalist predators in highly altered habitats [12,13] like the PPR. Loss of cover, concentration of nests in limited habitat, ease of travel by predators and loss of landscape heterogeneity can enhance foraging efficiency of avian and mammalian predators [7,14–16]. A rich guild of nest predators, arising from anthropogenic changes to the environment, will have a diversity of foraging behaviours that increases the risk to all nests regardless of nest distribution strategy [17,18].

Where substantial numbers of ducks breed in areas of suitable habitats, but nest survival remains suppressed due to high nest predation rates, intensive predator management can be an effective tool to mitigate nest losses [19]. The goals and policies outlined in the North American Waterfowl Management Plan [20] aim to improve waterfowl populations across the continent using strategies based on habitat conservation. However, for some areas, habitat-based strategies alone have proven inadequate in meeting local management goals; in such cases, short-term intensive management might be warranted and can be beneficial [6]. Lethal trapping of predators is flexible in its application in regards to space and time [19] and has been shown to increase nest survival for waterfowl and other avian species [21,22]. For example, predator removal resulted in increased dabbling duck nest survival in prairie ecosystems of Saskatchewan [23] and North Dakota [19,24–26], even when done at the relatively small scale of 259 ha [27]. In the Saskatchewan parklands, however, predator removal was associated with higher dabbling duck nest survival in only one of three monitored years [28]. Prevalence of results indicating successful implementation of predator removal may reflect publication bias towards significant results, otherwise known as the "file drawer effect" [29]. Most evaluation of predator removal to improve duck nest survival in North America has been conducted in prairie ecosystems dominated by agriculture with fewer data from parkland habitats.

Predator removal is done at substantial economic, social and potential ecological cost, and often must be continued perpetually to maintain results [22]. Documenting its effects is essential prior to implementation, to avoid unintended consequences and because predator removal can result in economic trade-offs with other initiatives such as habitat acquisition [6,30]. Potential exists for predator removal to be ineffective due to compensatory predation [31–33], immigration [34] or increased reproductive output by predators in response to higher mortality [35,36]. Other unintended but potential consequences of perturbing complex ecosystems with predator removal include competitive release of alternative prey [37] or trade-offs within vital rates of the species meant to benefit. For example, nesting exclosures were found to be successful in increasing hatching rates of snowy plovers (*Charadrius alexandrinus*), but were associated with increased adult mortality, the vital rate to which snowy plover populations are most sensitive [38].

Nest survival may account for nearly half (43%) of the variation in annual population growth rates of midcontinent mallards in the PPR, according to sensitivity analyses by Hoekman et al. [1]. However, breeding hen and duckling survival also were important vital rates accounting for 19% and 14% of variation, respectively [1]. Outside the PPR, population growth of mallards in the Great Lakes region of the United States was most affected by non-breeding hen survival (36%), duckling survival (32%) and nest success (16%; [39]). Presumably, nest success, duckling and breeding hen survival also are important parameters for other species of upland-nesting ducks in the PPR, and possible correlation among them will further enhance their impact on population trajectories [40]. Therefore, it is important to assess the influence of a management action on multiple population parameters [26], especially due to the potential for opposing effects on multiple vital rates [38,41]. Apparent competition is an example of a mechanism that may be unintentionally induced by predator removal with negative consequences for adult hen or duckling survival. Apparent competition arises when enhanced predator abundance results from an increase in a primary prey species and predation on other, secondary prey species increases collaterally [42–44]. McCarter [45] found slightly higher raptor abundance on plots where mammalian predators were reduced, because raptors were possibly attracted to these plots by increased abundance of shared prey (though McCarter [45] suggests predominance of bottom-up trophic forces). McCarter [45] illustrates an example of how a predator community could shift in favour of principal hen and duckling predators with the removal of primarily egg predators.

Duck nest success in the Canadian PPR is generally below that seen in the American portion, due largely to differences in habitat management [46–48]. At the northern extent of the PPR, the parklands of Alberta contain important nesting habitats and predator removal has not been thoroughly evaluated as a method for improving nest success. Most studies of predator removal to enhance dabbling duck nest survival have occurred in prairie ecosystems, and the most recent evaluation in parkland habitats did not find supporting evidence warranting predator removal [28]. Though both ecosystems are dominated by agriculture, three-dimensional vegetation structure distinguishes the parklands from the prairies and the increased structural complexity provides more opportunity for compensatory predation. Socio-economic constraints in Alberta further reduce the probability of effectiveness of predator removal. Legal constraints necessitate partial predator removal, because species of conservation concern including long-tailed weasel (*Mustela frenata*) and American badger (herein referred to as badger; *Taxidea taxus*) could not be removed following provincial permit stipulations. Logistic constraints in the form of fragmentation of land tenure restrict predator removal to small, isolated land plots where access can be obtained and retained. Due to increased habitat complexity and different socio-economic forces, findings from prairie-based studies in American jurisdictions cannot be generalized to Canadian parkland habitats. Investigation of predator removal for enhanced duck nest survival in the aspen parklands is needed prior to its implementation as a management practice.

Our primary objective was to evaluate the null hypothesis that predator removal would not improve nest survival of upland-nesting ducks in central Alberta parklands as it has in U.S. prairie habitats. Due to enhanced potential for compensatory predation resulting from abundance of three-dimensional vegetation and constraints imposed by socio-economic forces, we predicted that nest survival would not differ significantly between predator removal and control plots. In conducting our experiment, we establish baseline nest survival estimates for our study areas in the absence of predator removal. Additionally, we tested the null hypothesis that predation of nesting hens also would not be affected by predator removal.

2. Materials and Methods

2.1. Study Area and Design

In June 2014, Delta Waterfowl Foundation biologists conducted ground and fixed-wing reconnaissance surveys of aspen parkland habitats in central Alberta. High densities of both breeding ducks (>25 pairs/km^2) and small (<2 ha) semi-permanent and permanent wetlands were confirmed near the communities of Bashaw and Viking (unpublished data, [49]). Near each community, 30 quarter sections (~64.7 ha parcels) were selected randomly with some constraints to serve as predator removal (“trapped;” $n = 20$) and control ($n = 10$) plots. Quarter sections with more than 65% tree cover, complete absence of water or unsuitable for trapping due to an occupied dwelling were excluded. Trapped and control quarter sections were at least 3 km apart to maintain independence, a distance based on the 12-km^2 home range of a resident coyote (*Canis latrans*) [50], the farthest-ranging mammalian predator on the study areas. Within both sets of 20 predator removal plots, half were randomly chosen for nest searching (the remaining 10 were trapped without nest monitoring) and all control plots were monitored. Twenty-seven quarter sections were replaced during the study at the request of landowners. Throughout the study, predator removal was annually transposed on quarter sections provided access was retained; for example, a quarter section that was trapped in 2016 became a control plot in 2017 (Figure 1).

Both study areas (Bashaw and Viking) are dominated by agriculture which consists predominantly of cattle grazing, cereal and oil seed production fragmented by a one-mile by one-mile road network and interspersed with oil and gas infrastructure. The landscape is characterized by rolling hills, stands of trembling aspen (*Populus tremuloides*), lakes and numerous pothole wetlands. Overwhelmingly, land is privately owned; however, most data were collected on land managed for duck production by Ducks Unlimited Canada (DUC). Such land was managed for maintenance of nesting cover and any grazing or haying was delayed until after 15 July, when most nesting activity had ceased [51].

