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Efficacy of Killing Large Carnivores to Enhance Moose Harvests: New Insights from a Long-Term View

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Abstract: We analyzed harvest data to test hypotheses that nearly 4 decades of effort to reduce abundance of brown bears (*Ursus arctos*), black bears (*U. americanus*) and gray wolves (*Canis lupis*) in an 60,542 km^2 area in south-central Alaska (Game Management Unit [GMU] 13) was positively correlated with moose (*Alces alces*) harvests in some time-lagged fashion. Predator-reduction efforts were progressively more aggressive over decades (both *de facto* and officially designated predator control) and did not have clear starting points which complicated our post hoc analyses. We documented no positive correlations ($p > 0.05$) between harvests of brown and black bears and subsequent moose harvests for any time lag. Moose harvest was negatively correlated with the previous years' wolf harvest, but the relationship was weak (correlation = -0.33, $p < 0.05$). Consequently, we reject our hypotheses that harvest of predators was positively correlated with moose harvests. We also observed no differences in mean moose harvests during periods of officially designated wolf control (2005–2020) and a previous period ($p > 0.50$). We recommend that predator reductions designed to improve hunter harvests of moose be conducted within a research framework that will permit improved interpretations of results and the implementation of an adaptive-management approach to achieve management objectives.

Keywords: Alaska; black bear; brown bear; case history; intensive management; moose; predator control; wolves

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1. Introduction

Understanding the population dynamics of wild ungulates and the large carnivores that prey upon them is central to the wise management of both predators and prey [1]. How large carnivores might regulate the dynamics of their ungulate prey, however, remains a point of contention; correctly answering this question holds importance for both basic and applied ecology [2,3]. The population dynamics of large ungulates and the density-dependent processes that promote resilience of their populations to predation (or harvest) have been well-documented ([4,5] for reviews). Gray wolves (*Canis lupis*), brown (grizzly) (hereafter brown bears) (*Ursus arctos*), and black bears (*U. americanus*) can be important predators on young (<1 year old) moose (*Alces alces*) [6–12]. Survivorship of young often is a critical density-dependent mechanism regulating ungulate populations [13–16]. Under some circumstances populations of moose may be regulated at low density by heavy predation by large carnivores on both young and adult moose [2,17–24]. A low density of moose caused by intense predation may represent a point of strong equilibrium, a "predator pit" (similar to population dynamics near ecological carrying capacity, *K*), making it difficult for populations to "escape" from the pit [1,21]. Releasing moose from suspected low-density equilibria by killing wolves and bears in the hope of providing more moose or other ungulates for harvest by hunters has been a primary and widespread goal of wildlife management in Alaska for decades [25].

Other models than predator pits have been proposed to explain dynamics of ungulates and their predators [3,26]. Nonetheless, Alaska law since the 1994 Alaska Intensive Management Statute (Alaska Statutes §16.05.255 e–g) effectively has mandated predator reductions to enhance human harvests of wild ungulates for meat. Across 61% of Alaska, moose are the species targeted to benefit from Intensive Management of predators [25]. This prioritization exists wherever the politically appointed Alaska State Board of Game has identified geographic areas as being important for "high levels of human consumptive use" of one or more ungulate species, where hunter demand for wild ungulate harvests exceeds supply, and where ungulate populations are deemed to be "depleted" [27]. The Intensive Management law also identifies improvement of ungulate habitat as an allowed mechanism to achieve targeted levels of ungulate harvests, but such efforts (e.g., controlled burns or mechanical clearing for moose habitat) have not been conducted at a meaningful scale in Alaska [25]. Effectively, efforts to comply with the Intensive Management law have involved predator-reduction programs for one to three species of large carnivores in different parts of Alaska [25]. All Alaska residents, regardless of race, culture, or place of residency are equally eligible beneficiaries of the Intensive Management law.

The Alaska Department of Fish and Game confusingly defines "predator control" as occurring on only officially designated Predator Control Areas. Predator Control Areas are small areas where special-take techniques are authorized under permit, including shooting from fixed-wing aircraft for wolves and snaring for bears. The far more extensive form of predator reduction efforts, however, occurs from liberalization of general hunting and—for wolves— trapping regulations that are not officially defined as being "predator control" but are nevertheless usually adopted to achieve desired predator reductions and hoped for increased harvests of ungulate [25]. Regardless of the official definition of predator control, both the special techniques for killing predators in Predator Control Areas and regulation liberalizations are identified as being appropriate techniques to achieve Intensive Management objectives in the Alaska Department of Fish and Game's Intensive Management Protocol [27]. For bears, the Alaska Department of Fish and Game's management protocol specifically identifies "Favor[ing] conventional hunting seasons and bag limits to manage bear numbers" ([28] (p. 4)). Miller et al. described long term trends in the liberalizations of hunting regulations for brown bears to increase moose harvests [29]. Herein, we recognize and define both approaches as predator control. In the study area we analyze here, there is an officially described Predator Control Area for wolves that allow aircraft-assisted take techniques and, since 1980, progressively more aggressive efforts to reduce bear numbers by adoption of more liberal bearhunting regulations.

With rare exceptions [18,22], predator-reduction efforts to benefit moose in Alaska have not been conducted within a research framework that monitors abundance or other critical attributes of both predators and prey over long-enough periods to determine if or why objectives related to increased ungulate harvests were achieved. Such shortcomings in the design of predator-prey research in Alaska were recognized in 1997 by a National Research Council panel review [20]. In most instances, determination of a need for predator control and monitoring its effects are based on harvest data alone. Harvest data often are the only data collected consistently over long periods for both predator and prey species. This is the case for Game Management Unit 13 (GMU 13), for which we provide a retrospective analysis. We chose to examine available harvest data for moose, wolves, and bears because they span almost 4 decades. This period should be sufficiently long to identify relationships between numbers of predators killed and numbers of moose harvested while avoiding confusion from short-term changes in moose harvest that might be unrelated to numbers of predators killed. Moose harvests are an appropriate response variable for our analysis because increasing this harvest is the management objective for the predator-reduction efforts.

