Hunting as a Management Tool? Cougar-Human Conflict is Positively Related to Trophy Hunting

Kristine J. Teichman  
*University of Victoria*

Bogdan Cristescu  
*University of Cape Town*

Chris T. Darimont  
*University of Victoria*, darimont@uvic.ca

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Hunting as a management tool?
Cougar-human conflict is positively related to trophy hunting

Kristine J. Teichman1,2*, Bogdan Cristescu3† and Chris T. Darimont1,4,5

Abstract

Background: Overexploitation and persecution of large carnivores resulting from conflict with humans comprise major causes of declines worldwide. Although little is known about the interplay between these mortality types, hunting of predators remains a common management strategy aimed at reducing predator-human conflict. Emerging theory and data, however, caution that such policy can alter the age structure of populations, triggering increased conflict in which conflict-prone juveniles are involved.

Results: Using a 30-year dataset on human-caused cougar (Puma concolor) kills in British Columbia (BC), Canada, we examined relationships between hunter-caused and conflict-associated mortality. Individuals that were killed via conflict with humans were younger than hunted cougars. Accounting for human density and habitat productivity, human hunting pressure during or before the year of conflict comprised the most important variables. Both were associated with increased male cougar-human conflict. Moreover, in each of five regions assessed, conflict was higher with increased human hunting pressure for at least one cougar sex.

Conclusion: Although only providing correlative evidence, such patterns over large geographic and temporal scales suggest that alternative approaches to conflict mitigation might yield more effective outcomes for humans as well as cougar populations and the individuals within populations.

Keywords: British Columbia, Mountain lion, Predator-human coexistence, Puma, Puma concolor, Skull size, Trophy hunting, Wildlife

Background

Exploitation and persecution related to conflict with humans form major causes of predator declines worldwide [1–4]. Killing takes several forms and its ecological and evolutionary effects might be more severe than the number of removed predators suggests [5]. Expansion of human activities into previously undisturbed areas enables increased killing through facilitated human access; roads, cut lines and trails associated with extractive industries facilitate hunting of predators during and/or after resource extraction [6, 7]. As human populations expand, the likelihood of wildlife-human conflict also increases [8].

When conflicts involve large mammalian predators that pose a perceived or real threat to humans and property, a common outcome is the lethal removal of the predator by management agencies or sometimes by land owners, for example in response to predation on livestock [9]. In addition, conflict is often managed through increasing human-caused killing of carnivores, under the premise that human hunting can reduce conflict incidence over predation or decrease predation on wild ungulates sought by hunters (hereafter, ‘human hunting hypothesis’; e.g., [10–12]).

In the case of predator-human conflict over predation, Treves and Naughton-Treves [13] suggested that
carnivore killing by hunters may actually promote conflict. The process is thought to operate via shifts in age composition to younger age animals, which might depreciate more because of higher encounter rates with livestock. This process is thought to occur via the increased mobility of juvenile age classes of carnivores caused by decline in adult male territory tenure [14]. Young individuals become locally more abundant and thereby have increased chance of encountering livestock—and/or young animals might be bolder, more curious or lacking experience in interactions with people [15] or in capturing wild prey effectively [16]. Collectively these factors suggest that younger animals are more conflict-prone (hereafter, ‘young animal hypothesis’). Moreover, hunting, culling or other lethal control targeted at specific individuals (e.g. those involved in livestock predation) may reduce conflict (‘problem individuals hypothesis’; e.g., [16]), which has been challenged by the assertion that dispersing individuals often quickly recolonize conflict areas, offering only temporary relief [17].

To confront these hypotheses, we examined a long-term dataset on human hunting of cougars and conflict involving cougars in BC, Canada. Cougar-human conflict and cougar hunting are relatively widespread and common, the latter attracting both local BC hunters as well as foreign hunters for guided hunts. We used this system to test whether: (1) cougars killed by hunters would be larger than those that came into conflict with people (young animal hypothesis); and (2) human hunting mortality and conflict incidence would be related (problem animal and human hunting hypotheses).