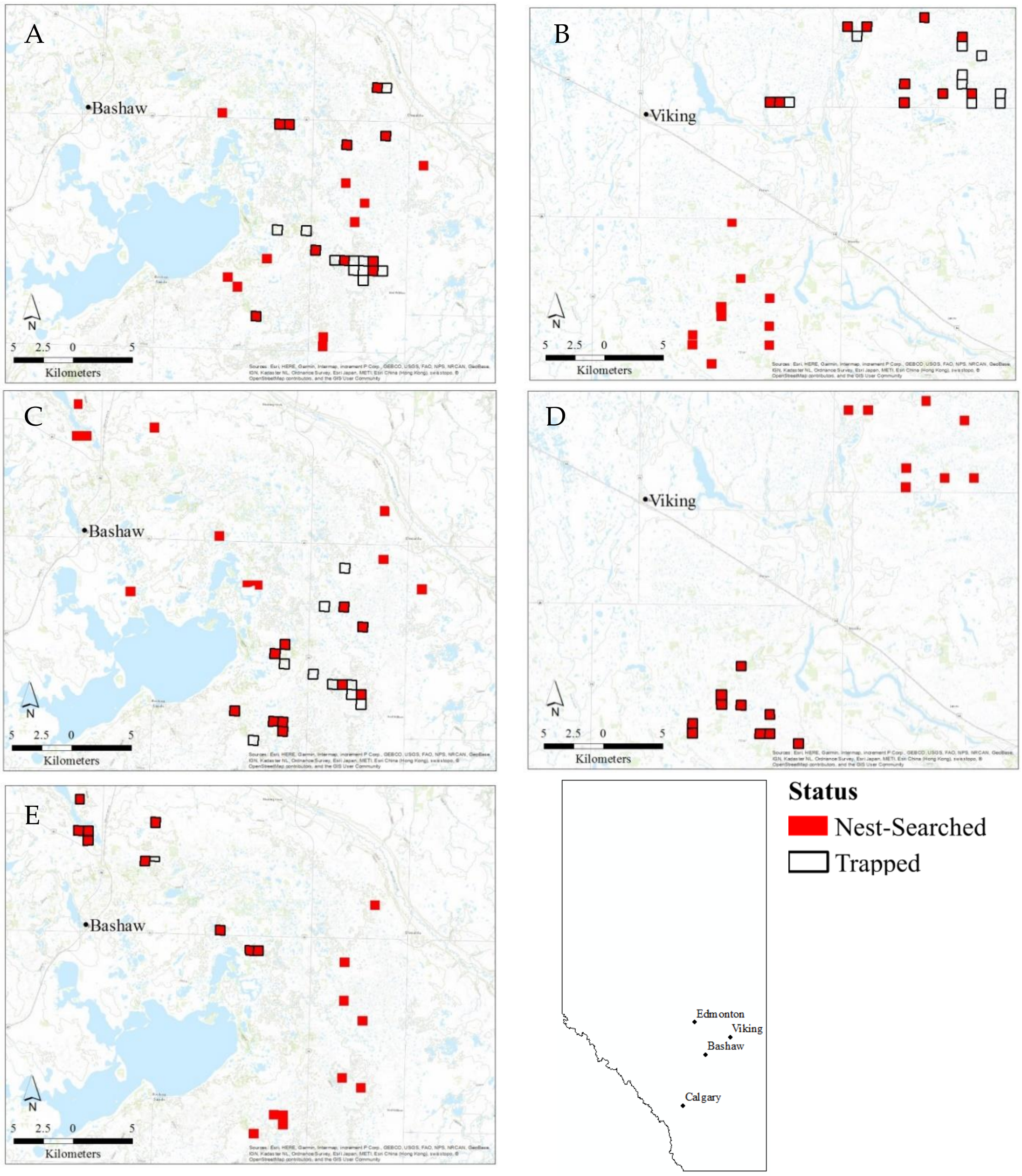

Figure 1. Maps of Bashaw and Viking study areas through 2015–2017, where (**A**) Bashaw 2015; (**B**) Viking 2016; (**C**) Bashaw 2016; (**D**) Viking 2017; and (**E**) Bashaw 2017. Red indicates nest-searched areas; black borders indicate predator removal.

In 2015, nest searching was limited to the Bashaw study area with 45% on privately tenured land actively grazed or hayed and 55% on land managed for duck production by conservation groups. Beginning in 2016, work was expanded to the Viking study area. During 2015–2018, 61 quarter sections were nest searched; most sites were managed as rotational pasture, with the remainder used for hay production. A total of 32 quarters were monitored for nests under both treatment conditions for at least one 3-month season each.

Dabbling ducks that were the focus of this research included mallard, northern pintail (*A. acuta*), northern shoveler (*A. clypeata*), blue-winged teal (*A. discors*), American green-winged teal (*A. crecca carolinensis*), gadwall (*A. strepera*) and American widgeon (*A. americana*). Nest or hen predators observed daily by field technicians included American crow (herein referred to as crow; *Corvus* *brachythynchos*), black-billed magpie (herein referred to as magpie; *Pica hudsonia*), red-tailed hawk (*Buteo jamaicensis*), Swainson's hawk (*B. swainsoni*) and northern harrier (*Circus cyaneus*), while common ravens (herein referred to as raven; *Corvus corax*) and great-horned owls (*Bubo virginianus*) also were often observed. Other nest or hen predators occurring in our study areas were striped skunks (herein referred to as skunks; *Mephitis mephitis*), raccoons (*Procyon lotor*), coyotes, red foxes (herein referred to as foxes; *Vulpes vulpes*), Franklin's ground squirrels (*Poliocitellus franklinii*), 13-lined ground squirrels (*Ictidomys tridecemlineatus*), badger, long-tailed weasel, short-tailed weasel (*Mustela erminea*), American mink (*Neovison vison*), Northern Goshawk (*Accipiter gentilis*), California gulls (*Larus californicus*) and ring-billed gulls (*L. delawarensis*). Nest predators notably absent from our study areas include rats (*Rattus* spp.) and egg-eating snakes [52,53].

2.2. Field Methods

One professional trapper was hired to remove nest predators in each study area, Bashaw and Viking, and predator removal took place from 15 March to 15 July of each study year. Crows, ravens and magpies were shot and targeted with Larsen and ladder traps. Skunks, raccoons, coyotes, foxes and ground squirrels were targeted with snares, box traps, foothold traps and body-gripping traps. Trapping was not standardized, and each professional trapper chose placement, density, type of trap and use of bait based on preference. As per provincial permit guidelines, badgers were not specifically targeted because they are provincially categorized as Sensitive [54]. Weasels (*Mustela* spp.) were not targeted because the long-tailed weasel is provincially listed as May Be at Risk [54]. California gulls and ring-billed gulls are other nest predators [55] that were excluded from removal efforts.

Upland nest-searching was conducted on each quarter section 2 to 3 times a season between 1 May–15 July, by dragging a 30-m chain between 2 ATVs [56]. Nest searching was limited to upland areas; forested and riparian areas were not searched. Upon flushing, the hen was identified to species and the nest was marked by GPS and with a thin metal rod at the nest bowl and a painted wooden lathe 10-m north. In 2017, lathes were placed randomly at variable directions and distances [57] in an effort to avoid "trap-lining" by corvids as reported by Picozzi [58], Buler and Hamilton [59] and others. Upon discovery and during weekly nest visits, we candled eggs to determine incubation stage [60] and monitored clutch sizes. At detection, visual obstruction was measured with a Robel pole at the nest bowl from 4 m in 4 cardinal directions [17,61]. Nests were left covered and conspicuously marked with 2 pieces of crossed vegetation; if the vegetation remained on the subsequent visit it indicated that the hen had not returned after being disturbed and investigator-induced abandonment was assigned. We revisited nests every 5–7 days to track incubation, until the nest either hatched or failed due to predation or other causes. Reconyx HC500^{TM} (Holmen, WI, USA) trail cameras were deployed opportunistically at a small subsample of 35 nests to identify predators. Cameras were deployed at both study areas on both predator removal and control plots and only on quarter sections where data for at least ten nests had been collected. To reduce abandonment risk, cameras were restricted to nests undergoing incubation [62,63] and limited to one per quarter section at a time to reduce the risk of search-image formation by predators [63,64].

Nest fates were determined from egg shell condition and other observations at the nest [56]. Nests were deemed either successful or failed, and failed nests were categorized 1 of 5 ways: (1) destroyed by a predator; (2) abandoned due to a predator; (3) abandoned due to investigator activity; (4) abandoned for unknown reasons; or (5) destroyed by an investigator. Abandoned nests contained intact eggs that were cold and no longer developing when characterized as failed. Predator-induced abandonment required evidence of predator activity in the form of missing eggs, partial egg depredation or remains of depredated hens. Investigator-induced abandonment was concluded when vegetation left conspicuously on the nest by investigators remained on the subsequent visit, indicating no return of the hen post-disturbance. Nests abandoned for unknown reasons were revisited by hens following the latest visit (ruling out investigator-induced abandonment) and were subsequently abandoned but showed no evidence of predator activity. Destroyed nests had no intact eggs remaining when failure was determined. A nest was deemed successful if evidence indicated that at least one egg hatched. Nests abandoned during the hatching phase (i.e., all ducklings died while pipping) were categorized as failed nests. When eggs were damaged by investigators they were removed from the nest bowl to reduce olfactory cues.

Nest monitoring was approved by University of Alberta's Animal Care and Use Committee (AUP00001473) and permitted by Alberta Environment and Parks (Research Permit #57638 & Collection Licence #57639). Predator removal was implemented by Delta Waterfowl Foundation and permitted by Canadian Wildlife Service (Permit #15-AB-SC004) and Alberta Environment and Parks (Research Permit #57626 and Collection Licence #57624).

2.3. Nest-Survival Modelling

Nests that were successful, or failed through destruction or abandonment due to predators, were included in nest survival analyses; nests that failed due to investigator activity or unknown causes were excluded. Nests that were monitored by a trail camera also were excluded from analyses because the presence of a camera can positively bias nest survival by reducing predation by neophobic predators [63]. Alternatively, cameras can negatively bias nest survival if they are used as visual cues by predators [57–59].

The RMark [65] nest survival package [66] was used to evaluate competing models describing daily survival rates (DSR) of nests as a function of individual-, group- and time-specific covariates [67,68]. This generalized linear modelling approach is equivalent to a known fate model with staggered entry, and uses the logit link to relate DSR and selected covariates [68,69]. Thus, DSR was estimated by back transformation as:

$$DSR = \frac{1}{1 + \exp\left\{-\left[\hat{\beta}_0 + \hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \ldots + \hat{\beta}_n x_n\right]\right\}} \tag{1}$$

where $\hat{\beta}_0$ is the intercept and $\hat{\beta}_i$ is the coefficient of covariate x_i for n covariates [67]. We made five assumptions in using this nest-survival model: (1) nests were accurately aged; (2) nest fates were attributed correctly; (3) discovery and monitoring of nests did not bias survival; (4) nest fates were independent of each other; and (5) daily survival rates were homogeneous [67,68]. All analyses were carried out in R [70] using the RMark package [65].