Factors other than predation may affect dynamics of moose populations [1,4,30,31]. Rigorously collected data on those factors such as winter severity and forage, however, were not consistently available in GMU 13. Harvest of moose also may depend upon a variety of factors including hunting regulations (e.g., quotas, season length and timing, effort, motivation, use of guides, equipment, and other variables) [31,32]. For predator control to be an effective mechanism to increase moose harvest, however, it must do so under all those exigencies. Thus, we analyze only the relationship between harvests of moose and previous years' harvests of predators.

Our analysis tests the hypothesis that numbers of predators killed resulted in subsequent increased moose harvests in GMU 13 in a time-lagged fashion across the duration of the study. We further test this outcome for different geographic groupings of harvest data based on the types of wolf killing techniques that were authorized and for which data were available.

2. Study Area

GMU 13 encompasses 60,542 km^2 of south-central Alaska and is subdivided into five subunits (A–E) (Figure 1). GMU 13 incorporates the upper reaches of the Susitna River that flows into Cook Inlet and the Nelchina River that flows into the Copper River and ultimately into Prince William Sound. The area is between the human population centers of the Anchorage Borough (398,328 residents) and the Matanuska-Susitna Borough (107,081 residents) to the south, and the Fairbanks North Star Borough (31,427 residents) to the north. These three areas contain 70.3% of Alaska's human population. The crest of the Alaska Range is the northern boundary of GMU 13. Thirty-one percent of GMU 13 is above 1,200 m in elevation, which is poor habitat for the ungulates and the large carnivores that prey upon them [11]. Lower elevations are a diverse mix of dense spruce (*Picea* spp.) forest encompassing numerous lakes and ponds. Other common plant communities include birch (*Betula nana* and *B. glandulosa*), heath (*Cassiope* spp., *Ledum* spp., *Vaccinium* spp., and *Arctostaphlos* spp.), and sedge (*Carex* spp.) meadows. Willows (*Salix* spp.), an important forage for moose, occur across a variety of plant communities, but are most common in riparian zones [11]. The climate is slightly milder and precipitation somewhat greater than in interior Alaska. Temperatures range from an average of 12 °C in July to −21 °C in December; average precipitation is 24 cm with snow depths ranging from 76–173 cm, although considerable weather variability occurs [11]. Fires play an important role in the ecology of moose [9,30,33], but major fires have not occurred in GMU 13 since at least the 1960s and prescribed fires have been small in extent (174 km^2 during 2003–2004 in Subunits 13A and 13B) [34].

GMU 13 is heavily used by moose and caribou (*Rangifer tarandus)* hunters. Many hunters are from the population centers with some flying into or using all-terrain vehicles and boats to gain access to interior areas as well as accessing the area from the road system with vehicles. GMU 13 was among the first group of areas designated for Intensive Management to benefit moose harvest through reduction of bears and wolves following passage of the 1994 Intensive Management statute. There have been many regulation changes during our period of analysis for the three predator species and for moose and these changes undoubtedly affected harvest numbers. Nevertheless, the details of these changes are not variables directly considered in our assessments. They are indirectly incorporated via our time-series analyses. For clarity, we provide the general pattern of these regulatory changes below.

The trend for moose-hunting regulations for resident hunters has been toward increasingly shorter seasons and more restrictive definitions of what is a legal moose for hunters to harvest. Antler-size restrictions designed to prevent shooting males with antlers smaller than 36 inches (~91 cm) started in 1980, but spike- or fork-antlered males also could be harvested (at least in a portion of GMU 13 during 1985–1992 and elsewhere in the GMU during 1993–2021). For large moose, legal minimum antler spread changed to 50 inches (127 cm) in 1993 and these antlers also needed to have $\geq$3 brow tines on at least one antler.

Starting in 2001, these large-antlered moose had to have ≥4 brow tines on at least one side. Hunting seasons during autumn generally have been short (10–30 days). Since 2003, the State of Alaska objectives are for 1050–2180 moose to be taken in GMU 13 under state regulations [34].

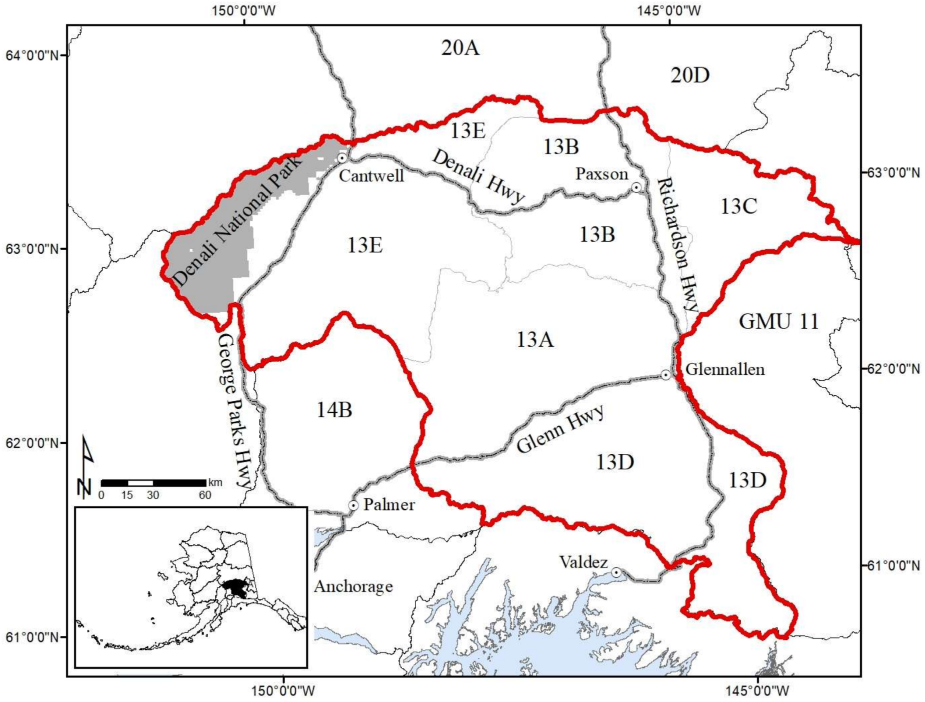

Figure 1. Game Management Unit (GMU) 13 (red outline), including subunits A, B, C, D, and E (grey lines are highways) in south-central Alaska, USA.