Methods

Cougardata

We used a 30-year dataset (1979–2008) on recorded cougar mortality in BC, Canada provided by the BC Ministry of Environment, wherein all records had an associated date. We used cougar kill records resulting from conflict and legal hunting events. For analyses involving age of conflict and legally hunted cougars [(1) above] we used only those records with associated spatial data, sex and skull sizes. The other analyses [(2) above] were carried out using the larger dataset of spatially-referenced conflict and legal hunting mortalities of cougars with known sex, irrespective of whether skull size had been recorded. Only 96 illegal kills were recorded during 1979–2008, of which 35 had associated skull length and width data and these were not used in analyses. We consider this a minimum estimate because evaluations of the frequency of illegal cougar kills have not been performed. We do not expect illegal killing to vary across regions. Additional spatially-referenced mortality records of cougars with known sex (356, of which 139 had associated skull information) had unclear or unrecorded cause of death and were not used in analyses.

Spatial data included universal transverse mercator (UTM) coordinates and we considered only conflict and legal hunting records occurring within the 5 of 8 total ‘development regions’ of BC (region size mean ± SE, 72,173 ± 19,388 km²) in which mortality was highest (Cariboo, Kootenay, Lower Mainland South-West (SW), Thompson Okanagan and Vancouver Island). After plotting kill locations by region in ArcGIS v.10.3 (ESRI, Redlands, USA) for validation and discarding records occurring outside the 5 regions or in water, as well as a small number of erroneous records (e.g., skull width > skull length), the final dataset for cougar age analysis consisted of 3665 records. The data included records of kills by BC resident hunters and non-resident guided hunters (n = 3219) as well as conflict-related cougar deaths (n = 449). ‘Conflict’ was defined as any incident of cougar road mortality, predation on livestock, perceived risk to people such as cougars sighted in urban areas, or recorded attack on humans. More male (n = 2240) than female (n = 1428) mortality records occurred in the data. The larger dataset for analysis of cougar conflict in relation to human hunting levels included 8788 records. The data were dominated by hunting mortalities (n = 7550), with conflict-related kills being less frequent (n = 1238). The dataset had more male (n = 5348) than female records (n = 3440).

Skull size data (length and width in mm) were collected by BC Ministry of Environment personnel as a proxy for age. These variables are positively correlated [18] with the skull growth continuing long into adulthood [19]. Skull size has been used as a proxy for age/body size in other large felids, such as African lion [20], leopard [21] and jaguar [22]. Because skull length and width were highly correlated for males (Pearson r = 0.761, df = 2239, P < 0.001) and females (r = 0.669, df = 1427, P < 0.001), we used an index known as the total skull length (or total skull size) for all analyses. This index is the sum of length and width [22] and is the standard age/body/trophy size metric used by the Boone and Crockett Club and the International Council for Game and Wildlife Conservation when assessing cougar and jaguar trophies [23].

Statistical analyses

To assess if skull sizes varied in relation to different human-caused mortality types, we first assessed if the variable was normally distributed with Shapiro–Wilk tests. Separate assessments were carried out for each sex and region. For males and females in all regions, the skull size variable was not normally distributed. Therefore we used two-sample Wilcoxon rank-sum (Mann–Whitney) tests to compare mean skull size for conflict and hunter
kills. Separate testing was performed for each sex and region for a total of 10 tests (2 sexes × 5 regions).

We used time series analysis to test factor combinations hypothesized a priori to influence annual conflict frequency across time (Additional file 1: Table S1). Newey-West Heteroskedasticity and Autocorrelation (HAC) standard errors were computed in multiple linear regression to account for potential variability and temporal autocorrelation in the models’ error terms. Conflict incidence (dependent variable) was standardized per 10,000 km² and square root-transformed prior to modelling to reduce skewness. Predictor variables included human density (D), human hunting pressure (annual number of cougars hunted) in the year of conflict (Ht0) and the Normalized Difference Vegetation Index (NDVI; a proxy for plant and prey productivity) in the year of conflict (Nt0). A squared term was included for human density (D²) to account for possible thresholds in human availability. Human hunting pressure was standardized per 10,000 km² and included hunting by residents and non-residents of BC. Because habitat quality and prey availability can influence large carnivore-human conflict [24, 25], but such data over our broad temporal and spatial extents were not available, we used NDVI as a habitat productivity surrogate [26–28]. These data came from the National Oceanic and Atmospheric Administration (NOAA) Climate Data Records (CDR), which derived NDVI from surface reflectance data acquired by the advanced very high resolution radiometer (AVHRR) sensor ([29]; details in Additional file 2). Highly correlated variables (r > 0.8) were not included together in the same model structure.