Nest survival analysis was restricted to nests from quarter sections that were studied under both control and predator removal treatments (n = 32). Spatial and habitat differences were largely accounted for by transposing treatment, so model covariates focused on temporal variation in nest survival: initiation date, age found, seasonal trends and year. Study area (Bashaw or Viking) and treatment (trapped/control) also were included as covariates. Year was treated as a fixed effect because we were interested in the transposition of trapping, represented by the combination of year and treatment. A linear time trend was modelled to represent increasing [19] or decreasing [46] survival through the season. A quadratic time trend represented a peak of nest predation corresponding with a peak for nest density at mid-season [51], or conversely, increased survival with nest density resulting from predator swamping [25]. In models including factorial covariates, the intercept was removed to avoid over-parameterization [65]. We used Pearson's r coefficient to test for collinearity and did not include covariates in the same model where $|r| > 0.6$ [71].

Akaike information criterion corrected for small sample sizes (AICc) was used to select the most parsimonious model [72] from which maximum likelihood estimates of DSRs were derived. On average, nests in our study (species pooled) took 34 days to hatch, so DSRs were raised to the power of 34 to estimate nest survival. To evaluate differences between predator removal and control plots, final nest survival estimates were compared within 2015 and across 2016–2017 using a series of z-tests and application of a Bonferroni correction [73].

2.4. Nesting Hen Mortality

We compared the number of nesting hens found depredated on transposed Bashaw control and trapped plots using Cochran–Mantel–Haenszel (CMH) statistics. We excluded nests from the Viking study area in hen mortality evaluation, because low trapping effort in 2016 (Table S1) and potential observer-enhanced nest predation in 2017 [57] introduced biases. We analysed all nests from transposed quarter sections in the Bashaw study area (n = 467) and stratified trapped and control plots by year. The Breslow-Day test for homogeneity was used to determine whether the likelihood of hen depredation in trapped versus control plots varied significantly across years [74]. A two-tailed CMH test employing Yates' continuity correction [75] was used to evaluate common odds ratios and 95% confidence intervals for hen depredation in trapped versus control plots after adjusting for year [76]. The odds ratio produced reflected odds of breeding hen mortality in the predator-removal conditions observed in our study, which we converted to probability of mortality following Equation (2):

$$P = \frac{o}{o+1} \tag{2}$$

where p is probability and o is odds. Analyses were carried out in R [70] using the vcd and DescTools packages.

Hoekman et al. [1] conducted sensitivity analyses of a stage-based matrix model describing the relationship between vital rates and population growth rate (λ) for female midcontinent mallards. We adjusted breeding hen survival for both stage classes (second year (SY) and after second year (ASY) to reflect our estimated probability of mortality in predator removal conditions. We retained Hoekman et al.'s [1] original parameter values for all other vital rates, including nest survival (0.13 for both SY and ASY) and re-calculated the fecundity and survival transitions constituting the stage-based matrix. We then calculated stable stage distributions and projected population growth rates using stage-based matrices representing our lower, upper and mean estimates of breeding hen survival. This was done as an exercise to demonstrate and contrast population impacts of lowered breeding hen survival and was not intended to represent accurate population growth estimates for reasons discussed below. Analysis was done using the popbio package [77] in R [70].

3. Results

Through 2015–2017, a total of 1136 nests were found and monitored; of these 1041 were suitable for analyses. Nests that were completely destroyed by investigators (n = 25), abandoned due to investigator activity (n = 38), monitored with a trail camera (n = 35) or found during hatching (n = 1), were excluded from analyses. Nests that were partially damaged by investigators (n = 48) were retained, as a chi-square test showed no significant difference in fates (hatch vs. failure) of damaged and undamaged nests (χ^2 = 1.3746, p = 0.241, df = 1, n = 1041). A total of 893 nests occurred on quarter sections that had treatment transposed at least once. Blue-winged teal nests were the most common (n = 555); fewer than 30 nests were found for green-winged teal, American widgeon and northern pintail (Table 1). Mean nesting period for all nests pooled was 34 days.

A large proportion of nests were depredated or abandoned with evidence of predator activity (60.1%); see Table 1 for nest fates by duck species. Within the Bashaw study area between 2016 and 2017, the number and proportion of nests hatching and failing were very similar despite the transposition of predator removal (Figure 2). Private land under active hay and cattle production comprised a substantial portion (45%) of the 2015 study area, compared to 2016 and 2017 where 97.5% and 100% of quarter sections were owned by DUC, respectively. DUC delays haying or grazing until 15 July, after the nesting season, so differences in management regimes affecting nests studied in 2015 eliminates a direct comparison of nest fates between 2015 and 2016–2017 (Figure 2).

Table 1. Species composition of fates and total count of nests monitored in Bashaw and Viking study areas, 2015–2017. Nests abandoned or destroyed due to investigator activity not included. Reason for nest abandonment was attributed to predator if there was evidence of predator activity, and as unknown cause otherwise.

Species	Destroyed	Hatched	Abandoned		Total
			Predator	Unknown	
American green-winged teal	1	4	0	0	5
American widgeon	8	4	1	2	15
Blue-winged teal	275	192	41	47	555
Gadwall	57	49	15	7	128
Mallard	58	30	10	8	106
Northern pintail	1	0	0	0	1
Northern shoveler	94	58	22	7	181
Unidentified	41	4	2	3	50
All species combined					1041

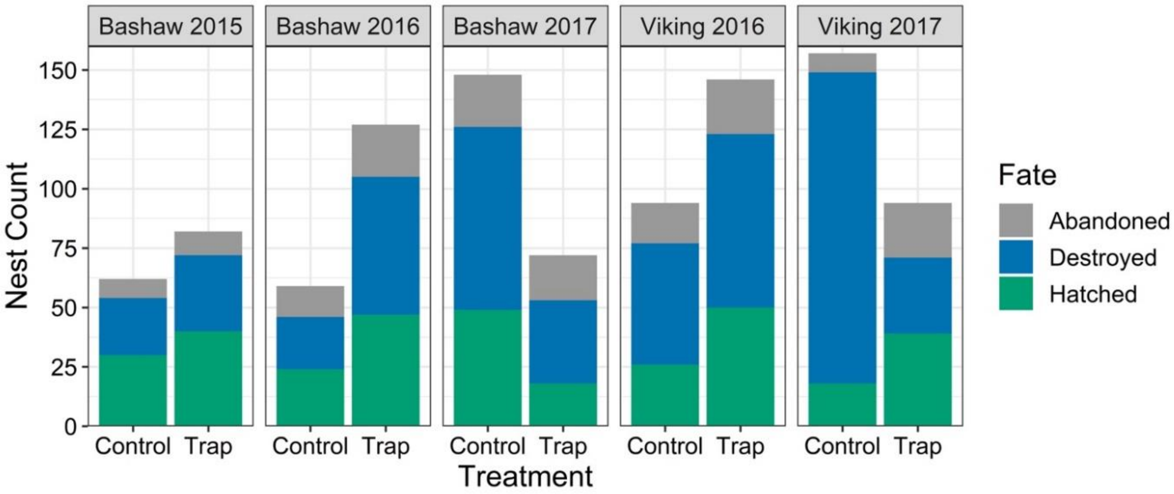

Figure 2. Fates of duck nests (abandoned, destroyed by predator or hatched) in central Alberta parklands by study area, year and treatment ($n = 1041$).

Through 2015–2017, 940 predators were removed. Removals consisted primarily of coyotes (17.2%), skunks (15.1%), black-billed magpies (20.9%), American crows (22.6%) and common ravens (21.7%); the latter 3 species herein referred to collectively as corvids. Red fox (0.4%), Franklin's ground squirrels (1.2%), raccoon (0.3%), American badger (0.5%) and long-tailed weasel (0.1%) were removed in negligible numbers between 2015–2017 (Figure 3). See Table S1 for complete summary of predator removals.

3.1. Nest Cameras

Between 2016–2017, Reconyx HC500^{TM} wildlife cameras were deployed at 35 individual nests for varying amounts of time. Predators were photographed at 12 nests; near Bashaw these included corvids, striped skunks and long-tailed weasels, while 13-lined ground squirrels and striped skunks were detected near Viking (see Table S2 for complete summary). Predators commonly made multiple visits to a nest over hours or days, and multi-species predation events occurred at 33% of the nests where predation was photographed. Two nests were abandoned following camera deployment. Over time, vegetation often obscured the lens, and smaller predators low to the ground would not have been captured by most cameras.

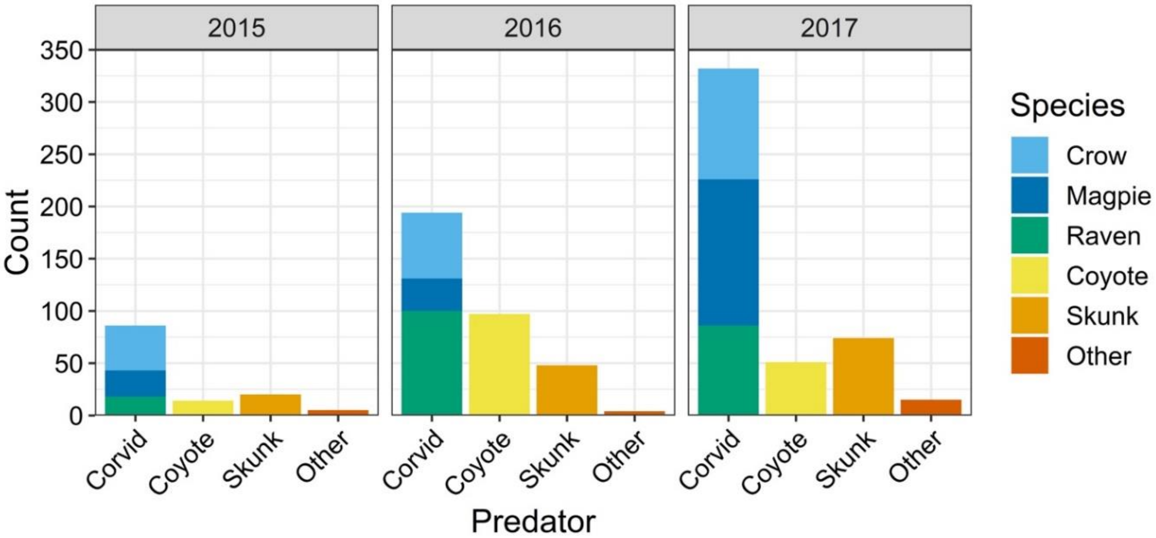

Figure 3. Nest predator species removed through 2015–2017 from Bashaw and Viking, Alberta study areas (*n* = 940).