For wolves the pattern of regulatory changes over time has been to facilitate or encourage the killing of more wolves since 1974. For hunters, the annual kill quota for wolves was unlimited (1975–1987), varied between four and unlimited (1988–1991), five wolves (1992–1998), and 10 wolves per day (1999–2020). Quotas for wolf trappers has been unlimited during 1972–2020. Starting in 2005, Intensive Management regulations were adopted authorizing wolf hunters and trappers also to take wolves by aerial shooting from fixed-wing aircraft (officially defined predator control). Aerial shooting of wolves was not authorized in Subunit 13D in 2005 or subsequently [34].

Following research in 1979 and the early 1980s indicating that brown and black bears frequently preyed upon neonatal moose [6,7,35], hunting regulations for brown bears became progressively more liberal. In GMU 13, all regulation changes since 1986 were designed to facilitate more harvests (Figure S1). These included no closed season for brown bear hunting, changing the annual quota to one bear per year (instead of one per four years), allowing killing over bait, and eliminating the requirement that resident hunters needed to purchase a tag to hunt brown bears (Figure S1). The management objective for brown bears in GMU 13 is to maintain a minimum unit-wide population of at least 350 bears. In 1993, the GMU 13 population bears was estimated to be 1228 [36]. A population of 350 brown bears would represent a 71% reduction from that number. Density estimates in a relatively remote portion of 13E indicated no change during a period of liberalized hunting regulations between 1985 and 1995 but detected a change in population composition favoring females [37,38]. Replicate density estimates in more accessible 13A during 1998 and 2011 reported a decline in density of 20–45% (4% per year) and, based on harvest data, a shift in population composition toward adult females [39]. In contrast to brown bears, most hunting regulations for black bear in GMU 13 were liberal prior to 1980 but also exhibited a trend toward becoming increasingly more liberal. Hunting seasons for black bear were open year-round since 1970, with a bag limit of three per year since 1973 (changed to five per year in 2022), no tag fee for resident hunters, and baiting was legalized in 1980. The current management goal in Unit 13 is to provide the greatest sustained opportunity to participate in hunting black bears [40].

3. Materials and Methods

3.1. Harvest Data

We obtained harvest data for moose, wolves, brown bears, and black bears from the Alaska Department of Fish and Game through requests and, for historical data, from Survey and Inventory Reports and Species Management Reports available on the state Fish and Game website. Brown and black bear harvests were obtained by the Alaska Department of Fish and Game from mandatory hide and skull inspection requirements ("sealing") for hunters and, for wolves, trappers of those predator species. Starting in 2009, sealing of black bears was not required in GMU 13, and hunters were asked to report kills and hunting activities with harvest-ticket reports. Harvest tickets must be obtained prior to hunting a species and have no limit on number issued. Bear kill numbers we report did not include kills made in defense of life or property, road or other accidental kills, or illegal kills. Harvest data included wolves taken by persons with hunting or trapping licenses and by aircraft-assisted (predator control) permits. Alaska Department of Fish and Game derived the moose harvest data we used from harvest ticket reports from resident and non-resident hunters. In GMU 13, only harvest tickets, with no quota on number issued, were required of Alaska resident moose hunters in GMU 13. our moose-harvest data also included moose killed in federally authorized subsistence hunts. Alaska Department of Fish and Game reports to the Board of Game on Intensive Management activities in GMU 13 for moose harvests included constants added since 2008 for "unreported kills, "illegal kills," and "train or vehicle mortalities" (e.g., [34]). These constants averaged 125 moose/year since 2011 and are not included in our moose-kill numbers.

3.2. Statistical Analyses

Our goal was to produce regression models that best predicted observed moose harvest from predator-harvest data that had reliable and interpretable coefficients for testing our hypothesis that past predator harvest would be positively related to increases in moose harvest. Our process had three steps. First, we tested harvest data for each species for serial correlation. Strong serial correlation within harvest data for a species could affect the sign and magnitude of regression coefficients in models including that species, and thereby confound our ability to interpret those coefficients [41,42]. When serial correlations occurred, we took steps during model building to mitigate these effects. The second step was to examine correlations between moose harvest and harvest of a predator species in a preceding year to identify which predator species and which past year's harvests likely predicted the moose harvest. Our third step was to use those predator harvests we identified as likely candidates to build regression models that best predicted moose harvest. We repeated this three-step procedure for harvest data from the entire GMU 13 (1973–2020) and for harvest data from two subunit areas (13D and the other four subunits) for years when subunit data were available for all species (1983–2020). We included this analysis excluding 13D because special "predator control" aerial shooting permits were not issued in 13D starting in 2005 but were for the other 4 subunits.