We evaluated candidate models using Akaike’s Information Criterion for small sample sizes (AICc) [30]. We estimated relative importance of variables by applying multi-model inference to rank variables in the supported model set (ΔAICc ≤ 7) by their summed AICc weights [31]. We used the proportion of variance explained (R²) to evaluate model performance. For all models that received support we plotted residuals against fitted values and inspected for patterns in the residual distribution. We used Stata v.14.1 (StataCorp, College Station, USA) and an alpha level of 0.10 for all statistical analyses.

The Newey-West HAC standard errors were computed in Stata using the hacreg command [32].

**Results**

**Skull size comparisons between hunter- and conflict-killed cougars**

At the provincial level, conflict-killed male cougar skulls were smaller than those of hunter-killed animals (Two-sample Wilcoxon rank-sum z = −5.376, df = 2239, P < 0.001). Skull sizes differed between kill types for males in 4 of the 5 BC regions, similarly larger for hunter-killed than for conflict-killed males for Cariboo (Two-sample Wilcoxon rank-sum z = −1.959, df = 329, P = 0.050), Lower Mainland SW (Two-sample Wilcoxon rank-sum z = −2.195, df = 113, P = 0.028), Thompson Okanagan (Two-sample Wilcoxon rank-sum z = −2.210, df = 763, P = 0.027) and Vancouver Island (Two-sample Wilcoxon rank-sum z = −2.762, df = 571, P = 0.006) (Fig. 1a).

At the provincial level, skull sizes of females were similarly smaller among conflict animals compared with hunter-killed individuals (Two-sample Wilcoxon rank-sum z = −3.464, df = 1427, P < 0.001). Skull sizes likewise differed between kill types in 2 of the 5 BC regions (Lower Mainland SW; Two-sample Wilcoxon rank-sum z = −1.701, df = 114, P = 0.089; Thompson Okanagan; Two-sample Wilcoxon rank-sum z = −4.311, df = 520, P < 0.001) (Fig. 1b).

**Predictors of cougar-human conflict**

Regional models (see Additional file 3) that received substantial support explained roughly half of the variation in cougar-human conflict for males (R²: mean = 0.504; range = 0.258–0.816; all P < 0.10) as well as females (R²: mean = 0.507; range = 0.124–0.772; all P < 0.10). For both sexes, models that received substantial support were of intermediate or low complexity (with 1–4 parameters, including the intercept; Table 1). Only for males in the Lower Mainland SW did the intercept-only model receive substantial support, but two candidate models were superior. All supported models (ΔAICc ≤ 7) [33] are listed in Additional file 4: Tables S2–S6, provided their ΔAICc was smaller than that of the corresponding null model.

Human hunting pressure in both current (Figs. 2, 3) and lagged periods (Fig. 2) had the most relative importance for predicting cougar-human conflict for male cougars across the five regions. Human hunting was positively associated with conflict involving this cougar sex. Variables for human hunting during the conflict year or hunting lagged occurred in all but one male model that received substantial support and which had AICc less than the null model’s AICc (Table 1).
Human hunting pressure was also the most important factor associated with cougar-human conflict for female cougars in 2 of 5 BC regions. Only for one model (female cougars, Thompson-Okanagan) was increased human hunting (lag 2) associated with decreased conflict. Overall, increased human hunting was related to greater conflict for 16 of 17 models that included hunting variables with estimates that did not overlap zero and that received substantial support (Table 2; Additional file 4: Tables S7–S11).

Human density was the key variable associated with conflict for female cougars in 3 BC regions (Fig. 2) and was also important for male cougar-human conflict in 1 BC region (Table 2). Years with intermediary human densities were generally associated with conflict (Additional file 4: Tables S9, S10). For both cougar sexes, NDVI was the least important variable tested in relation to conflict (Fig. 2), but three substantially supported models revealed conflict increases in years when habitat productivity was low (Table 2).