3.2. Nest Survival

A total of 830 nests were used to test 13 candidate models characterizing nest survival. The top-performing model of daily survival rates included year, study area and treatment as fixed-effects (model weight = 1.00; Table S3). Mean 34-day nest survival in Bashaw control plots in 2015, 2016 and 2017, respectively was: 27.12% (95% CI = 15.24%–47.79%, *n* = 45); 28.79% (95% CI = 16.62%–49.42%, *n* = 39) and 16.71% (95% CI = 11.44%–24.31%, *n* = 140; Figure 4). Mean nest survival in Bashaw trapped plots in the same respective years was: 28.71% (95% CI = 17.98%–45.46%, *n* = 59), 19.52% (95% CI = 13.04%–29.07%, *n* = 111) and 9.09% (95% CI = 3.47%–23.18%, *n* = 35; Figure 4). In Viking control plots in 2016 and 2017, respectively, mean 34-day nest survival was 15.76% (95% CI = 8.97%–27.46%, *n* = 65) and 0.44% (95% CI = 0.17%–1.16%, *n* = 153; Figure 4). In the same respective years, mean nest survival in Viking trapped plots was 17.14% (95% CI = 11.11%–25.98%, *n* = 112) and 30.30% (95% CI = 20.10%–44.81%, *n* = 71; Figure 4). See Table S4 for corresponding daily survival rates.

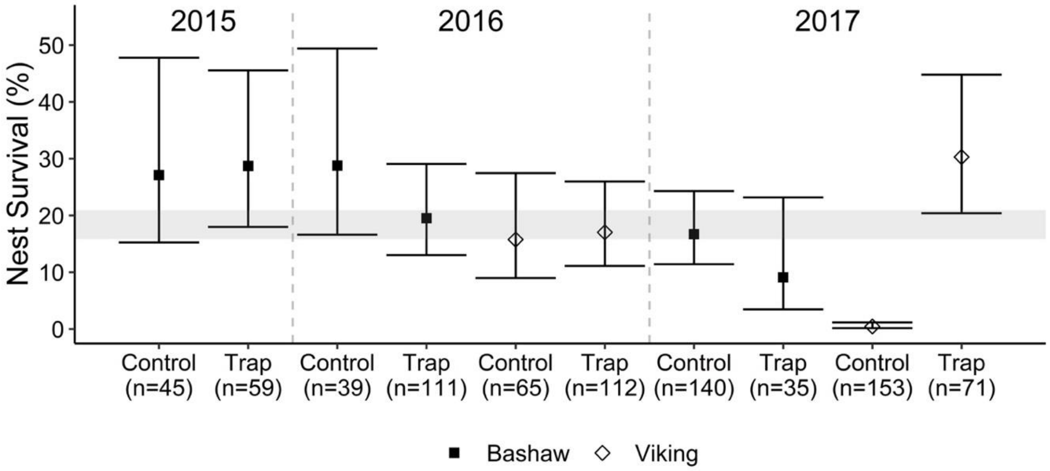

Figure 4. Nest survival over 34 days on trapped and control plots (trapping transposed between years) over 3 years in the central Alberta parklands. Threshold for stable population maintenance of 15%–20% nest survival [2–4] converted to 34-day nest survival shown in grey. Confidence intervals = 95%, *n* = 830.

Except for the Viking 2017 control group, all 95% confidence intervals for 34-day nest survival overlap each other and include the 15%–20% threshold required for maintenance of stable populations [2–4] (Figure 4). Converted to 34-day nest survival, this threshold is 15.84%–20.94%. A series of five z-tests using a Bonferroni-corrected α-value of 0.01 revealed a significant difference in mean nest survival only for the Viking 2016 trap-Viking 2017 control spatial-pairing. For this cohort, nest survival was significantly lower under control conditions ($z = 7.13$, $p < 0.001$, Table 2) due to observers negatively affecting nest survival in the control group [57]. No other significant differences were found among the 5 pairings of nest survival estimates (Table 2).

Table 2. Statistics generated from five z-tests comparing mean nest survival within 2015 and across transposed 2016 and 2017 treatments, using a Bonferroni correction of $\alpha = 0.01$.

Study Area	Year-Treatment Pairing	*z*-Score	*p*-Value
Bashaw	2015 control-2015 trapped	−0.16	0.88
	2016 control-2017 trapped	2.12	0.03
	2016 trapped-2017 control	0.56	0.57
Viking	2016 control-2017 trapped	−1.92	0.06
	2016 trapped-2017 control	7.13	0.00

Exceptionally low nest survival in Viking 2017 control plots appeared to drive model selection, so we modelled nest survival a second time in the absence of that cohort. With the removal of these outlier values, model weight was more distributed, and 5 candidate models had ΔAIC values of <2 (Table S5). Models containing treatment as a covariate performed poorly with model weights of <0.02 (Table S5). Of the top 5 performing models, we selected nest survival as a function of nest age at the time of discovery as the most parsimonious model. Nest age upon discovery was positively skewed, with median age of 10 days (interquartile range = 6–17). Mean 34-day nest survival for nests found at 10 days of age was 21.12% (95% CI = 17.92%–24.87%, $n = 677$). Age of nest when found was weakly associated with higher daily survival rates (Figure 5), with 34-day nest survival estimates ranging from 19.60% (95% CI = 8.60%–43.84%) to 23.55% (95% CI = 9.73%–55.76%) with a mean of 21.66% (95% CI = 21.23%–22.10%).

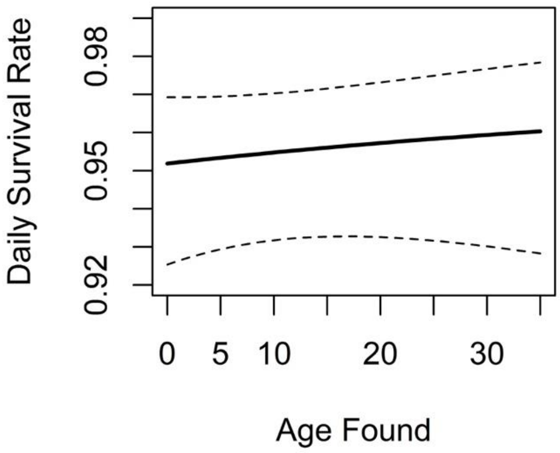

Figure 5. Daily survival rate (DSR) as a function of nest age when found, derived from the top-performing model when 2017 Viking control nests were excluded. Solid line is mean DSR; dashed lines represent 95% confidence intervals.

3.3. Nesting Hen Mortality

Controlling for year and transposing treatment, the common odds of nesting hen mortality due to predation were significantly higher in trapped plots (OR = 2.60, 95% CI = 1.03–6.58, $n = 467$, Table 3) for the Bashaw study area. The increased odds of hen mortality in trapped plots were similar in all 3 years (Breslow-Day $\chi^2 = 0.7133$, $p = 0.7$, df = 2, $n = 467$, Table 3) and significantly higher relative to control plots when year is controlled (Cochran-Mantel-Haenszel $\chi^2 = 3.7413$, $p = 0.0531$, df = 1, $n = 467$; Table 3). See Table S6 for a species breakdown of depredated hens.

Table 3. Counts of surviving and depredated nesting hens by treatment and year from transposed plots near Bashaw, Alberta.

Treatment	Hen Killed	Year		
		2015	2016	2017
Predator Removal	Yes	4	9	5
	No	60	115	33
Control	Yes	1	2	6
	No	50	40	142

The probability of survival for nesting hens in predator removal plots was 0.50 (95% CI = 0.28–0.71). Should an entire population experience the rate of breeding hen survival observed in our predator removal plots, population growth rate (λ) estimated for female midcontinent mallards would be 0.566 (95% CI = 0.320–0.813; Figure 6). For comparison, Hoekman et al.'s [1] λ estimate of 0.824 was based on 0.72 probability of breeding hen survival and represented an approximate population growth rate in the absence of predator removal. Our highest estimate of breeding hen survival in predator removal conditions (0.71) results in a 1.1% lower population growth rate compared to Hoekman et al.'s [1] benchmark estimate.