We estimated autocorrelation and partial autocorrelation functions [43] to examine the strength and form of serial correlation within the harvest data for each species. Harvest data are reported by Alaska Department of Fish and Game designated regulatory years, which overlap calendar years. For example, regulatory year 2019 includes 1 July 2019–30 June 2020 (denoted here as "2019"). Moose hunting occurred only in autumn but most wolf harvest occurred in winter. Bear hunting during Intensive Management was legal year-round (e.g., Figure S1). Consequently, we only compared moose harvest with predator harvests from previous regulatory years because most predator harvest in a regulatory year (especially for wolves) happened after the moose harvest. One of the most efficient ways to examine correlations between current moose harvest and past predator harvest is to use cross correlations, which are standard Pearson correlations between the current moose harvest and predator harvest 1 year ago, 2 years ago, 3 years ago, 4 years ago and so on until the beginning of each time series [41]. We used those correlations to identify lagged predator harvests that likely were predictors of moose harvest and should be considered in our regression functions. We also combined all three predator harvests together into a single variable for consideration. We used a significance level for correlations of $p \leq 0.05$)

We explored models containing different combinations of harvest data for each species to determine the combination that best predicted moose harvest. We used conditional Akaike Information Criteria (AICc) [44] to select the best models for predicting moose harvest. We only considered a model if the difference (AICc Δ) between its AICc score and that of the model with lowest AICc in the suite of potential models was <4.0. Our selection criteria were generous and inclusive with respect to accepting models and covariates to avoid mistakenly rejecting a marginal covariate for predator kill. Nonetheless, we risked including models containing uninformative covariates, a common problem when using any AIC-mediated model selection [45]. Therefore, we took advantage of the link between AICc and log-likelihood ratio tests to reduce that risk and exclude uninformative covariates. The AICc Δ values are approximations of log-likelihood ratio test scores and their probabilities can be approximated by a chi-square distribution [45]. The AICc selection process adds a penalty of 2 to the AICc score for every covariate in a model. If we compare two models that are the same except one has an additional covariate, and they have the exact same log likelihood values, that additional covariate is uninformative. The AICc Δ value for the more complex model would be ~2. That approximates a log-likelihood ratio chi-square score of 2 with 1 degree of freedom and $\alpha = 0.15$. Therefore, 85% confidence limits ($1 - 0.15 = 0.85$) about the coefficients of potential regression covariates coincide with the AIC selection process and can be used to identify covariates that are likely uninformative but were not excluded by the AIC criteria used during model selection [45,46]. Consequently, if the 85% confidence intervals for any coefficient of a covariate encompassed 0, we did not consider that covariate to be an important predictor. We used Durbin-Watson statistics (D-W) to indicate the strength of serial correlation among regression-model residuals to assure our steps to mitigate serial correlation in harvest data were successful. If the D-W value was $\geq$1.75 and $\leq$2.25, we assumed serial correlation among residuals was not significant—we only considered those models. Our models were built on the best fit for historical data and are not necessarily predictive [45].

In addition to our AIC evaluation, we also compared mean harvest of moose for the officially recognized predator control area (13A, 13B, 13C, 13E) during the officially recognized wolf predator control period (2005–2020) with mean harvests prior to that period (1983–2004) in the same area. We used Student's *t*-test for detecting difference in the means, however, if strong serial correlation was detected in the harvest data, we modified the test accordingly [47]. Several years may be necessary before effects from intense wolf harvests would result in increased moose harvests. Therefore, we repeated our means-comparison test but allowed 3 years to elapse from the implementation of officially recognized predator control for wolves (1983–2004 compared with 2008–2020). These means-comparison tests provided another way to evaluate whether Intensive Management resulted in more moose harvests.

4. Results

4.1. Game Management Unit 13

Harvests of moose varied greatly during 1973–2020 but never reached the peak harvests of the previous decade (Figure 2). We only used data during 1973–2020 for our analyses because that period had complete harvest data for all the species of predators we investigated. The lowest moose harvest occurred in 2001 (a year with a change to a more restrictive definition of what was a legally harvestable moose) and it trended higher from then until 2016 (harvest of 1083 moose) followed by a decline (Figure 2). The minimum "target" set for moose harvests in GMU 13 under Intensive Management regulations is 1050 moose [34]; other than in 2016 and 2015 (1051 moose harvested), this target was last previously met in 1993 (1993 moose harvested, Figure 2). During 1977–2020, 99.5% of annual moose harvests in GMU 13 were males (range 94.8–100%, SE = 0.12).

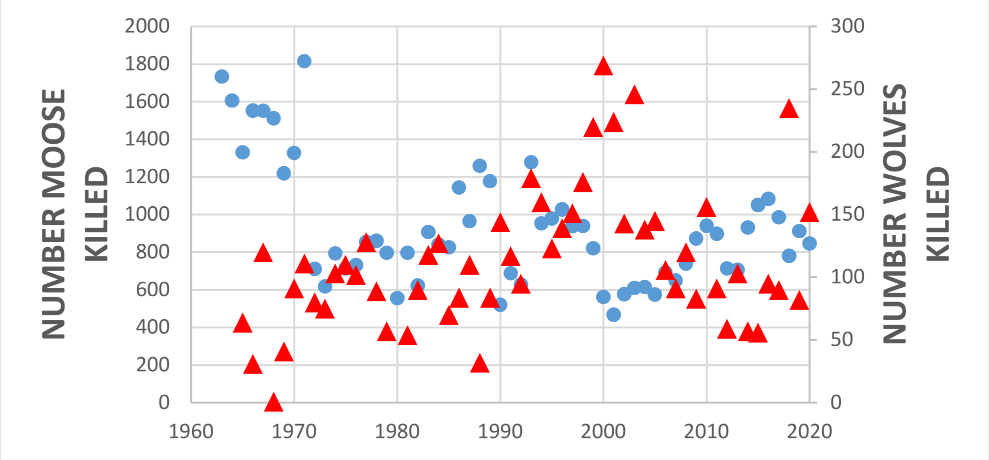

Figure 2. Hunter harvests of moose and hunter and trapper harvests of wolves in Game Management Unit 13, in south-central Alaska, USA (moose = blue circles; wolves = red triangles). Our statistical analysis includes data from 1973 onward.