Discussion

With expanding human populations and influence, conflict between carnivores and humans is expected to increase, which requires evidence-informed approaches to conflict mitigation. A long-term data set on human-caused cougar mortality allowed us to confront...
fundamental hypotheses on the relationship between human hunting, cougar-human conflict and cougar population demography, including testing of the commonly accepted but under-examined assumption that hunting of large carnivores could result in decreased conflict incidence (see [34] for an overview and call for inquiry into the relationship between hunting of carnivores and conflict).

As we expected, we found support for the young animal hypothesis in most comparisons, with individuals that came into conflict with humans younger compared to those hunted. Human encroachment into cougar habitat increases conflict potential [35–37] and young animals are more likely to occur in areas used by people than other age classes [38]. Dispersing juveniles are more likely to come into conflict on travel routes through fragmented habitats and high risk areas including human inhabited areas, roads [39] and ranches [24, 40]. In addition, food resources may be limited while dispersers attempt to establish home ranges [41]. As a result, when available, cougars may attack livestock [42] (however, see [43] for an alternative documentation of old cougars being disproportionately involved in livestock predation). Finally, hunters might be more likely to forgo killing small individuals for trophies, particularly if they are treed by trained hounds, although this has not been examined.

The manner by which carnivore populations respond to regulated hunting depends on social structure, reproductive strategies and dispersal patterns [14]. Human hunting of old individuals can increase immigration of juveniles from neighboring areas [14, 44], which could result in increased conflict. We therefore hypothesized that increased human hunting pressure would be associated with increased conflict via social disruption and younger population age structure (problem animal and human hunting hypotheses). We demonstrated that high hunting-related mortality in the same or preceding time period is positively associated with cougar-human conflict for at least one sex in all five regions tested (Table 2; Figs. 2, 3), with the most consistent pattern (both sexes: regression $P < 0.10$) for Thompson-Okanagan and Vancouver Island. While Thompson-Okanagan is an inland region, Vancouver Island is a large land mass off the British Columbia mainland known to be the world’s ‘hotspot’ of cougar-human conflict [45]. Our results corroborate and extend recent findings on impacts of human hunting on cougar complaints and depredations in Washington State [46]. In British Columbia, male cougars appeared most susceptible to conflict if hunted more intensively and conflict records involving males were almost double...
Vancouver Island Male
Thompson Okanagan Male
Lower Mainland SW Male
Kootenay Male
with females appeared related to variation in human den-

sity. Females might use suboptimal areas with human
density, as we detected. Selection of areas close
to human development by females with offspring presum-
ably to avoid males has been recently documented for cou-
gars in California [50] and grizzly bears in Alberta [51].
Thompson-Okanagan was the only region where human
density was related with conflict for both sexes, with con-
flicts most likely at intermediary densities of people. Such
intermediate densities are typically found in exurban or
suburban areas and are thought to have high levels of cou-
gar-human conflict in California [52]. Despite high human
populations in Lower Mainland SW, human density in this
region did not influence frequency of conflict involving
males. The documented decreases in conflict associated
with decreased human hunting of males in this region sug-
gest that, similar to other carnivores [53], cougar popu-
lations can persist in regions with high human densities as
long as human hunting pressure is low.

