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RESEARCH ARTICLE

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Wildlife whodunnit: forensic identification of predators to inform wildlife management and conservation

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Abstract

Genetic evidence at predation sites is rapidly improving predator-prey interaction studies and can provide information beyond field-based investigations. However, factors contributing to the retention of genetic evidence have received limited investigation in a field setting, and researchers have yet to leverage genetic evidence to improve traditional field investigations. Using data from 61 mortality investigations of mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and elk (*Cervus canadensis*), we evaluated factors influencing predator DNA amplification success and misidentification of predators in field investigations. We found that predator DNA was detected more for prey with higher body mass (18.5% increase per standard deviation [23.1 kg] in carcass body mass above the mean [32.8 kg]). Predator DNA was also 27.0% more likely to amplify when collected from kill sites that had not undergone a freeze-thaw cycle between the mortality and the investigation. The delay between the kill and the investigation, the swabbing surface, and the amount of precipitation did not influence amplification of predator DNA. Misidentifications of the predator based on the field ID were not influenced by the investigation delay or investigator confidence level, suggesting that investigators should collect genetic evidence even when they feel certain about the predator. Errors in identifying the

predator during the field investigation increased for prey with smaller body mass, and the predator was actually more likely to be misidentified than correctly identified for fawns and calves < ~21 kg. Black bears (*Ursus americanus*), bobcats (*Lynx rufus*), cougars (*Puma concolor*), coyotes (*Canis latrans*), and wolves (*C. lupus*) were equally likely to be missed in a field investigation, but bobcats tended to be falsely assigned more than expected and cougars were falsely assigned as the predator less than expected. Using genetic evidence as validation, we showed how patterns of predation and the field signs left by predators differed for some species depending on the size of the prey. Our findings should help researchers and managers to optimize their use of genetics to enhance field investigations.

KEYWORDS
carnivore, DNA, forensic analysis, genetic, mortality, predation, predator identification, saliva, ungulate

Carnivores can affect the structure and dynamics of prey populations, with impacts extending throughout the ecological community (Sih et al. 1985, Sinclair et al. 2003). Researchers and wildlife managers are often interested in understanding food-web dynamics and identifying the factors regulating populations, with potential implications for predators and prey. For species below population targets that are limited by predation, management options have included increasing harvest of and relocating predators. For instance, the removal of bears (*Ursus* spp.) and wolves (*Canis lupus*) in Alaska increased survival and abundance of moose (*Alces alces*) and caribou (*Rangifer tarandus*; Boertje et al. 1996, Keech et al. 2011). For research to be informative, and management to be effective and ethical if predator removal is considered (Santiago-Ávila et al. 2018), it is essential to correctly identify the predators of prey.

To quantify the consumptive effects of predators on prey populations, cause-specific mortality rates are often estimated by monitoring a sample of radio-collared prey (Steigers and Flinders 1980, Ballard et al. 1981). When a mortality is detected, methods of inference such as evaluating carnivore tracks, scat, predator hair, associated predator signs (i.e. caching, scrapes, tree scratching), and the pattern of consumption of the prey are used to identify the most likely species of predator (Elbroch 2003, Eacker et al. 2016, Elbroch and McFarland 2019). Traditional field methods are imprecise, leading to unclassified mortality sites, and can contribute to misidentification of predator species (Onorato et al. 2006). Errors may result from investigator experience or over confidence, the challenge of distinguishing predator species based on scat and hair samples (Onorato et al. 2006, Morin et al. 2016), limited evidence available for examination (Peelle et al. 2019), interference of scavengers (Bauer et al. 2005), and similar carcass handling styles between predator species (Mumma et al. 2014, Elbroch and McFarland 2019).

Genetic techniques allow for the identification of predators based on DNA evidence at kill sites and can provide valuable insights when used in conjunction with field investigations (Williams et al. 2003, Onorato et al. 2006, Sundqvist et al. 2008). Predators can be identified from DNA left at kill sites in the form of saliva (Williams et al. 2003), hair (Onorato et al. 2006), and scats (Höss et al. 1992). Onorato et al. (2006) used genetic methods to identify predator hair and scats at elk (*Cervus canadensis*) calf mortality sites with 88.5% accuracy, while field-only

methods were accurate for only 58% of predator hairs and 79% of predator scats. As a result, genetic identification is rapidly becoming a standard component of kill site investigations, particularly in predator-prey systems. Further, DNA can provide additional information such as sex and individual identification (Williams et al. 2003, Blejwas et al. 2006), yielding better management insight than field investigations alone.

Unfortunately, genetic identification can be costly, and there is little guidance on when and where to prioritize DNA collection if resources are limited. Additionally, knowledge about common misidentifications in kill site investigations can and should be leveraged to improve the training of field investigators and refine field investigations. To address these limitations, we collected predator DNA at the kill sites of collared deer (*Odocoileus* spp.) and elk by swabbing saliva from bite marks, collars and ear tags, and epithelial cells from predator scats. We aimed to (1) identify external factors such as weather, sample collection location, delays in sample collection, and the size of the individual prey that influence the efficacy of obtaining genetic material, (2) identify factors contributing to misidentifications of the predator species when using field evidence alone, (3) identify which predator species are most commonly misidentified in the field, and (4) describe species-specific patterns of predation for prey of different sizes.

We expected that DNA samples collected with the shortest time since mortality would have less time to degrade and have a higher rate of amplification success (Harms et al. 2015, Piaggio et al. 2020). We predicted that DNA collected from artificial surfaces (i.e. the collar and ear tags) would have higher rates of success in amplifying predator DNA (Peelle et al. 2019), and we expected that samples of predator DNA collected from the carcasses of larger prey (i.e., adult deer versus elk calves and deer fawns) would also be more successful in providing genetic information because the predator may spend more time handling and feeding on large prey, depositing more saliva. We expected that precipitation could wash away predator saliva and would reduce success of genetic identification (Brinkman et al. 2010), and that DNA undergoing a freeze-thaw cycle in the field would also be less likely to amplify (Takahara et al. 2015).