Killing of wolves peaked between 1999 and 2001 but kills increased gradually after 1990 and then declined after 2004, except for another peak in 2018 (Figure 2). Harvest of wolves in GMU 13 increased somewhat after 2012 but remained lower than previously reported (Figure 2). Killing of black bears and brown bears, likewise, increased over the course of our study (Figure 3) as a consequence of regulation liberalizations [25].

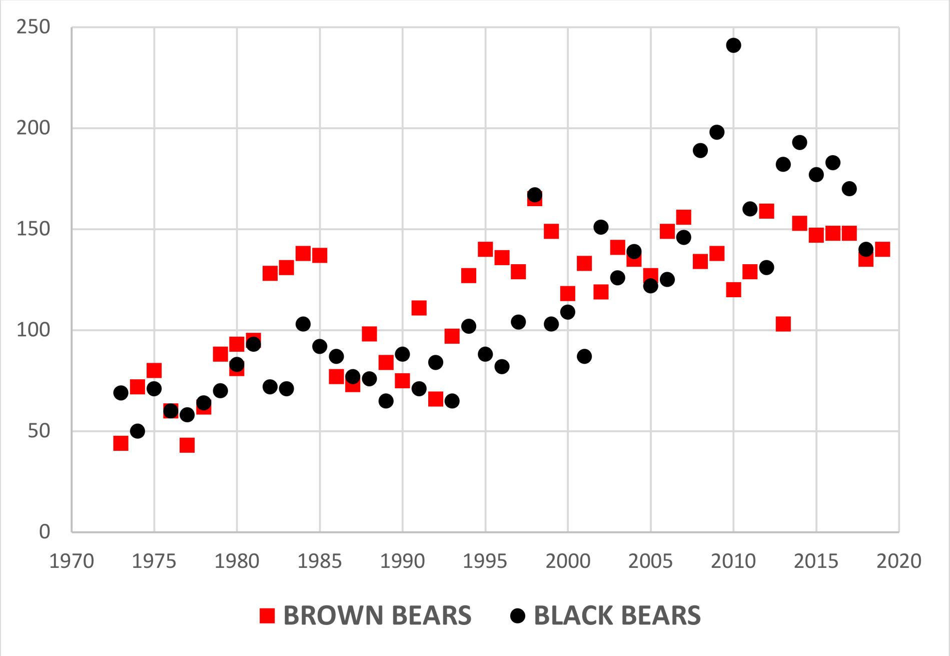

Figure 3. Number of hunter kills of brown bears and black bears in Game Management Unit 13, south-central Alaska, USA, 1973–2019.

Autocorrelation and partial autocorrelation functions for the harvest of moose during 1973–2020 exhibited strong serial correlation (Figure 4, Table S1). Indeed, the decay of correlation as time lags increased indicated serial correlation in data and the single significant spike in the partial autocorrelation function at time lag (year—1) indicated current moose harvest was significantly correlated with moose harvest the previous year but not beyond that single year time lag. Likewise, harvest data for wolves, brown bears, and black bears exhibited similar patterns of serial correlation (Figure 4). Consequently, we did not include multiple lagged terms for the same species within the same model to avoid problems interpreting regression coefficients caused by significant correlations among those terms.