We found limited relationship with NDVI, our proxy
for habitat productivity. Decreased productivity was
hypothesized to be associated with increased cougar-
human conflict. Conversely, a positive relation between
conflict and NDVI might have been expected due to
increased productivity resulting in increased reproduct-
ive output [54], with the indirect effect of increased sub-
adult dispersal and greater conflict potential. Kootenay
was the only region where decreased productivity was
associated with increased conflict for both males and
females. This region comprises substantial high elevation
mountain ranges compared to the other regions and habi-
tat productivity in the Kootenay is possibly an important
limiting factor for cougars and their prey. Future moni-
toring of the associations between habitat productivity
and carnivore-human conflict should not be neglected,
given increased variability in vegetation conditions/
NDVI associated with climate change, which might have
implications for future predator-human conflicts that
have yet to be explored. When possible, finer scale prey
availability metrics should be incorporated, because prey
use differences among cougar sexes [55] could influence
conflict incidence. Furthermore, it is important to rec-
ognize that inferences from this study should be placed
in the context of the relative coarseness of covariate data
utilized, which is to be expected when focusing on broad
spatiotemporal extents such as the one we considered.
Our results showed that human-related variables had
the strongest association with conflict. We acknowledge
that the patterns of association we reveal do not neces-
arily imply causation. Our results, however, are generally
consistent with the hypothesis that high hunter mortal-
ity leads to young animals becoming involved in con-
dict. Unlike natural agents of mortality (other predators,
competitors, disease), hunters typically target adult individuals. The ability of resident males to maintain territories means that sub-adults are more likely to come into conflict, likely because of their movements during dispersal in search for vacant territories [56]. Human hunting can disrupt social structure leading to increased juvenile immigration from surrounding source populations [14] and result in younger age structure [57, 58] exacerbating conflicts between cougars and humans. With increasing human populations, interactions between predators and humans are expected to become more common, underlining the need for research into patterns and mechanisms of conflict, conflict prevention and non-traditional management strategies to facilitate coexistence.

Conclusions
Wildlife managers often prescribe hunting of carnivores to reduce competition with hunters for prey and to minimize conflicts with humans and their property [8]. If lethal control such as through human hunting is to facilitate coexistence between wildlife and humans, control must minimize wildlife-human conflict or increase tolerance of the public towards wildlife, without compromising wildlife population viability [13]. In some situations lethal management focused on targeted individuals associated with conflict (e.g., individuals that injure or kill people in predatory attacks) offers one route to address large carnivore-human conflicts. However, we showed that overall increased human hunting in fact can be associated with increased conflict, especially for males. Although our results are only correlative, we caution against the universal use of hunting as a tool for managing conflict with large predators.

Additional files

**Additional file 1:** Table S1. Hypotheses for frequency of cougar-human conflict.

**Additional file 2.** Information on NDVI and human density data.

**Additional file 3.** Information on regional models of cougar-human conflict.

**Additional file 4:** Tables S2–S11. List of all cougar-human conflict models that received support (ΔAICc ≤ 7). Estimated coefficients from substantially supported (ΔAICc < 2) models are also listed.

Abbreviations
AICc: Akaike’s information criterion for small sample sizes; AVHRR: advanced very-high resolution radiometer; BC: British Columbia; CDR: climate data records; D: human density; HAC: heteroskedasticity and autocorrelation; Ht0: very high resolution radiometer; BC: British Columbia; CDR: climate data records; NOAA: national oceanic and atmospheric administration; Nt0: NDVI; Nt1: NDVI (lag 1); Nt2: NDVI (lag 2); NW: north–west; UTM: universal transverse mercator; ΔAICc: difference between the model AICc and the lowest AICc for the model set.

Authors’ contributions
KJT and BC conceived and designed the study and CTD helped to refine it. KJT obtained the cougar mortality dataset from the British Columbia Ministry of Environment. KJT and BC performed the statistical analyses. KJT, BC and CTD wrote the manuscript. All authors reviewed and approved the final manuscript.

Author details
1 Department of Geography, University of Victoria, PO Box 3060, STN CSC, Victoria, BC V8W 3M4, Canada. 2 Biology Department, University of British Columbia, 3333 University Way, Kelowna, BC V1V 1V7, Canada. 3 Department of Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch 7701, South Africa. 4 Raincoast Conservation Foundation, PO. Box 77, Bella Bella, BC V0T 1B0, Canada. 5 Hakai Institute, PO. Box 309, Heriot Bay, BC V0P 1H0, Canada.

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Competing interests
The authors declare that they have no competing interests.

Availability of data and materials
The dataset used is available upon request from the authors, pending permission to redistribute from the British Columbia Ministry of Environment, Canada.

Ethics (and consent to participate)
This study did not require ethics approval as it made use of an existing dataset collected by the British Columbia Ministry of Environment, Canada.

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