We expected that misidentifications would increase with the duration of time between the mortality and the field investigation because there would be more time for scavengers to destroy or contaminate the physical evidence at the site (Bauer et al. 2005). We also predicted that genetic evidence would be most beneficial where investigator confidence was low (i.e., misidentification rates would be lower with higher investigator confidence). If this were the case, it would indicate that researchers should prioritize collecting genetic information when they were uncertain about an investigation, but genetic information would be less important if investigators were confident in their classification of the predator. Additionally, we predicted that smaller prey (i.e., deer fawns and elk calves) would be more likely to have a misassigned predator from the field investigation because there should be less field evidence left to interpret compared to larger (i.e., adult) prey. We expected that predators would be most frequently misidentified for species within the same taxonomic family due to a similarity in prey handling styles, and that predators may handle smaller prey differently than larger prey due to shorter killing and feeding times.

STUDY AREA

We investigated mortalities of mule deer (*O. hemionus*), white-tailed deer (*O. virginianus*), and elk, in 2 northern Washington, USA, study areas (Figure 1). Black bears (*U. americanus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), cougars (*Puma concolor*), and wolves occurred in both study areas. Mule deer were captured in winter along the Methow Valley of Okanogan County (Okanogan Study Area) and ranged across the coniferous forests and shrub-steppe habitat of northcentral Washington through their annual migrations (latitude: *c.* 48.050° to 49.150°; longitude: *c.* −120.900° to −119.700°). Elevations ranged from 230–2830 m. In Mazama, WA, an average of 57 cm of rain and 292 cm of snow falls annually. Winters there were typically cold (average low of −7°C, average high of 1°C from December–March), while summers were warm (average low of 9°C to average high of 26°C from June–September; https://www.usclimatedata.com/climate/mazama/washington/united-states/uswa0264).

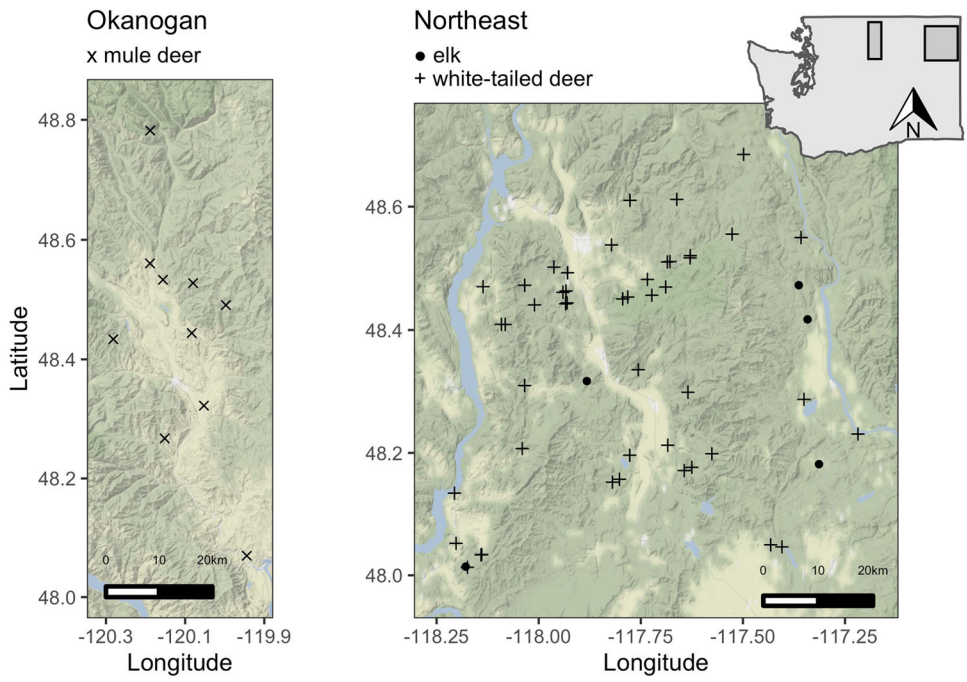

FIGURE 1 Locations of predation mortalities across northern Washington, USA, where lethal bite wounds (identified as hemorrhaged punctures) were swabbed for predator saliva DNA from 2017 to 2021.

Elk and white-tailed deer were captured in Stevens, Pend Oreille, and Spokane counties of northeastern Washington (northeast study area; latitude: *c.* 47.900° to 48.720°; longitude: *c.* −118.300° to −117.200°). Montane conifer forests managed for timber production dominated the mid-to-higher elevations of the region, while valley bottoms were predominately converted to agriculture. Elevations ranged from 370–2080 m. Chewelah, WA, at the center of the study area, received an average of 152 cm of rain and 114 cm of snow annually, with cool winters (average low of −6°C, average high of 4°C from December–March) and warm summers (average low of 7°C to average high of 27°C from June–September; https://www.usclimatedata.com/climate/chewelah/washington/united-states/uswa0074).