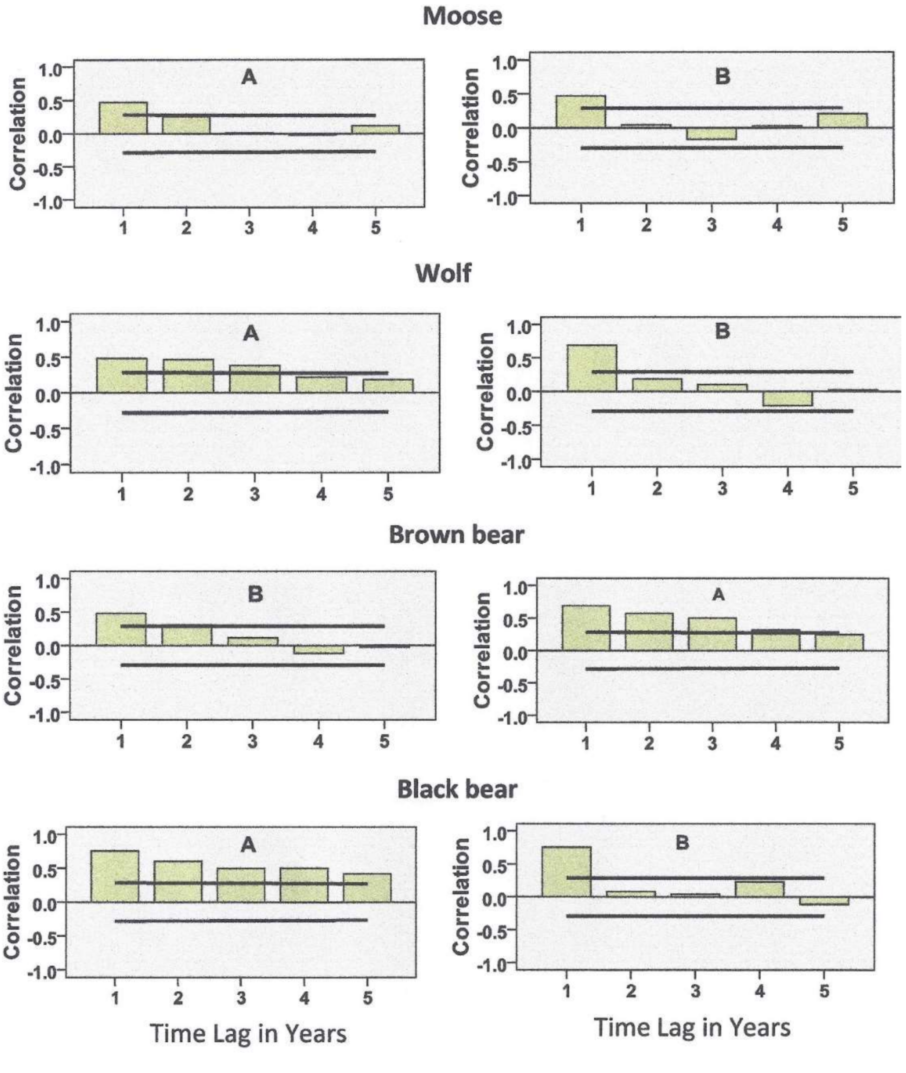

Figure 4. Autocorrelation (A) and partial autocorrelation (B) functions for time lagged (1–5 years) for moose, wolf, brown bear, and black bear harvest data from GMU 13 south-central Alaska, USA, 1973–2020. Correlations (bars) extending beyond bracketing lines are significant ($p \leq 0.05$). We only show lags up to 5 years because all significant correlations occurred within those years.

Cross correlation functions exhibited significant negative correlations between moose and lagged wolf harvests from the previous 5 years, but that relationship was weak (Figure 5). Nevertheless, we included lagged wolf harvests for the length of our study as possible covariates in our regression functions predicting moose harvest (only 1–5 year lags shown in figures). The same analysis of moose and brown bear harvest, and moose and black bear harvest showed no significant correlations between moose harvest and lagged bear harvests (Figure 5). In addition, an analysis combining kills of all three predators into a single variable failed to exhibit a significant relationship (Figure 5). As a result, we excluded brown and black bear harvest from our regression functions for all of GMU 13.

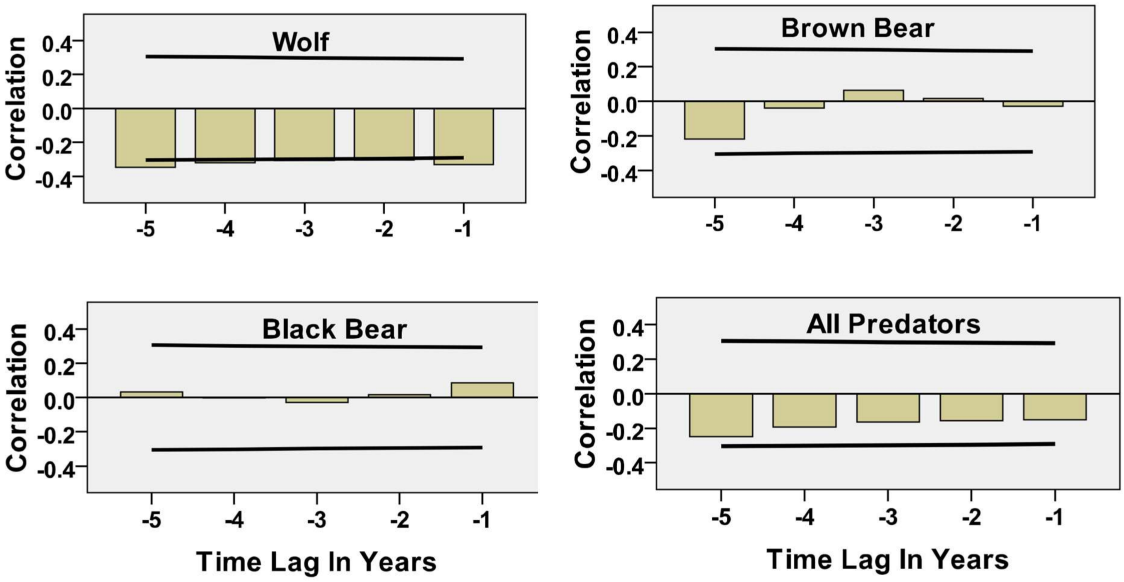

Figure 5. Cross-correlation functions for moose harvest versus previous (1–5 year lag) for wolf, brown bear, black bear, and all predators combined in GMU 13 south-central Alaska, USA, 1973–2020. We only show lags up to 5 years because all significant correlations occurred within those years.

We included the previous year's moose harvest as a covariate in every model because that variable was always a significant predictor of current year's moose harvest and it conditioned out most effects of serial correlation in the moose-harvest time series. Moreover, this method enabled each model to track effects, albeit in a time-lagged fashion, of factors extraneous to our analyses that affected moose harvest, such as regulation changes, without the need to explicitly partition those effects. Hence, we could examine the significance of predator harvest independent of those other influences. The two best models explaining harvest of moose contained the previous year's moose harvest alone, and the previous year's moose and wolf harvest. For the second model that included the wolf covariate, the coefficient for wolves was negative (Table S1). We did not consider the other models because the 85% CIs for the coefficients of wolf harvest overlapped 0. The AICc weights (w) for the two best models differed little (0.463 and 0.537, respectively) indicating that including wolf harvest (with a negative coefficient) only marginally improved model fit.

4.2. GMU 13D and Subunits A, B, C, and E

Because officially designated wolf predator control was not authorized in subunit 13D, we evaluated moose harvest with and without data from 13D for the period 1983–2020 when data for all species were available by subunit and 13D could be excluded. For the aggregate group containing designated wolf control subunits A, B, C, and E, cross correlations again indicated moose harvest was negatively correlated with wolf harvest for the previous 2 years. Moreover, moose harvest was not correlated with previous brown or black bear harvests. Our regression model results were similar to those for the entire GMU noted previously for the time period starting in 1973 (Table S2) The best model included moose and wolf harvests for the previous year and the coefficient for wolf harvest was again negative indicating that an increase in wolf harvest predicted lower moose harvests the next year (Table S2). Moreover, no wolf harvests > 1 year in the past had a significant effect on moose harvests.