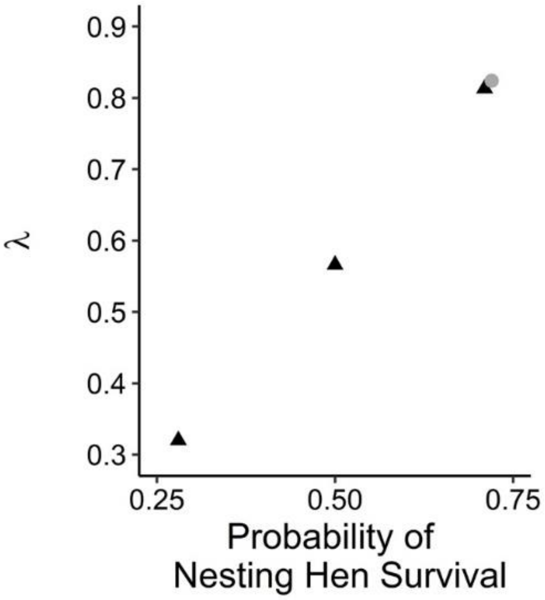

Figure 6. Population growth rate (λ) as a function of nesting hen survival. Black triangles represent our estimates from predator removal plots, and the grey circle represents estimate by Hoekman et al. [1], for reference.

4. Discussion

In accordance with our hypothesis, nest survival patterns indicated that predator removal was ineffective. In all but one study area-year combination, we found no significant difference in nest survival between control and predator removal plots (Table 2). The majority of research evaluating predator removal to increase dabbling duck nest survival has found it to be effective when applied in prairie habitats [19,23–27]; but publication bias towards significant results might have influenced the prevalence of positive findings [29]. Ours is the third study to date demonstrating ineffectiveness of predator removal for duck nest survival in Canadian parkland habitats [28,78], while Guyn [79] found conditioned taste aversion ineffective in Saskatchewan parklands. Like Clark et al. [78] and Dassow [28], we conducted partial predator removal within a rich predator community characteristic of the parkland region [80] where ample opportunity for compensatory predation exists. Three-dimensional habitat structure (aspen stands) and socio-economic drivers may enhance the potential for compensatory predation relative to U.S. prairie habitats, where most successful studies have been carried out. Nest abundance and proportion of fates was largely preserved within study area across years, regardless of treatment (Figure 2), indicating that nest survival was driven by habitat characteristics, for which we controlled by treatment transposition. Associations of habitats with nest predation risk are examined in Blythe [81] and Blythe and Boyce [82].

A lack of response in nest survival does not necessarily preclude the depression of predator abundance because of potential compensatory nest predation by species that were not removed [31–33]. Trail camera evidence demonstrated that species that were not targeted for removal were consuming duck eggs (long-tailed weasels, 13-lined ground squirrels). Assuming effective removal of skunks, coyotes and corvids, we believe other species might have been responsible for compensatory nest predation which could have been facilitated through multiple mechanisms. Mesopredator release, the expansion of distribution or density of a mid-trophic level predator resulting from the decline of an apex predator (in our system, coyotes) [83,84], is known to benefit foxes (e.g., [85]), skunks [83], ravens [86] and other nest predators. Given the short 4-month timeframe of predator removal each year, a distribution expansion of the community of nest predators, induced by mesopredator release, would probably occur largely through behavioural mechanisms [10,87]. The removal of more efficient nest predators might have increased opportunity afforded to less-efficient species that do not key in on duck eggs as readily [32,37].

The compressed temporal and spatial scale of our predator removal plots provided ample opportunity for immigration and the creation of a core, predator-free area was unlikely [19]. Similar to our study, Manton et al. [88] describe a predator assemblage shaped at the landscape scale by socio-economic factors; in both cases a landscape approach is required to address impacts of anthropogenic land use. The spatial scale and distribution of our predator removal was constrained by land tenure; landowner concerns about the spread of clubroot (*Plasmodiophora brassicae*), a fungal disease of canola, led to restrictions on accessing private land. The duration of predator removal was constrained by cost; our implementation of predator removal represents the inherent logistic constraints that also would characterize a long-term predator removal program in the Alberta parklands. When applying small-scale predator removal on the prairies, Chodachek and Chamberlain [27] increased duck nesting success on 259 ha parcels, while Sargeant et al. [89] saw slight increases when trapping 61–301 ha plots. The parklands are more complex in habitat structure than prairie ecosystems and effective predator removal is challenging when conducted at small, widely distributed plots across a productive landscape that supports many predator species [89]. The Alberta parklands may be more vulnerable to the creation of a source-sink system where non-managed areas provide source populations for immigration into predator-removal areas [36,90]. Lieury et al. [91] suggested that immigration would quickly negate the effects of reducing red foxes at scales less than 10 km^2, and that spring culling is more conducive to compensatory immigration than post-dispersal culling.

Wide confidence intervals preclude us from determining whether baseline nest survival in our study areas is above or below that required for population maintenance. All but one of our 10 nest survival estimates encompassed the 15.84%–20.94% 34-day threshold required for maintenance of stable populations [2–4] and none fully exceeded it (Figure 4). As concluded in several other studies [19,67,92], we observed that nest survival increased linearly with nest age. The 2017 Viking trapped plots had the highest minimum survival estimate at 20.10%. With a maximum estimate of 1.16% nest survival and 18 successful nests out of 153, the 2017 Viking control plot had the lowest survival. These results indicate that predator removal in the Viking area might prove effective at increasing nest survival, but this requires further investigation, especially because the 2017 Viking control plot was negatively affected by nest marking [57]. In contrast, predator removal was ineffective in the Bashaw study area and did not appear to be an effective management strategy.

We were surprised that significantly more nesting hens were depredated on trapped plots, although low incidence and minimal influence on estimates of λ ultimately rendered this pattern nonsignificant. Though predator removal did not depress nest predator abundance sufficiently to improve nest survival, it appears to have influenced predator assemblage in favour of principal hen predators, thereby increasing hen mortality. Mesopredator release and competitive release might have shifted the relative abundance of mammalian predators. Coyotes were the apex predator in our system but are not principal hen predators especially in comparison to red fox [55,85]. Coyotes limit red fox abundance through interference competition that includes direct killing and instilling fear [10,85,93,94]. Areas where coyotes were reduced might have become attractive refuges for more important hen predators like red fox and weasels [10,55], resulting in increased nesting hen mortality relative to control plots. The dietary breadth of skunks is relatively high [95] and their niche overlaps that of red fox [7], so competitive release resulting from skunk removal also could have benefited weasels and foxes.

Apparent competition [42] in the form of increased rodent abundance attracting duck predators is another potential consequence of predator removal that could have occurred to the detriment of nesting hen survival. Rodent species are an important prey for both coyotes and skunks [95], the removal of which could have resulted in increased rodent abundance through both numerical and behavioural responses [10,87,96]. Red fox, weasel and raptors are shared predators of rodents and adult ducks [95,97–100] and an increase in their abundance is a plausible explanation for significantly higher nesting hen mortality on trapped plots. In North Dakota, McCarter [45] observed slightly higher abundance of raptors where mammalian predators were reduced, presumably in response to increased prey.

Future evaluation of predator removal for increased duck production would be improved by the collection of additional data. Information on predator abundance is essential for evaluating the presence and degree of a decline induced by predator removal, and inferences are limited in its absence. Beyond population size, trapper removals are influenced by effort which encompasses trapper experience, and type and placement of traps and attractants [101], none of which were standardized in our study design. Predator-removal methods must be standardized to allow for comparisons [102,103], thus tracking trapping effort as well as removals over time could allow for indirect estimates of predator abundance to be made through depletion modelling (T. Arnold, University of Minnesota, personal communication). Relative importance of each nest predator species might help to elucidate aspects of compensatory predation, but such data are difficult to obtain [104–106]. Disturbance from trapping activity might cause nest abandonment; spatially recording trapper's trails and sets could allow researchers to quantify possible impacts of trapping on nest abandonment.

The failure of predator-removal programs intended to increase bird abundance because of compensatory predation is well documented [45], especially when predator removal does not encompass all predator species [22]. Where predator removal does increase nest survival, enhancements may not translate into increases in recruitment to the local population due to a combination of low duckling survival, limitations in breeding philopatry and territorial behaviour of breeding pairs [26,107]. A measure of recruitment is critical to truly evaluate the effectiveness of predator removal intended to increase not only nest survival but duck productivity [26,107]. A long-term predator removal program in North Dakota has produced marginal gains in population growth at high monetary cost, in part due to low duckling survival dampening the effectiveness of high nest survival [26]. Duckling survival benefited from predator removal in Saskatchewan [108] but not in North Dakota [109], where duck populations appear to be controlled predominantly by bottom-up trophic forces not addressed by predator removal [45]. In our study, duckling survival could have been reduced unintentionally through the same mechanisms that led to a reduction in breeding-hen survival. Limitations in carrying capacity due to finite food and habitat resources place constraints on recruitment that might ultimately prevent increases in fall duck abundance resulting from increased nest survival [26,45].

5. Conclusions

Predator removal was ineffective at increasing duck nesting success and at time of writing there are no plans to continue the predator-control program in the Alberta parklands. Prior to implementing any form of predator management, the benefits should be assessed using a rigorous study design and weighed against potential consequences, including those that might be unintentional or counterintuitive [30]. The substantial resources required to implement predator removal could be redirected at non-lethal mitigation methods that often can be more effective and less controversial [30] with less risk of inducing unintended negative consequences. Predator removal should be continuously monitored to ensure desired outcomes are being achieved. Determining prey survival at multiple life stages is important due to the potential for opposing effects on different vital rates this study, [38,41]. Finally, retaining coyotes on the landscape might increase the success of a predator-removal program [25] because coyotes effectively reduce the abundance of fox and other mesopredators, and coyote presence is associated with higher nest survival [85].