METHODS

Field methods

From winter 2017 to spring 2021 we captured and collared adult female mule and white-tailed deer, white-tailed deer fawns, and elk calves. Adult female mule deer were captured by drive netting and aerial net-gunning (Kock et al. 1987) and fitted with GPS radiocollars (Model Vertex Plus, Vectronic Aerospace, Berlin, Germany). We captured adult female white-tailed deer and 6–8 month old white-tailed deer (both sexes) using a suspended net gun (Wildlife Capture Services, Flagstaff, Arizona, USA) or clover traps (Clover 1954, Hawkins et al. 1968, VerCauteren et al. 2000). Ground darting was also used to capture adult female white-tailed deer (Peterson et al. 2003). We fit adult female white-tailed deer with GPS radio-collars (Models Vertex Plus or Survey, Vectronic Aerospace, Berlin, Germany), and tested a subset of captured individuals for pregnancy with a portable ultrasound (Ibex Pro, E.I. Medical Imaging, Loveland, CO, USA). When pregnancy was detected, we inserted vaginal implant

transmitters (VIT; VERTEX Natal-Link Vaginal Implant Transmitter, Vectronic Aerospace, Berlin, Germany) that triggered email and SMS notification on expulsion (Rice 2016). We used VIT expulsions to target neonates for capture, and we also captured white-tailed deer neonates opportunistically. White-tailed deer fawns were fitted with expandable, very high frequency (VHF) radio collars at capture (Model M4210, Advanced Telemetry Systems, Isanti, MN, USA and Model Vertex Natal-linked, Vectronic Aerospace, Berlin, Germany). We captured neonatal elk opportunistically and by targeting VIT expulsions from collared adult female elk (Bassing et al. 2022). Adult elk were not included in our study as none were confirmed to die by predation. Neonatal elk were fitted with expandable GPS (Model Survey, Vectronic Aerospace, Berlin, Germany) or VHF (Model M2230B, Advanced Telemetry Systems, Isanti, MN, USA) radiocollars. Neonatal deer and elk were weighed during capture. We used ANOVA to determine if the body mass of neonates varied by sex and year of capture and assigned the mean capture weight from the appropriate category if body mass at capture was unknown.

Each GPS collar was equipped with mortality sensors that sent an email and SMS notification after 9 hours of inactivity. White-tailed deer fawn VHF collars were set to a 6-hour mortality delay, and elk calf collars were set to an 8-hour mortality delay. The VHF collars were programmed to transmit a code indicating the time of death. We monitored VHF collared individuals with radiotelemetry daily for the first 3 months of life, biweekly to 6-months old, and weekly from 6-months to 1-year old. Adults with GPS collars were monitored remotely. Mortalities were investigated as rapidly as possible upon detection to determine cause of death through June 2021.

We confirmed predation by skinning the carcass and finding evidence of lethal hemorrhage associated with bite marks (Williams et al. 2003). When predation was confirmed, we evaluated the predator tracks, sign and patterns of consumption following Elbroch (2003), Washington Department of Fish and Wildlife (2014), Stonehouse et al. (2016), and Elbroch and McFarland (2019) to determine the species of predator ostensibly responsible for the kill. We also noted the presence or absence of 12 indicators to identify the predator species. Indicators included blood on trails/vegetation, broken and crushed bones, caching or burial of the carcass, clipped or plucked hair, disarticulated limbs, a dispersed carcass, a drag trail, other dead animals, a peeled hide, an intact rumen, scratches on the hide, and predator tree scratching. Upon concluding the field investigation of the predation mortalities, investigators reported confidence in their assessment of the predator, ranging from 0 to 1, with a 0 assigned to cases where the predator was unidentifiable.

We swabbed the puncture wounds associated with the predation (identified by subcutaneous hemorrhage) for salivary DNA when these sites were uncovered in the skinning process to minimize the potential risk of contamination from scavenger DNA (Williams et al. 2003). Skinning knives were sterilized with bleach between mortality investigations and researchers wore sterile gloves while swabbing DNA; gloves were changed between swabbing sites if they became dirty or contamination was suspected. We wet sterile swabs (PurFlock Ultra®; Puritan Diagnostics LLC, ME, USA) by dispensing 1 to 2 drops of phosphate buffered saline solution (pH 7.4) from a sterile eyedropper, and rolled the swabs over areas of predator saliva (Caniglia et al. 2013, Mumma et al. 2014) associated with lethal bites (i.e., the periphery of the hemorrhaged puncture), as well as collars, ear tags, and presumed predator scats. Presumed predator scats were identified by freshness, and collar, ear tag and predator scat swabs were collected as a supplement to salivary DNA collected from hemorrhaged punctures. Each swab was air dried and inserted individually into a coin envelope; the swab and envelope were preserved in desiccant before laboratory analysis. We did not sample bites without subcutaneous hemorrhage, as these could not be distinguished from the bites of scavengers. For each sampling site, swab replicates (labeled A and B) were collected. The first swab collected (A) was prioritized for extraction, and the second swab (B) was extracted if the A swab failed.

Laboratory analysis

All DNA swabs were sent to the School of Environmental and Forest Sciences genetics lab at the University of Washington (http://sefsgeneticslab.weebly.com) that was specifically designed to process low-copy, degraded