For subunit D, where officially designated wolf control was not implemented in 2005, cross-correlation functions indicated that previous wolf, brown bear, and black bear harvests were not correlated with moose harvest from 1983 to 2020. The only suitable candidate covariate in our regression model was moose harvest the previous year (Table S3).

4.3. Moose Harvest Means Comparisons, Subunit A, B, C, and E

The mean harvest of moose in subunits A, B, C, and E during 1983–2004, before intensive wolf harvest was implemented, was 768.8 (SD = 228.2) moose. After intensive wolf harvest was implemented (2005–2020) the average harvest was 761.1 (SD = 138.6) moose. Moose harvest was strongly serially correlated with a coefficient of 0.496 between current harvest and harvest the previous year. To accommodate that serial correlation, we calculated effective sample size, Ne, and used that rather than observed sample size when determining the significance of the *t*-test [47]. The observed sample size of 37 was multiplied by scaler $(1 - 0.496)/(1 + 0.496) = 0.34$. Thus, Ne = 12. The variances about each mean differed (Levene's test $F = 4.46$, $p = 0.042$) so we computed *t*-test scores for unequal variances. The *t*-score was 0.129 and p (2-tailed) = 0.90. Because positive effects on moose harvests may lag behind increased wolf harvests, we also conducted a means comparison for moose harvests 3 years following implementation of officially designated wolf predator control (2008–2020) and the prior period (1983–2004). The mean harvest 2008–2020 was 803.6 (SD = 114.1) moose. The *t*-score of differences between the means and Ne = 12, was -0.600 and p (2-tailed) = 0.561.

5. Discussion

5.1. Predator Kill and Moose Harvest

Our analysis failed to support our hypothesis that moose harvests in Alaska's GMU 13 would be positively correlated with harvests of wolves, brown bears, or black bears. No matter how we examined those data, we observed no evidence that any past predator harvest was positively correlated with subsequent moose harvests in GMU 13. Our best model included the previous year's wolf harvest but, the coefficient was negative. The next most strongly supported model, with almost the same AICc value, included only the previous year's moose harvest as an explanatory variable. Any effect of wolf harvest on moose harvest was weak; our models probably reflected that the peak in wolf harvest during 1999–2001 also coincided with the lowest moose harvests in 2000, 2001, and 2002 (Figure 2). That outcome likely caused the negative correlation between those harvest numbers. Perhaps the high wolf harvest was somehow related to the increase in moose harvest after 2005. Nevertheless, if that occurred, then we would expect to observe positive correlations between moose harvest and wolf harvest 5–6 years previously—we did not. This outcome indicated that whatever factors caused fluctuations in moose harvests over time in GMU 13, the number of predators killed was not significant as being one of them. This conclusion is further supported by the absence of a significant difference in mean harvests of moose before and during the period of officially implemented predator control (for wolves) that started in 2005.

Our analysis was complicated by the absence of a good experimental design with clear stopping and starting points for predator control in different geographic areas and with different techniques allowed for taking predators. Consequently, we examined different time periods and geographic areas to avoid missing a potentially significant signal that predator control of a species was "working" as intended. This was especially true for wolves, which were officially identified as a target for reduction in GMU 13 under Alaska's 1994 Intensive Management law. Regulations designed to reduce abundance of bears that started in 1980, in contrast, were not officially classified as "predator control," even though management objectives were to significantly reduce their numbers (by up to 70% for brown bears).

Regardless of how we sorted the available data we were unable to detect a positive relationship between kill numbers of any predator species and subsequent moose harvests. Neither did we find significant increases in mean moose harvests during two periods of official wolf predator control and *a priori* period. The long period encompassed by our analyses calls into question conclusions from shorter-term studies indicating that predator control in GMU 13 resulted in increased moose harvests (e.g., [34]). In short-term studies, there is a danger of accepting an apparent fit of observations to a preferred explanation [48].

Our analyses demonstrate that a focus only on increased killing of predators to enhance harvests of moose can be a poor paradigm for management of moose in GMU 13 (and likely other areas). The 1997 National Research Council report evaluating predator control in Alaska concluded that, in part, many predator-control experiments had been insufficiently monitored, and that design of those experiments did not allow firm conclusions regarding the causes of subsequent changes in ungulate populations [20]. The Council also recommended that wolves, bears, and ungulates be managed with an adaptive-management approach [49]. Those previously identified shortcomings in research design and implementation remain for most predator-reduction efforts conducted in Alaska prior to and after passage of the Intensive Management Statute.

Wolves and bears can be potent predators of young moose. What conditions then might lead to the absence of a strong relationship between the killing of bears and wolves and the subsequent harvest of moose? One possibility is that the moose population was not in a predator pit and, hence, would not experience an ecological release from killing predators. Predators also might immigrate from adjacent areas and replace harvested individuals [50], which also would lessen the effect of killing predators to bring about higher moose harvests. In GMU 13, however, adjacent areas and about 84% of the entire state have similar liberal take regulations for large carnivores [25], likely reducing the potential of this explanation to be of value.

Historic declines in moose harvest following the 1960s (Figure 2) have been attributed to a population crash associated with severe winters and perhaps heavy harvest by hunters [8]. Population declines subsequently also were associated with severe winters with deep snow (1988–1994 and 1999–2000) and reported high wolf populations; circumstances that led to wolf-control efforts starting in 2003 [51,52]. Winters have been relatively mild since 2000 and this, along with reduced wolf predation, were identified as causes for modest moose population increases since then [51]. Populations near K would be expected to be most susceptible to adverse effects from severe weather because of their poor nutritional condition [5,48,51]. Predator control under such conditions would be unlikely to affect moose populations because of compensatory mortality [4,5]. Despite substantial variation in moose harvest over a considerable span of years with variable weather conditions, no detectable relationships occurred between previous brown bear, black bear, and wolf kill, and moose harvest, despite efforts over 3 decades to reduce brown bear and wolf abundance by liberalizing hunting regulations [29,39].