In conclusion, current nest survival in the central Alberta parklands might be lower than required for maintenance of stable populations [2–4] but our results do not indicate that nest survival would benefit from local-scale predator removal. Our observations of a possible increase in nesting hen mortality on predator removal sites raise new concerns and add to a growing body of literature suggesting minimal gains from predator removal intended to increase duck production [26,45,107,109]. Habitat-based management alternatives might be a more effective approach for reducing nest-predation risk [81,82].

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/12/3/119/s1, Table S1: Total nest predators removed from Bashaw and Viking trapped sites, 2015–2017, Table S2: Summary of wildlife trail cameras deployed at individual nests and predator species photographed, Table S3: RMark nest survival models for daily survival rates of duck nests (n = 830) on plots where predator removal was transposed over >2 years in central Alberta parklands in 2015–2017, ranked by corrected Akaike's Information Criterion (AICc), Table S4: Daily survival rate (DSR) and standard error (SE) derived from top-performing RMark nest survival model for daily survival rates of duck nests on plots where predator removal was transposed over >2 years in central Alberta parklands in 2015–2017, Table S5: RMark nest survival models for daily survival rates of duck nests on plots where predator removal was transposed over >2 years in central Alberta parklands in 2015–2017, excluding Viking Control 2017 plots. Ranked by corrected Akaike's Information Criterion (AICc), Table S6: Counts of depredated nesting hens (n = 27) by species and treatment plot on which they were found.

Author Contributions: All authors have read and agreed to the published version of the manuscript. Conceptualization, E.M.B. and M.S.B.; methodology, E.M.B. and M.S.B.; formal analysis, E.M.B.; visualization, E.M.B.; investigation, E.M.B.; resources, M.S.B.; data curation, E.M.B.; writing—original draft preparation, E.M.B.; writing—review and editing, M.S.B.; supervision, M.S.B.; project administration, E.M.B.; funding acquisition, E.M.B. and M.S.B.

Funding: This research was generously funded by Delta Waterfowl Foundation (DWF), with additional funding from Mitacs Accelerate Internship, Alberta Fish & Game Association (AFGA), and Northern Alberta Chapter of Safari Club International.

Acknowledgments: Initial conceptualization, in-kind support, training and valuable insights were provided by DWF; F. Rohwer, J. Brice, M. Buxton, and M. Chouinard were exceptionally helpful. Predator removal was managed by DWF. Essential land access was granted by Ducks Unlimited Canada, as well as AFGA, Alberta Conservation Association, and a number of private landowners. K. Norton collected 2015 data. R. Marcil provided field support. Field technicians J. Melsted, T. Vilalta, S. Andrews, J. Hewlett, E. Healey, and S. O'Donovan were essential to this project's success. S. Hoekman provided insight and help with lambda calculations. C. Paszkowski, T. Nudds, and S. Green provided helpful critique and revisions.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Hoekman, S.T.; Mills, S.; Howerter, D.W.; Devries, J.H.; Ball, I.J. Sensitivity Analyses of the Life Cycle of Midcontinent Mallards. *J. Wildl. Manag.* **2002**, *66*, 883–900. [CrossRef]
2. Cowardin, L.M.; Gilmer, D.S.; Shaiffer, C.W. Mallard Recruitment in the Agricultural Environment of North Dakota. *Wildl. Monogr.* **1985**, *92*, 3–37.
3. Greenwood, R.J.; Sargeant, A.B.; Johnson, D.H.; Cowardin, L.M.; Shaffer, T.L. Factors Associated with Duck Nest Success in the Prairie Pothole Region of Canada. *Wildl. Monogr.* **1995**, *128*, 1–57.
4. Klett, A.T.; Shaffer, T.L.; Johnson, D.H. Duck Nest Success in the Prairie Pothole Region. *J. Wildl. Manag.* **1988**, *52*, 431–440. [CrossRef]
5. Beauchamp, W.D.; Koford, R.R.; Nudds, T.D.; Clark, R.G.; Johnson, D.H. Long-Term Declines in Nest Success of Prairie Ducks. *J. Wildl. Manag.* **1996**, *60*, 247–257. [CrossRef]
6. Sovada, M.A.; Anthony, R.M.; Batt, B.D.J. Predation on Waterfowl in Arctic Tundra and Prairie Breeding Areas: A Review. *Wildl. Soc. Bull.* **2001**, *29*, 6–15.
7. Crimmins, S.M.; Walleser, L.R.; Hertel, D.R.; McKann, P.C.; Rohweder, J.J.; Thogmartin, W.E. Relating Mesocarnivore Relative Abundance to Anthropogenic Land-Use with a Hierarchical Spatial Count Model. *Ecography* **2016**, *39*, 524–532. [CrossRef]
8. Sargeant, A.B.; Raveling, D.G. Mortality during the Breeding Season. In *Ecology and Management of Breeding Waterfowl*; Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.F., Krapu, G.L., Eds.; University of Minnesota Press: Minneapolis, MN, USA, 1992.
9. Ricklefs, R.E. An Analysis of Nesting Mortality in Birds. *Smithson. Contrib. Zool.* **1969**, *9*, 1–48. [CrossRef]
10. Ritchie, E.G.; Johnson, C.N. Predator Interactions, Mesopredator Release and Biodiversity Conservation. *Ecol. Lett.* **2009**, 982–998. [CrossRef] [PubMed]
11. Suraci, J.P.; Clinchy, M.; Dill, L.M.; Roberts, D.; Zanette, L.Y. Fear of Large Carnivores Causes a Trophic Cascade. *Nat. Commun.* **2016**, *7*, 10698. [CrossRef]
12. Rodewald, A.D.; Kearns, L.J.; Shustack, D.P. Anthropogenic Resource Subsidies Decouple Predator-Prey Relationships. *Ecol. Appl.* **2011**, *21*, 936–943. [CrossRef] [PubMed]
13. Borgo, J.S.; Conover, M.R. Influence of Shelterbelts on Success and Density of Waterfowl Nests within the Prairie Pothole Region of North America. *Waterbirds* **2016**, *39*, 74–80. [CrossRef]
14. Clark, R.G.; Nudds, T.D. Habitat Patch Size and Duck Nesting Success: The Crucial Experiments Have Not Been Performed. *Wildl. Soc. Bull.* **1991**, *19*, 534–543.
15. Pasitschniak-Arts, M.; Messier, F. Risk of Predation on Waterfowl Nests in the Canadian Prairies: Effects of Habitat Edges and Agricultural Practices. *Oikos* **1995**, *73*, 347–355. [CrossRef]
16. Wirsing, A.J.; Phillips, J.R.; Obbard, M.E.; Murray, D.L. Incidental Nest Predation in Freshwater Turtles: Inter- and Intraspecific Differences in Vulnerability Are Explained by Relative Crypsis. *Oecologia* **2012**, *168*, 977–988. [CrossRef]
17. Jiménez, J.M.; Conover, M.R.; Deuser, R.D.; Messmer, T.A. Influence of Habitat Patch Characteristics on the Success of Upland Duck Nests. *Hum. Wildl. Confl.* **2007**, *1*, 244–256.
18. Ringelman, K.M. Predator Foraging Behavior and Patterns of Avian Nest Success: What Can We Learn from an Agent-Based Model? *Ecol. Model.* **2014**, *272*, 141–149. [CrossRef]
19. Garrettson, P.R.; Rohwer, F.C. Effects of Mammalian Predator Removal on Production of Upland-Nesting Ducks in North Dakota. *J. Wildl. Manag.* **2001**, *65*, 398–405. [CrossRef]
20. *North American Waterfowl Management Plan: People Conserving Waterfowl and Wetlands*; Canadian Wildlife Service, Ottawa and US Fish and Wildlife Service: Washington, DC, USA, 2012.
21. Drever, M.C.; Wins-Purdy, A.; Nudds, T.D.; Clark, R.G. Decline of Duck Nest Success Revisited: Relationships with Predators and Wetlands in Dynamic Prairie Environments. *Auk* **2004**, *121*, 497–508. [CrossRef]
22. Smith, R.K.; Pullin, A.S.; Stewart, G.B.; Sutherland, W.J. Effectiveness of Predator Removal for Enhancing Bird Populations. *Conserv. Biol.* **2010**, *24*, 820–829. [CrossRef]