DNA (e.g., separate rooms for pre- and post-PCR processes to minimize contamination risk). The DNA was extracted from the swabs using Investigator Lyse&Spin and QIAamp DNA Investigator kits (Qiagen, Hinden, Germany) following the manufacturer's protocol. Species identification from samples was conducted using an assay that was optimized for detection of carnivore species that occur in Washington. The assay contained primers that amplified size-specific mitochondrial DNA fragments from different species of predators. Primers SIDL (Murphy et al. 2000) and Gulo1F (Dalén et al. 2004) were paired with reverse primer H3R (Dalén et al. 2004) to amplify canid, bear, and mustelid DNA at species-specific fragment lengths (De Barba et al. 2014). Primers FelidID F, Lruf R, and Pcon R (Davidson et al. 2014) were included to amplify cougar and bobcat DNA at species-specific lengths. Finally, primers DL1F and DL5R (Palomares et al. 2002) were included to amplify size-specific lynx DNA. The PCR reactions consisted of 0.12 μM FelidID F, 0.6 μM Lruf R, 0.6 μM Pcon R, 0.16 μM SIDL, 0.16 μM H3R, 0.08 μM Gulo1F, 0.16 μM DL1F, 0.16 μM DL5R, 4 μL of Qiagen Multiplex PCR Master Mix, 0.8 μL of Q solution, and 2 μL of extracted DNA for a final volume of 8 μL. The thermal cycling protocol consisted of an initial denaturation step of 95°C for 15 min, followed by 35 cycles of 94°C for 30 s, 46°C for 90 s, and 72°C for 60 s, followed by a final elongation step of 72°C for 15 min. Negative controls were used at both the DNA extraction and PCR stages to monitor for contamination, and positive controls were used to monitor the quality of PCR amplification. Two PCR replicates were amplified per sample, and PCR replicates were analyzed at Yale's DNA Analysis Facility using an ABI 3730 Fragment analyzer (Applied Biosystems, Foster City, CA, USA). The resulting sample electropherograms were checked for diagnostic species-specific amplification of predator DNA using GeneMapper 6 (Applied Biosystems, Foster City, CA, USA). Samples were assigned a genetic-based predator species ID if the electropherograms for both sample PCR replicates possessed the diagnostic amplified product for a particular predator species. If only 1 of the 2 PCR replicates for a sample exhibited amplification, 2 additional PCR replicates were run for that sample. Thus, we only accepted the species ID if at least 2 replicates returned the same ID. In cases where the initial genetic analysis yielded negative results or indicated the presence of multiple predator species, we processed additional swabs from the kill site using the same protocol. We then compared the predator species assigned during the field investigation to the species identified by the genetic evidence to find misidentifications. In cases where the genetic species identification did not match the field identification, we reviewed the investigation to ensure that the predator identified by genetics could be responsible for the evidence at the scene.

Statistical analysis

To examine factors influencing the success of genetic testing (positive ID), we used logistic regression to test the influence of the delay between the mortality and the field investigation (days), the estimated body mass of prey at death (kg), the surface that was swabbed, the amount of precipitation, and if a freeze-thaw cycle had occurred between the deposition of predator DNA during the kill and the investigation. We considered a sample successful if either replicate amplified predator DNA and did not count A and B swabs from the same swabbing site separately. We classified the surface as hard if the saliva was collected from an ear tag or collar, and soft if it was collected from the carcass or a scat. All continuous variables in our models were standardized with a mean of 0 and standard deviation of 1 to improve model fit, and we confirmed that the Pearson's correlation between model covariates did not exceed 0.7 (Dormann et al. 2013).

To determine if DNA amplification success and misidentification rates depended on the size and associated age class of prey, we used estimated body mass as a continuous variable to describe prey size. Mule deer were not weighed in our study, so we used mean winter body mass of adult female mule deer captured in Ferry County, WA ($\bar{x}$ = 70 kg, SD = 9, n = 25; J. Dellinger and A. Wirsing, The University of Washington, unpublished data). We assigned mean body mass of adult female white-tailed deer weighed in our study ($\bar{x}$ = 53, SD = 9 kg, n = 16; body mass recorded for 2017 captures only) if individual mass was not measured or used their individual mass if recorded during captures. For white-tailed deer fawns, we estimated body mass at death given a rate of increase of

0.16 kg day^{-1} from 0–150 days old and a gain of 0.07 kg day^{-1} from 150–350 days old (Berry 2017). Similarly, elk calves gain 0.7–0.9 kg day^{-1} for the first 4 months of life (Cook 2002), which was the maximum age at which calves in this study died by predation. Thus, we estimated the body mass of calves at death as the capture mass + 0.8 kg days^{-1} since capture. Projected body mass for fawns captured at 6–8 months were estimated assuming those animals were born on the mean date of neonate birth for that year at mean capture weight.

We used precipitation and temperature data from the Parameter-elevation on Independent Slopes Model (PRISM) to describe weather conditions at kill sites, with data modeled on a daily basis at 800 m resolution (http://prism.oregonstate.edu; Daly et al. 2008). We summed the total amount of precipitation during the delay between the mortality and the investigation and determined if the predator DNA had been through a freeze-thaw cycle based on the minimum and maximum temperatures during the delay.

To investigate the drivers of predator misidentification in the field, we used logistic regression to examine the effects of estimated prey body mass at death, the delay between the mortality and the field investigation, and the confidence of the investigators in their physical evidence assessment. In this framework, predator misidentification was the response variable such that a 1 represented a misidentified predator and 0 represented a correctly identified predator. We also tested for an interaction between the time lag and the size of the carcass, because we hypothesized that larger carcasses would have lower rates of misidentification despite delays in the investigation as compared to smaller carcasses (i.e., the delay would be more consequential for smaller-bodied prey).

We used chi-squared tests to determine if misidentifications occurred for particular predator species at rates different than based on random chance. Misidentification was considered both from the perspective of false positives and false negatives. For example, a bobcat determined to be the predator from the field investigation but found through genetics to not be responsible for the kill would be classified as a false positive, whereas a kill genetically determined to be caused by a bobcat but assigned to another carnivore in the field would be classified as a false negative. To improve the interpretation of evidence at future field investigations, we summarized the field signs of predation and consumption that were associated with each carnivore species. To ensure we were not interpreting signs that may have been due to scavengers, we excluded cases where DNA from more than one predator species was detected.