Fire also can improve K (ecological carrying capacity) for moose populations [30,33] and thereby effect harvest. Paucity of fires (wild or prescribed) since 1950 likely reduced the K for moose over extensive portions of Unit 13 [51]. In recent decades, only about 166 km^2 of prescribed fires have been set in Unit 13 (2003 and 2004) [34]. On Alaska's Kenai Peninsula, predation was a much less important factor for moose productivity in recently burned areas compared with older burns [9]. Research in GMU 13 reported that nutritional constraints on moose productivity were associated with population declines (1994–2000), but attributed population declines to high rates of summer mortality of young moose—modeling concluded that reducing predation would have a greater effect on population growth than increased reproduction [52]. Nonetheless, improved habitat would not be an important factor if moose were regulated at low density by intense predation because moose productivity already would be high [4,5].

5.2. Management Considerations

One difficulty with Intensive Management is that changes in management are linked with the harvest of moose, which is responding primarily to variables other than killing predators—clearly other data are needed for the sound management of moose. The most necessary yet challenging requisite for such management of moose is knowing where the population is with respect to ecological carrying capacity (*K*). Populations near *K* are composed of individuals in poor physical condition where mortality is mostly compensatory, wherein one source of mortality compensates for another—killing predators would have a minimal effect on recruitment of young, because those animals would have perished from other sources anyway [53]. Conversely, moose populations at low density are in good physical condition where mortality is primarily additive (i.e., potentially in predator pits), where sources of mortality would be summed and killing of predators could enhance recruitment into huntable cohorts. Notably, differences in population density among populations or changes of density within a population do not provide a reliable index of compensatory vs. additive mortality, because *K* can vary across areas or time periods, requiring other data to parametrize where the population is in relation to *K*.

Measures of moose nutritional condition, other population characteristics, and forage availability can be used to index the relationship of the moose population to *K* [1,4,5]. Nevertheless, forage-based methods, including those implemented in Alaska [18,54–57] for estimating *K* (or some reproductive variables related to *K*) are available, but these are labor intensive; forage measurements also may lag declines of ungulate populations [5]. Moreover, browsing intensity by moose was not predictive of calving success [58]. and measures of willow quality can vary markedly in response to annual patterns of weather [10]. Moose would be expected to respond reproductively to such variation in forage quality only when populations were near *K*, and forage was limited. In addition, the relationship between ungulate density and forage productivity may not be linear, especially at low densities of ungulates [58,59], which reduces the reliability of measuring forage to understand population dynamics of moose. Further, moose sexually segregate in spring and winter [60–62], necessitating that ranges used primarily by females be sampled to assess population productivity, a critical factor that often is ignored [63].

Some population parameters, such, young to female, male to female, or predator to prey can be used to judge population dynamics, but may be misleading because of the double-variable nature of those data [4,64–66]. Measures of physical condition of moose are extremely useful in determining where the population was in relation to *K*, without having to measure *K* directly [1,4,5]. Nonetheless, the use of weights of young or yearlings may be biased because of potential cohort or maternal effects whereby improvements in habitat quality are not immediately reflected in the size of adults or their young [12,46,56]. A suite of life-history and population characteristics are available to help judge the relationship of an ungulate population to *K* but are most useful when a variety of characteristics are collected from females [1,4,5]. Too few females have been included in the harvest of moose over the past 4 decades in Unit 13 to implement such an approach. Clearly, a suite of variables would be useful in making such judgments, and data on females are required for those analyses [5,66]. Those variables lend themselves well for implementing an adaptive-management approach as suggested by the National Research Council [20] and would benefit future management of moose in Alaska.

6. Conclusions

Our long-term case history offers new and important insights for managing moose via predator control, in any of its forms, which failed to achieve management objectives for moose harvests or otherwise affect the harvest of those large herbivores. This outcome clearly demonstrates that additional information regarding factors influencing moose abundance and harvests should be more fully considered before predator control is applied as a general management procedure on large geographic scales. We further caution that better data concerning the proximity of the moose population to *K* is necessary to effectively manage moose.

Estimates of abundance and trends for populations of large carnivores such as bears are expensive, difficult to obtain, and often imprecise [37,42]. Elsewhere in North America, aggressive efforts to reduce abundance of bears and wolves in the 19th and 20th Centuries have led to widespread declines in distributions and abundance of large carnivores and altered their effects on ecosystem function [29,67–72]. Alaskan habitats and populations are likely more resilient than many of the places around the world where large carnivores have declined or disappeared because of human activities including direct killing. In Alaska, large areas of wildlife habitat remain intact and unfragmented. Potential threats to large carnivore abundance at levels where the dynamics of their populations and their roles in ecosystem function are close to natural comes more from efforts to manipulate abundance of predators and prey than from habitat changes (excluding—perhaps—climate change). Our long-term view of the existing management paradigm for moose and their predators signals the need for further consideration for more well-rounded wildlife-management protocols in Alaska that consider more than just harvest of ungulates.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14110939/s1, Figure S1: Trends in annual number of brown bears harvested in GMU 13 overlain on extant hunting regulations; Table S1: Regression models of moose harvest (t) against moose harvest (t-1)[ml], wolf harvest (t-1) [wll], wolf harvest (t-2) [wl2], wolf harvest (t-3) [wl3], wolf harvest (t-4) [wl4], and wolf harvest (t-5) [wl5] for GMU 13, south-central Alaska, USA, 1973-2020. Table S2 Regression models of moose harvest (t) against moose harvest (t-1)[ml], wolf harvest (t-1) [wl1], wolf harvest (t-2) [wl2] for subunits A, B, C, and E of GMU 13, south-central Alaska, USA,1983-2020. Table S3. Regression model of moose harvest (t) against moose harvest (t-1)[ml] for subunit D of GMU 13, south-central Alaska, USA, 1983–2020.

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