23. Lester, V.G. Nest Site Selection Patterns of Dabbling Ducks in Response to Variation in Predation Pressure: An Experimental Study. Master's Thesis, University of Saskatchewan, Saskatoon, SK, Canada, 2004.
24. Pieron, M.R.; Darr, M.J.K.; Rohwer, F.C. Duck Nest Success Adjacent to Predator-Reduced Sites. *J. Wildl. Manag.* **2012**, *76*, 1450–1455. [CrossRef]
25. Pieron, M.R.; Rohwer, F.C. Effects of Large-Scale Predator Reduction on Nest Success of Upland Nesting Ducks. *J. Wildl. Manag.* **2010**, *74*, 124–132. [CrossRef]
26. Amundson, C.L.; Pieron, M.R.; Arnold, T.W.; Beaudoin, L.A. The Effects of Predator Removal on Mallard Production and Population Change in Northeastern North Dakota. *J. Wildl. Manag.* **2013**, *77*, 143–152. [CrossRef]
27. Chodachek, K.D.; Chamberlain, M.J. Effects of Predator Removal on Upland Nesting Ducks in North Dakota Grassland Fragments. *Prairie Nat.* **2006**, *38*, 25–37.
28. Dassow, J.A. Upland-Nesting Ducks in the Parklands of Saskatchewan: The Effect of Predator Reduction on Nest Success and Reproductive Investment. Master's Thesis, Southern Illinois University, Carbondale, IL, USA, 2010.
29. Rosenthal, R. The "File Drawer Problem" and Tolerance for Null Results. *Psychol. Bull.* **1979**, *86*, 638–641. [CrossRef]
30. Treves, A.; Krofel, M.; McManus, J. Predator Control Should Not Be a Shot in the Dark. *Front. Ecol. Environ.* **2016**, *14*, 380–388. [CrossRef]
31. Boyce, M.S.; Sinclair, A.R.E.; White, G.C. Seasonal Compensation of Predation and Harvesting. *Oikos* **1999**, *87*, 419–426. [CrossRef]
32. Ellis-Felege, S.N.; Conroy, M.J.; Palmer, W.E.; Carroll, J.P. Predator Reduction Results in Compensatory Shifts in Losses of Avian Ground Nests. *J. Appl. Ecol.* **2012**, *49*, 661–669. [CrossRef]
33. Errington, P.L. Predation and Vertebrate Populations. *Q. Rev. Biol.* **1946**, *21*, 144–177, 221–245. [CrossRef]
34. Porter, J.H.; Dueser, R.D.; Moncrief, N.D. Cost-Distance Analysis of Mesopredators as a Tool for Avian Habitat Restoration on a Naturally Fragmented Landscape. *J. Wildl. Manag.* **2015**, *79*, 220–234. [CrossRef]
35. Sterling, B.; Conley, W.; Conley, M.R. Simulations of Demographic Compenstation in Coyote Populations. *J. Wildl. Manag.* **1983**, *47*, 1177–1181. [CrossRef]
36. Minnie, L.; Gaylard, A.; Kerley, G.I.H.; Chapron, G. Compensatory Life-History Responses of a Mesopredator May Undermine Carnivore Management Efforts. *J. Appl. Ecol.* **2016**, *53*, 379–387. [CrossRef]
37. Ruscoe, W.A.; Ramsey, D.S.; Pech, R.P.; Sweetapple, P.J.; Yockney, I.; Barron, M.C.; Perry, M.; Nugent, G.; Carran, R.; Warne, R.; et al. Unexpected Consequences of Control: Competitive vs. Predator Release in a Four-Species Assemblage of Invasive Mammals. *Ecol. Lett.* **2011**, *14*, 1035–1042. [CrossRef] [PubMed]
38. Neuman, K.K.; Page, G.W.; Stenzel, L.E.; Warriner, J.C.; Warriner, J.S. Effect of Mammalian Predator Management on Snowy Plover Breeding Success. *Waterbirds* **2004**, *27*, 257–263. [CrossRef]
39. Coluccy, J.M.; Yerkes, T.; Simpson, R.; Simpson, J.W.; Armstrong, L.M.; Davis, J. Population Dynamics of Breeding Mallards in the Great Lakes States. *J. Wildl. Manag.* **2008**, *72*, 1181–1187. [CrossRef]
40. Pearse, A.T.; Lester, V.G. Correlation between Nest and Duckling Survival of Mallards Breeding in Saskatchewan. *J. Wildl. Manag.* **2007**, *71*, 1612–1616. [CrossRef]
41. Darrah, A.J.; Cohen, J.B.; Castelli, P.M. A Bayesian Multinomial Logistic Exposure Model for Estimating Probabilities of Competing Sources of Nest Failure. *Ibis* **2018**, *160*, 23–35. [CrossRef]
42. Holt, R.D. Predation, Apparent Competition, and the Structure of Prey Communities. *Theor. Popul. Biol.* **1977**, *12*, 197–229. [CrossRef]
43. Holt, R.D.; Lawton, J.H. The Ecological Consequences of Shared Natural Enemies. *Annu. Rev. Ecol. Syst.* **1994**, *25*, 495–520. [CrossRef]
44. DeCesare, N.J.; Hebblewhite, M.; Robinson, H.S.; Musiani, M. Endangered, Apparently: The Role of Apparent Competition in Endangered Species Conservation. *Anim. Conserv.* **2009**, *13*, 353–362. [CrossRef]
45. McCarter, J. Trophic Control of Duck Abundance in a Prairie Pothole Food Web. Master's Thesis, University of Guelph, Guelph, ON, Canada, 2009.
46. Arnold, T.W.; Craig-Moore, L.M.; Armstrong, L.M.; Howerter, D.W.; Devries, J.H.; Joynt, B.L.; Emery, R.B.; Anderson, M.G. Waterfowl Use of Dense Nesting Cover in the Canadian Parklands. *J. Wildl. Manag.* **2007**, *71*, 2542–2549. [CrossRef]

47. Howerter, D.W.; Anderson, M.G.; Devries, J.H.; Joynt, B.L.; Armstrong, L.M.; Emery, R.B.; Arnold, T.W. Variation in Mallard Vital Rates in Canadian Aspen Parklands: The Prairie Habitat Joint Venture Assessment. *Wildl. Monogr.* **2014**, *188*, 1–37. [CrossRef]
48. Drever, M.C.; Nudds, T.D.; Clark, R.G. Agricultural Policy and Nest Success of Prairie Ducks in Canada and the United States. *Avian Conserv. Ecol.* **2007**, *2*. [CrossRef]
49. Scarth, J.; Brice, J. *Hen House and Predator Reduction Research in Parkland Habitats of Alberta: Nest Success and Long-Term Population Responses of Dabbling Ducks*; Delta Waterfowl Foundation: Winnipeg, MB, Canada, 2014.
50. Roy, L.D.; Dorrance, M.J. Coyote Movements, Habitat Use, and Vulnerability in Central Alberta. *J. Wildl. Manag.* **1985**, *49*, 307–313. [CrossRef]
51. Larivière, S.; Messier, F. Effect of Density and Nearest Neighbours on Simulated Waterfowl Nests: Can Predators Recognize High-Density Nesting Patches? *Oikos* **1998**, *83*, 12–20. [CrossRef]
52. Russell, A.P.; Bauer, A.M.; Lynch, W.; McKinnon, I. *The Amphibians and Reptiles of Alberta: A Field Guide and Primer of Boreal Herpetology*, 2nd ed.; University of Calgary Press: Calgary, AB, Canada, 2000.
53. Bourne, J. *Rat Control in Alberta*; Alberta Agriculture and Forestry: Red Deer, AB, Canada, 2015.
54. Alberta Environment and Parks. *Alberta Wild Species General Status Listing*; Government of Alberta: Edson, AB, Canada, 2015.
55. Sargeant, A.B.; Sovada, M.A.; Greenwood, R.J. *Interpreting Evidence of Depredation of Duck Nests in the Prairie Pothole Region*; U.S. Geological Survey, Northern Prairie Wildlife Research Centre & Ducks Unlimited, Inc.: Jamestown, ND, USA, 1998; p. 72.
56. Klett, A.T.; Duebbert, H.F.; Faanes, C.A.; Higgins, K.F. *Techniques for Studying Nest Success of Ducks in Upland Habitats in the Prairie Pothole Region*; United States Department of the Interior Fish and Wildlife Service: Washington, DC, USA, 1986.
57. Blythe, E.M.; Boyce, M.S. Conventional Marking of Duck Nests May Increase Predation by Corvids. Unpublished.
58. Picozzi, N. Crow Predation on Marked Nests. *J. Wildl. Manag.* **1975**, *39*, 151–155. [CrossRef]
59. Buler, J.J.; Hamilton, R.B. Predation of Natural and Artificial Nests in a Southern Pine Forest. *Auk* **2000**, *117*, 739–747. [CrossRef]
60. Weller, M.W. A Simple Field Candler for Waterfowl Eggs. *J. Wildl. Manag.* **1956**, *20*, 111–113. [CrossRef]
61. Robel, R.J.; Briggs, J.N.; Dayton, A.D.; Hulbert, L.C. Relationships between Visual Obstruction Measurements and Weight of Grassland Vegetation. *J. Range Manag.* **1970**, *23*, 295–297. [CrossRef]
62. Garrettson, P.R.; Richkus, K.D.; Rohwer, F.C.; Johnson, W.P. Factors Influencing Investigator-Caused Nest Abandonment by North American Dabbling Ducks. *Can. J. Zool.* **2011**, *89*, 69–78. [CrossRef]
63. Richardson, T.W.; Gardali, T.; Jenkins, S.H. Review and Meta-Analysis of Camera Effects on Avian Nest Success. *J. Wildl. Manag.* **2009**, *73*, 287–293. [CrossRef]
64. Renfrew, R.B.; Ribic, C.A. Grassland Passerine Nest Predators near Pasture Edges Identified on Videotape. *Auk* **2003**, *120*, 371–383. [CrossRef]
65. Laake, J.L. *Rmark: An R Interface for Analysis of Capture-Recapture Data with Mark*; Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration, National Marine Fisheries Service: Washington, DC, USA, 2013.
66. White, G.C.; Burnham, K.P. Program Mark: Survival Estimation from Populations of Marked Animals. *Bird Study* **1999**, *46*, S120–S139. [CrossRef]
67. Dinsmore, S.J.; White, G.C.; Knopf, F.L. Advanced Techniques for Modeling Avian Nest Survival. *Ecology* **2002**, *83*, 3476–3488. [CrossRef]
68. Rotella, J.J.; Dinsmore, S.J.; Shaffer, T.L. Modeling Nest–Survival Data: A Comparison of Recently Developed Methods That Can Be Implemented in Mark and Sas. *Anim. Biodivers. Conserv.* **2004**, *27.1*, 187–205.
69. McCullagh, P.; Nelder, J.A. *Generalized Linear Models*, 2nd ed.; Chapman and Hall: London, UK, 1989.
70. R Core Development Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2016.
71. Dormann, C.F.; McPherson, J.M.; Araújo, M.B.; Bivand, R.; Bolliger, J.; Carl, G.; Davies, R.G.; Hirzel, A.; Jetz, W.; Kissling, W.D.; et al. Methods to Account for Spatial Autocorrelation in the Analysis of Species Distributional Data: A Review. *Ecography* **2007**, *30*, 609–628. [CrossRef]
72. Burnham, K.P.; Anderson, D.R. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed.; Springer: Berlin/Heidelberg, Germany, 2002.