RESULTS

We deployed mortality-sensitive tracking collars on 273 individual white-tailed deer (125 adults and 148 fawns), 148 adult mule deer, and 30 elk calves, for a total of 451 individual ungulates. There was no difference in body mass at capture for neonates between sexes (white-tailed deer: $F_{1,100} = 0.32$, $P = 0.6$; elk: $F_{1,21} = 1.8$, $P = 0.2$) or by year of capture (white-tailed deer: $F_{3,98} = 1.6$, $P = 0.2$; elk: $F_{2,20} = 0.25$, $P = 0.8$), so we assigned the mean neonate body mass at capture of that species across years if body mass at capture was unknown. Causes of mortality ($n = 215$ total mortalities investigated) included predation, malnutrition, disease, harvest, vehicle collision, and accidents (e.g., caught in a fence). Some causes of mortality remained unknown due to scavenger contamination, insufficient evidence remaining at the mortality site, or severe autolysis of tissues.

In total, we investigated 61 mortalities where genetic data were collected, and predation was confirmed as the proximate cause of death. We collected 202 samples, and on average, we were able to positively identify the predator for 76% of samples and 89% of all mortalities using DNA. On average, there was a 1.8-day delay (SD = 2.0, min–max = 0–10) between the mortality and the investigation. Genetic evidence improved inference at 21 mortalities using 3 different methods. First, there were 7 cases where the field evaluation was inconclusive, but we were able to identify the predator via genetic evaluation. Second, there were 13 cases where the predator was misidentified in the field but corrected with genetic information collected from swabbing lethal bites on the carcass. Third, there was one case where genetic methods identified 2 species of predator while the field investigators classified a different, third predator. In this case, we could not ultimately determine the responsible predator, but genetic evidence improved inference by avoiding a false positive.

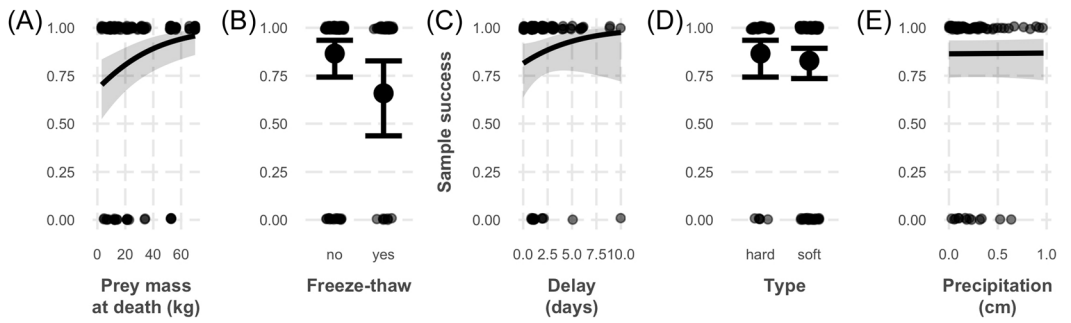

FIGURE 2 Factors influencing amplification of predator DNA at kill-sites of white-tailed deer (adult females and fawn), adult female mule deer, and elk calves in Washington, USA, from 2017 to 2021. Successful amplification was more likely for prey with larger mass at death (a) and if a freeze-thaw cycle did not occur between the kill and investigation (b). The delay between the predation event and the investigation (c), the sample collection location (hard refers to samples collected from collars and ear tags, soft refers to samples collected from the carcass and scats; d), and the amount of precipitation (e), did not influence if DNA was amplified from the sample. Coefficient estimates and odds ratios are presented in Table S1, available in Supporting Information.

Drivers of DNA amplification success

The DNA amplification success rates increased for larger prey, decreased if a freeze-thaw cycle occurred, and were unaffected by the delay, collection surface, and amount of precipitation. The likelihood of a positive genetic identification per sample increased by 18.5% (CI = 8.5–28.2%) with a standard deviation increase in carcass body mass (23.1 kg) above the mean (32.8 kg; Figure 2; Table S1, available in Supporting Information). If a freeze-thaw cycle occurred, the odds of success decreased by 27.0% (CI = 6.3–40.1%). Surprisingly, amplification success was not affected by the delay in the investigation ($z = 1.41$, $P = 0.16$; Table S2, available in Supporting Information). Samples collected from ear tags and the collar (i.e., hard surfaces; $n = 54$) rather than the carcass (i.e., soft surfaces; $n = 148$), had a slightly higher success rate of detecting DNA (86.6% vs. 82.8%), but the effect was not significant ($z = -0.73$, $P = 0.47$; Figure 2; Table S1). Precipitation ranged from 0.0 to 5.0 cm ($\bar{x} = 0.3$, SD = 0.7) and had no influence on DNA retention ($z = 0.12$, $P = 0.91$).

Drivers of misidentifications

After excluding samples where the genetic ID was inconclusive and removing data where predator confidence was not recorded (6 mortalities), we had 48 predation mortalities to examine factors contributing to predator misidentifications. Estimated prey body mass at death was the only significant predictor of misidentification. For every standard deviation (22.8 kg) below the mean prey body mass at death (41.1 kg), investigators were 33.3% (CI = 13.8–46.0%) more likely to misidentify the predator (Figure 3; Table S3, available in Supporting Information). Moreover, investigators at confirmed predation mortalities were more likely to misidentify the predator species when estimated prey body mass at death was below 21.26 kg, at which point fawns were approximately 3.5 months old and elk calves were 3–4 days old. Counter to our predictions, there was no significant effect of the delay between the mortality and the investigation ($z = -0.39$, $P = 0.70$) on rates of misidentification based on field evidence. Likewise, there was no effect of investigator confidence in their assessment of the predator ($z = 0.16$, $P = 0.87$), which ranged from 0 to 1 ($\bar{x} = 0.76$, SD = 0.35), nor was there an interaction between the investigation delay and prey body mass at death ($z = -1.17$, $P = 0.24$).

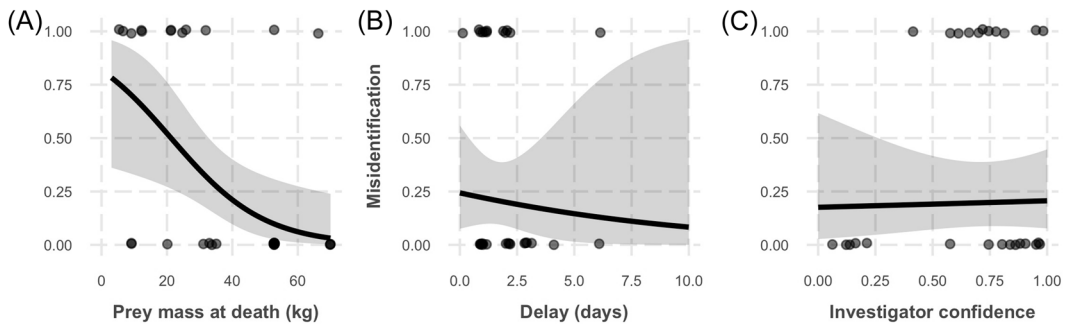

FIGURE 3 Factors influencing misidentifications of predators based on field evidence at mortalities of white-tailed deer (adult females and fawns), adult female mule deer, and elk calves in Washington, USA, from 2017 to 2021. The probability of misidentification of the predator from field evidence alone increased as prey mass at death decreased (a). The delay between the predation event and investigation (b) and the confidence of the investigator in their assessment of the predator (c) were unrelated to the misidentification of the predator when based on field evidence alone. Coefficient estimates and odds ratios are presented in Table S3, available in Supporting Information.

TABLE 1 Cases of predations of white-tailed deer (fawns and adult females), adult female mule deer, and elk calves in Washington, USA, from 2017 to 2021, where the genetic information from the predator differed from the assessment of the field investigators (i.e., misidentifications). False positives refer to species that were assigned in the field, but genetic information revealed that they were not associated with lethal bites. False negatives refer to the species identified by genetic information but misidentified in the field investigation. Where the genetic ID is classified inconclusive, more than one species of predator was positively identified on samples collected from hemorrhaged bites, but none were the species identified in the field investigation.

	Genetic ID						Total false positives
	Bear	Bobcat	Cougar	Coyote	Wolf	Inconclusive	
Field ID							
Bear	0	0	1	0	0	1	2
Bobcat	0	0	4	2	0	0	6
Cougar	0	2	0	1	0	0	3
Coyote	0	1	2	0	0	0	3
Wolf	0	0	0	0	0	0	0
Inconclusive	1	0	3	2	0	1	7
Total false negatives	1	3	10	5	0	2	21

False negatives and false positives

All predators were equally likely to be missed by the field investigators and assigned to a different, incorrect predator (i.e., a false negative; $\chi^2 = 2.56$, df = 4, $P = 0.6$). Rates of being falsely assigned in the field when a different predator was responsible for the kill (i.e., false positives) varied significantly at the $\alpha = 0.10$ level ($\chi^2 = 8.87$, df = 4, $P = 0.06$) but not at the $\alpha = 0.05$ level. Bobcats were 2.4 times more likely to be misattributed as the predator than expected with 6 false positives observed and only 2.5 expected. The 6 mortalities misattributed to bobcats in the field had cougar ($n = 4$) and coyote ($n = 2$) DNA associated with hemorrhaged bite wounds, indicating that cougars and coyotes were the true predators (Table 1). Cougars were less likely to be misassigned as a predator in the field than was expected; false positives were 0.46 times the expected rate (3 observed, 6.5 expected) at kill sites.

Predator sign

We successfully amplified predator DNA at 54 kills. Of these, we detected DNA from more than one species of predator at 7.4% of mortalities, indicating scavengers may have contaminated these sites. Evidence of scavenging was detected only at kills of juvenile prey (<1 year old) and not at adult predations (>1 year old) but included fawns and calves ranging from 8 to 102 kg ($\bar{x}$ = 38.8, SD = 28.9 kg). After eliminating kills with evidence of scavenging and removing one mortality where no indicators of predator sign were recorded, we had a sample of 49 confirmed predations. Because the probability of misidentification was greater than 50% for prey ≤21.26 kg at death, we used this body mass as the threshold to categorize small versus large prey. A summary of predation sign (Table 2)

TABLE 2 Sign associated with each predator for confirmed mortalities of white-tailed deer (fawns and adult females), adult female mule deer, and elk calves in Washington, USA, from 2017 to 2021, where there was no evidence of scavenging. Predator sign is compared for large prey (>21.26 kg) and for small prey (≤21.26 kg, the size of the average white-tailed deer fawn at 3.5 months old or a 3–4-day old elk calf) as this was the threshold below which investigators were more likely to misidentify the predator than correctly identify the predator if only using field evidence. The total number of predations is indicated as *n*, while each predation sign reports the number of cases where that sign was recorded/the number of cases where data was collected for that indicator. There were no confirmed wolf predations of small prey without evidence of scavenging.

	Predator	*n*	Blood trail/on vegetation	Broken and crushed bones	Buried/ cached	Clipped/ plucked hair	Disarticulated Limbs	Dispersed carcass
Large Prey (>21.26 kg)	Bear	3	2/3	3/3	0/3	1/3	3/3	2/3
	Bobcat	5	3/5	2/5	4/5	4/5	3/5	0/5
	Cougar	23	5/23	6/23	17/23	17/23	8/23	2/18
	Coyote	2	1/2	1/2	0/2	0/2	2/2	2/2
	Wolf	1	1/1	0/1	0/1	0/1	1/1	0/0
Small Prey (≤21.6 kg)	Bear	2	1/2	2/2	0/2	0/2	2/2	1/2
	Bobcat	1	1/1	0/1	1/1	0/1	0/1	0/1
	Cougar	7	4/7	4/7	3/7	2/7	5/7	1/7
	Coyote	5	2/5	4/5	3/5	1/5	4/5	3/5