73. Zar, J.H. *Biostatistical Analysis*, 5th ed.; Pearson: Upper Saddle River, NJ, USA, 2010.
74. Breslow, N.E.; Day, N.E. *Statistical Methods in Cancer Research. Volume 1-the Analysis of Case-Control Studies*; International Agency for Research on Cancer (IARC Scientific Publications: No. 32): Lyon, France, 1980.
75. Yates, F. Contingency Tables Involving Small Numbers and the X2 Test. *Suppl. J. R. Stat. Soc.* **1934**, *1*, 217–235. [CrossRef]
76. Agresti, A. *Categorical Data Analysis*, 2nd ed.; Wiley-Interscience: New York, NY, USA, 2002.
77. Stubben, C.; Milligan, B. Estimating and Analyzing Demographic Models Using the Popbio Package in R. *J. Stat. Softw.* **2007**, *22*, 2–23. [CrossRef]
78. Clark, R.G.; Meger, D.E.; Ignatiuk, J.B. Removing American Crows and Duck Nesting Success. *Can. J. Zool.* **1995**, *73*, 518–522. [CrossRef]
79. Guyn, K.L. Sources of Variation in Waterfowl Nest Predation. Master's Thesis, University of Saskatchewan, Saskatoon, SK, Canada, 1994.
80. Sargeant, A.B.; Greenwood, R.J.; Sovada, M.A.; Shaffer, T.L. *Distribution and Abundance of Predators that Affect Duck Production-Prairie Pothole Region*; U.S. Fish and Wildlife Service Resource Publication 194: Washington, DC, USA, 1993.
81. Blythe, E.M. Trappings of Success: Predator Removal & Habitat Associations with Dabbling Duck Nest Survival in Alberta Parklands. Master's Thesis, University of Alberta, Edmonton, AB, Canada, 2019.
82. Blythe, E.M.; Boyce, M.S. Duck Nest Predation Risk in Alberta Parklands. Unpublished work.
83. Crooks, K.R.; Soulé, M.E. Mesopredator Release and Avifaunal Extinctions in a Fragmented System. *Nature* **1999**, *400*, 563–566. [CrossRef]
84. Prugh, L.R.; Stoner, C.J.; Epps, C.W.; Bean, W.T.; Ripple, W.J.; Laliberte, A.S.; Brashares, J.S. The Rise of the Mesopredator. *Bioscience* **2009**, *59*, 779–791. [CrossRef]
85. Sovada, M.A.; Sargeant, A.B.; Grier, J.W. Differential Effects of Coyotes and Red Foxes on Duck Nest Success. *J. Wildl. Manag.* **1995**, *59*, 1–9. [CrossRef]
86. Mezquida, E.T.; Slater, S.J.; Benkman, C.W. Sage-Grouse and Indirect Interactions: Potential Implications of Coyote Control on Sage-Grouse Populations. *Condor* **2006**, *108*. [CrossRef]
87. Lima, S.L.; Dill, L.M. Behavioral Decisions Made under the Risk of Predation: A Review and Prospectus. *Can. J. Zool.* **1990**, *68*, 619–640. [CrossRef]
88. Manton, M.; Angelstam, P.; Naumov, V. Effects of Land Use Intensification on Avian Predator Assemblages: A Comparison of Landscapes with Different Histories in Northern Europe. *Diversity* **2019**, *11*, 70. [CrossRef]
89. Sargeant, A.B.; Sovada, M.A.; Shaffer, T.L. Seasonal Predator Removal Relative to Hatch Rate of Duck Nests in Waterfowl Production Areas. *Wildl. Soc. Bull.* **1995**, *23*, 507–513.
90. Novaro, A.J.; Funes, M.C.; Walker, R.S. An Empirical Test of Source-Sink Dynamics Induced by Hunting. *J. Appl. Ecol.* **2005**, *42*, 910–920. [CrossRef]
91. Lieury, N.; Ruette, S.; Devillard, S.; Albaret, M.; Drouyer, F.; Baudoux, B.; Millon, A. Compensatory Immigration Challenges Predator Control: An Experimental Evidence-Based Approach Improves Management. *J. Wildl. Manag.* **2015**, *79*, 425–434. [CrossRef]
92. Klett, A.T.; Johnson, C.J. Variability in Nest Survival Rates and Implications to Nesting Studies. *Auk* **1982**, *99*, 77–87. [CrossRef]
93. Gosselink, T.E.; Van Deelen, T.R.; Warner, R.E.; Joselyn, M.G. Temporal Habitat Partitioning and Spatial Use of Coyotes and Red Foxes in East-Central Illinois. *J. Wildl. Manag.* **2003**, *67*, 90–103. [CrossRef]
94. Nelson, J.L.; Cypher, B.L.; Bjurlin, C.D.; Creel, S. Effects of Habitat on Competition between Kit Foxes and Coyotes. *J. Wildl. Manag.* **2007**, *71*, 1467–1475. [CrossRef]
95. Azevedo, F.C.C.; Lester, V.; Gorsuch, W.; Larivière, S.; Wirsing, A.J.; Murray, D.L. Dietary Breadth and Overlap among Five Sympatric Prairie Carnivores. *J. Zool.* **2006**, *269*, 127–135. [CrossRef]
96. Henke, S.E.; Bryant, F.C. Effects of Coyote Removal on the Faunal Community in Western Texas. *J. Wildl. Manag.* **1999**, *63*, 1066–1081. [CrossRef]
97. Richkus, K.D.; Rohwer, F.C.; Chamberlain, M.J. Survival and Cause-Specific Mortality of Female Northern Pintails in Southern Saskatchewan. *J. Wildl. Manag.* **2005**, *69*, 574–581. [CrossRef]
98. Sargeant, A.B.; Eberhardt, R.T.; Allen, S.H. Red Fox Predation on Breeding Ducks in Midcontinent North America. *Wildl. Monogr.* **1984**, *48*, 1–41.
99. Simms, D.A. North American Weasels: Resource Utilization and Distribution. *Can. J. Zool.* **1979**, *57*, 504–520. [CrossRef]

100. Thomas, P.J.; Mineau, P.; Shore, R.F.; Champoux, L.; Martin, P.A.; Wilson, L.K.; Fitzgerald, G.; Elliott, J.E. Second Generation Anticoagulant Rodenticides in Predatory Birds: Probabilistic Characterisation of Toxic Liver Concentrations and Implications for Predatory Bird Populations in Canada. *Environ. Int.* **2011**, *37*, 914–920. [CrossRef] [PubMed]
101. Ruette, S.; Stahl, P.; Albaret, M. Factors Affecting Trapping Success of Red Fox *Vulpes Vulpes*, Stone Marten *Martes Foina* and Pine Marten *M. Martes* in France. *Wildl. Biol.* **2003**, *9*, 11–19. [CrossRef]
102. DeVink, J.; Berezanski, D.; Imrie, D. Comments on Brodie and Post: Harvest Effort: The Missing Covariate in Analyses of Furbearer Harvest Data. *Popul. Ecol.* **2011**, *53*, 261–262. [CrossRef]
103. McKelvey, K.S.; Lofroth, E.C.; Copeland, J.P.; Aubry, K.B.; Magoun, A.J. Comments on Brodie and Post: Climate-Driven Declines in Wolverine Populations: Causal Connection or Spurious Correlation? *Popul. Ecol.* **2011**, *53*, 263–266. [CrossRef]
104. Hernandez, F.; Rollins, D.; Cantu, R. An Evaluation of Trailmaster® Camera Systems for Identifying Ground-Nest Predators. *Wildl. Soc. Bull.* **1997**, *25*, 848–853.
105. Larivière, S. Reasons Why Predators Cannot Be Inferred from Nest Remains. *Condor* **1999**, *101*, 718–721.
106. Larivière, S.; Messier, F. Characteristics of Waterfowl Nest Depredation by the Striped Skunk (*Mephitis Mephitis*): Can Predators Be Identified from Nest Remains? *Am. Midl. Nat.* **1997**, *137*, 393–396. [CrossRef]
107. Pieron, M.R.; Rohwer, F.C.; Chamberlain, M.J.; Kaller, M.D.; Lancaster, J. Response of Breeding Duck Pairs to Predator Reduction in North Dakota. *J. Wildl. Manag.* **2013**, *77*, 663–671. [CrossRef]
108. Pearse, A.T.; Ratti, J.T. Effects of Predator Removal on Mallard Duckling Survival. *J. Wildl. Manag.* **2004**, *68*, 342–350. [CrossRef]
109. Amundson, C.L.; Arnold, T.W. The Role of Predator Removal, Density-Dependence, and Environmental Factors on Mallard Duckling Survival in North Dakota. *J. Wildl. Manag.* **2011**, *75*, 1330–1339. [CrossRef]