	Predator	*n*	Drag trail	Other dead animals	Peeled hide	Rumen intact	Scratches on hide	Predator tree scratching
Large Prey (>21.26 kg)	Bear	3	0/3	0/3	1/3	0/3	3/3	0/3
	Bobcat	5	3/5	0/5	0/5	4/5	2/5	0/5
	Cougar	23	11/23	2/23	1/13	19/20	13/23	3/23
	Coyote	2	1/2	0/2	1/1	1/2	1/2	0/2
	Wolf	1	0/1	0/1	0/0	0/0	0/1	0/1
Small Prey (≤21.6 kg)	Bear	2	0/2	0/2	2/2	0/2	1/2	1/2
	Bobcat	1	1/1	0/1	0/1	0/1	0/1	0/1
	Cougar	7	3/7	0/7	0/7	4/7	4/7	1/7
	Coyote	5	1/5	1/5	0/5	1/5	3/5	0/5

associated with different species highlights the difference in the sign left from black bears, bobcats, cougars, and coyotes for large (>21.26 kg) and small (<21.26 kg) prey.

DISCUSSION

Our study adds to recent evidence indicating that genetic data markedly improve the classifications of predation mortalities by adding important data to that collected during field investigations (Onorato et al. 2006, Mumma et al. 2014). Our findings indicated that considering predator DNA in addition to the field evidence can be important in identifying the predator for smaller-bodied prey. We found that prey weighing less than ~21 kg at death (i.e., deer fawns ~3.5 months old and elk calves 3–4 days old) were more likely to be misidentified than correctly identified during field investigations despite well-trained field crews that systematically recorded 12 indicators of predator identity. Our findings highlight that genetic methods are especially valuable in regions with diverse carnivore assemblages due to the high likelihood of misidentification based on field sign alone. Overall, genetic evidence improved mortality investigations at 34% of kill sites, similar to rates observed by Onorato et al. (2006) and Mumma et al. (2014).

Contrary to our expectation, we found that a delay in sample collection did not reduce DNA amplification success across our 0–10 day range. We investigated most carcasses within 2 days, but some investigations occurred up to 10 days after the mortality event. Our results demonstrate that genetic evidence can still be valuable even if the investigation is substantially delayed. Mumma et al. (2014) similarly investigated most carcasses within 1–2 days of mortality but some investigations occurred up to 6 days post-mortem, and they also found no effect of the delay on sample retention. Most studies documenting DNA degradation over time have focused on degradation from 0–48 hours since deposition (Blejwas et al. 2006, Sundqvist et al. 2008, Harms et al. 2015, Piaggio et al. 2020), a time frame that may be unachievable to access a carcass despite best efforts for many field studies. It is possible that samples degrade in the first 2 days and then stabilize, which could explain the difference between our findings and those of Blejwas et al. (2006), Sundqvist et al. (2008), Harms et al. (2015), and Piaggio et al. (2020). While our findings suggest that genetic evidence can still be useful even after a long delay, we emphasize that mortalities should be investigated as rapidly as possible because the evidence needed to confirm predation may be destroyed by consumption of the carcass and scavengers have more time to contaminate the site.

Of all the environmental and biological factors we hypothesized could affect the success of amplification and identification, prey size was most influential. Successful amplification of DNA decreased with prey size, and field investigators also misidentified predators most often for the smallest prey (i.e., deer fawns and neonatal elk). Thus, despite lower amplification success rates at neonatal mortality sites, DNA evidence is most valuable in investigating these mortalities. As Sundqvist et al. (2008) and Mumma et al. (2014) have pointed out, it is important to collect multiple samples at predation mortalities, and we further recommend that investigators focus on collecting additional samples at mortalities of smaller prey (i.e., younger age classes) to increase the chances of positively identifying a predator.

We found that in-field freeze-thaw cycles reduced DNA amplification success, indicating that investigators should prioritize rapid investigations of carcasses when temperatures fluctuate above and below 0°C. Takahara et al. (2015) similarly found that freezing and thawing reduced detection of eDNA in water samples. Surprisingly, increased precipitation did not reduce amplification success in our study, perhaps because many samples were cached or covered in snow which could have helped preserve DNA. To our knowledge, effects of precipitation on retention of salivary DNA have not been tested but could be considered in an experimental context. However, DNA collected from the exterior of deer scats has been shown to degrade marked with rainfall (Brinkman et al. 2010). We did not explore differences in rain versus snow because we could not distinguish which occurred when there was precipitation and temperatures fluctuated above and below freezing. Of the 202 samples, 105 were collected from

mortalities receiving precipitation in the field, and half of those mortalities (52) were exposed to a minimum temperature below freezing, so the precipitation could have been snow. It is reasonable to expect that snow could help preserve DNA while rain could wash it away which may explain the lack of a net effect from precipitation.

Peelle et al. (2019) found that amplification success of predator DNA from snowshoe hare kills was more successful when samples were collected from hard surfaces, such as the plastic collar box, compared to soft surfaces such as bite wounds. In contrast, we did not detect an effect of the swabbing surface on amplification success. We therefore recommend that investigators swab both hard and soft surfaces to maximize the potential of obtaining predator DNA. Hemorrhaged bites are the best way to ensure DNA is collected from the predator and not a scavenger, and these samples should be weighted more heavily in the evaluation of the mortality if they positively identify a carnivore. However, DNA collected from the collar or ear tags can be exceedingly valuable if these are the only evidence found. Positive genetic classification from a hard surface can be used to indicate that a collar is from a probable mortality with the detection of predator or scavenger DNA rather than a potential dropped collar if no DNA is detected. This is especially important in studies of neonates, where expandable collars are designed to drop off the individual after a certain period. While not included in this study because they could not be confirmed as predation events, we documented 8 instances where carnivore DNA was amplified from the radio-collar when only the collar was found. While it is possible that DNA on a collar alone could occur when a carnivore finds and carries a dropped collar, such occurrences are likely rare (Windell et al. 2019), and it is far more likely that detection of DNA on collars represents cases where prey died and the saliva was from the predator or a scavenger.

Misidentification rates were not significantly affected by the delay between the mortality and the investigation or the confidence of the investigator. Delay may indeed be important, and the lack of significance could have reflected a small sample size (13 misidentifications out of 48 considered mortalities). We suspect that investigators were hesitant to make a classification for cases with long delay, and only assigned a predator in those cases when the evidence was exceptionally clear, otherwise classifying the cause of death as inconclusive. This would have reduced the misidentification rate associated with the delay between the kill and the investigation. Contrary to expectations, misidentifications rates were unaffected by investigator confidence. All investigators had been trained in ungulate necropsies, identifying predator tracks and sign, and identifying kill and consumption patterns for the predators in this study area, and they followed consistent protocols during predation investigations. The lack of effect is particularly important and implies that investigators are just as likely to misidentify the predator when they have high confidence in their field-based assessment. Thus, we recommend use of genetic methods to supplement field investigations regardless of investigator training or confidence.

We predicted that some predator species were more likely to be misidentified than others in the field. While we did not find a statistically significant difference, we suspect that the relatively small sample size of misidentifications limited our ability to detect such an effect and that species within the same taxonomic family are indeed more likely to be confused for one another. We noted frequent confusion between bobcats and cougars, which was likely due to their similar handling style of carcasses (Elbroch and McFarland 2019). In the field, investigators primarily differentiated between cougars and bobcats based on the size of their tracks and the distance between canine punctures (Stonehouse et al. 2016). One reason for a potential under identification of cougars in lieu of bobcats could be that juvenile cougars were mistaken to be bobcats due to their smaller size. We also saw that cougars more consistently cached larger adult deer and elk calves than fawns, and the rumen was more frequently found intact for large prey than small prey of cougars. Due to the small size of the prey, a cougar may consume most of a fawn in a single feeding bout rather than leaving signatures such as a cache. Intact rumens were ubiquitous at cougar and bobcat predations of adult deer, but this was only observed for half of cougar and bobcat predations of deer fawns and elk claves < ~21 kg at death (Table 2). Neonatal fawns dying from causes other than predators often had stomachs full of milk upon death, which may have been palatable to cougars while rumens of adult deer were not.

Although most misidentifications involved confusion among felids, bobcats and cougars were also mistaken for coyotes in several cases. In 3 out of 7 cases of predation mortality of fawns with no evidence of scavenging,

coyotes buried carcasses after partial consumption. These can be mistaken for carcass caches typically found at bobcat and cougar kill sites. Also, coyotes tend to disperse carcass parts, which makes the investigation difficult when attempting to find lethal wounds or evidence of a struggle. These feeding characteristics could make it more challenging to identify predation events caused by coyotes.

When applying forensic techniques, researchers need to remain vigilant to minimize the risk of contamination. Contamination can occur due to scavenger activity at the site, sources introduced during the investigation, while samples are in transit, or in the lab. Swabbing bite wounds with lethal hemorrhage reduces the risk of detecting scavenger DNA but does not eliminate the possibility. Indeed, in our study we detected DNA from 2 species of predator on lethal wounds at 4 out of the 61 confirmed predations. In 2 cases, we deduced the responsible predator versus the scavenger based on physical signs at the site, but we were ultimately unable to classify the predator at the other 2 mortalities. Additionally, it is possible that field researchers could introduce predator DNA to a site (e.g., through dirty clothes or equipment), so using sterile gloves and appropriately cleaning equipment is essential. We also recommend that researchers occasionally collect blank samples of PBS buffer (if using) in the field to process and ensure that the solution has not been contaminated. All genetic lab work should be done in sterile conditions, with separate rooms for pre- and post-PCR processes, and negative and positive controls used at all steps of the process to monitor for any contamination.

MANAGEMENT IMPLICATIONS

Forensic DNA analysis is rapidly advancing the understanding of complex predator-prey interactions and improving information available to inform research, conservation, and management. However, it is critical to remember that genetic evidence alone cannot distinguish between a predator and a scavenger at a kill site, and the field investigation remains an essential component in determining the cause of death. With this in mind, we make the following recommendations regarding genetic evidence:

1. Genetic evidence consistently improves kill-site investigations and should be a standard component of predation mortality studies, especially where there is a rich community of carnivores that may prey on ungulates and regardless of the confidence or training level of the investigators.
2. More genetic samples should be collected for smaller prey (i.e., deer fawns and neonatal elk versus adult deer) because their predators are more frequently misidentified, yet DNA samples are less likely to amplify. Additionally, investigators should be mindful that predator sign associated with small prey often differs from that of larger prey. For instance, cougars frequently cached the carcasses of large prey and left the rumen intact, while this was less common for small prey.
3. Rates of DNA amplification success decreased when a freeze-thaw cycle had occurred in the field. Investigators should collect more samples in these conditions to increase the likelihood of a positive identification.
4. Where the potential predators under consideration are in the same taxonomic family, collecting genetic evidence should be prioritized to help to distinguish the species and avoid misidentifications.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

White-tailed deer, mule deer, and elk were captured in accordance with protocols approved by the University of Washington Institutional Animal Care and Use Committee (IACUC Protocol No. 4226-01: Anti-Predator Behavior Effects) and adhered to the guidelines of the American Society of Mammologists for the use of live animals in research (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists 2016).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are archived at http://doi.org/10.5063/F1FX77W0.

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SUPPORTING INFORMATION

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