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# Integrated Stress and Community Perceptions: Toward an Understanding of Human-Cougar Tolerance

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# INTEGRATED STRESS AND COMMUNITY PERCEPTIONS: TOWARDS AN UNDERSTANDING OF HUMAN-COUGAR TOLERANCE

By

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**Abstract**

Evidence suggests that cougars (*Puma concolor*) are beginning to recolonize their traditional range in the Midwestern and Eastern US, returning to a landscape and a social environment that have changed drastically in a century of absence. Any hope of the cougar's persistence depends on both human tolerance of their presence and on cougar tolerance of disrupted habitat. In this thesis, we took advantage of diverse cougar policy in place in the Western US to explore variation in human attitudes and acceptability of cougars and in the cougar stress response. We validated a process to identify and extract cortisol from cougar hair and examined relationships between cougar stress and intrinsic, environmental, and anthropogenic variables. We also validated a definition of human tolerance adapted from the sociological literature – "putting up with wildlife and wildlife behaviors you don't like" – and tested its fit on data gathered from a social survey of rural communities in the West. After operationalizing tolerance, we explored whether permitting cougar hunting was likely to improve tolerance among the general public. In Chapter 2, we found that age class, season, precipitation, human population density, and hunting all significantly influenced cougar hair cortisol content, with cougars demonstrating higher cortisol when hunted and when inhabiting areas of lower human density. In Chapter 3, we identified four distinct typologies characterized by attitudes toward and acceptability of cougars among the general public – the "enthusiastic," the "pragmatic," the "intolerant," and the "tolerant." Finally, in Chapter 4, we found that while the general public had high attitudes and acceptability of cougars, hunters in California, where cougar hunting is banned, were intolerant of cougars compared to hunters elsewhere. Wildlife managers in eastern states should be aware that cougars do physiologically respond to anthropogenic disturbance and that hunters may chafe under restrictive cougar hunting regulations.

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**Table of Contents**

**Copyright** ... ii
**Acknowledgments** ... iv
**Chapter 1: Introduction** ... 1
Cougars Are Recolonizing The East ... 1
The Significance of Tolerance in Cougar Recovery ... 2
Measuring Tolerance ... 5
Cougars as a Case Study ... 8
Research Approach ... 9
Social-Ecological Systems ... 9
Measuring Human Tolerance through a Social Survey ... 10
Measuring Cougar Tolerance through Stress Hormones ... 11
Works Cited ... 12
**Chapter 2: Factors Influencing Cougar Stress Hormones in Hair** ... 17
Background ... 17
Rationale/Hypotheses ... 24
Methods ... 25
Results ... 29
Discussion ... 36
Works Cited ... 47
**Chapter 3: Operationalizing Human Tolerance of Wildlife** ... 55
Background ... 55
Rationale/Research Questions ... 65
Methods ... 65
Results ... 70
Discussion ... 81
Works Cited ... 85
**Chapter 4: Testing the Tolerance Metric Across Communities and Social Groups** 90
Background ... 90
Research Questions ... 96
Methods ... 97
Results ... 98
Discussion ... 101
Works Cited ... 105
Appendix ... 109
Survey Instrument ... 109
ANCOVA tables for Community Differences ... 119

# Chapter 1: Introduction

## Cougars Are Recolonizing The East

In 2015, after a review of genetic evidence, the US Fish & Wildlife Service (USFWS) declared the endangered eastern cougar (*Puma concolor couguar*) officially extinct. The declaration was long overdue, as experts agreed that the subspecies had almost certainly vanished over a century earlier (Cardoza & Langlois, 2002). Ironically, the eastern cougar first gained protection under the Endangered Species Act several decades after being extirpated by deforestation, loss of prey, and direct human persecution through a bounty harvest system (Racey et al., 2015; Sunquist & Sunquist, 2002).

The delay in removing the eastern cougar from the endangered species list was partially due to continuous and increasing cougar sightings east of the Mississippi River, leading some to speculate that the eastern cougar persisted in its historical range (LaRue et al., 2012). In 2011, a driver hit and killed a juvenile male cougar as it was crossing a highway in Connecticut, a state that had lost its cougar population at the end of the $19^{th}$ century. Microsatellite DNA analysis later showed that the individual was not an eastern cougar, but originated from a population in the Black Hills of South Dakota. The individual had seemingly dispersed over a thousand miles in search of unoccupied territory (Drake, 2011). A few years later, the state wildlife agency confirmed a cougar sighting in Tennessee, the first in a century (TWRA, 2016). These and other sightings have led researchers to propose a trend of Western cougars following deer along habitat corridors into the Midwest and beyond (See Figure 1.1), effectively recolonizing the historical range of the eastern cougar. However, sporadic individual dispersal is only the first step toward true population establishment, and thus far there is little evidence of *Puma concolor* breeding anywhere east of the Black Hills.


Figure 1.1 Cougars historically occupied most of the continental US from coast to coast; the dark shaded area indicates their current range. Points (n=178) indicate confirmed cougar sightings in the Midwest between 1990-2008. Figure from LaRue et al., 2012.

## The Significance of Tolerance in Cougar Recovery

Two factors will determine whether cougars are able to establish permanent reproducing populations in the eastern US. The first is the extent to which cougars, with their substantial home range requirements, will be able to thrive in the disrupted landscapes of the Midwest and East (LaRue & Nielsen, 2016). Cougars can adapt to modified environments by changing their behavior and movement patterns to accommodate human activities; for example, waiting to cross roads during periods of low traffic (Knopff et al., 2014). White-tailed deer, the cougar's main prey in many regions, forage in large numbers near the gardens, forest edges, and croplands of the wildland-urban interface, occasionally drawing cougars close to human development (Kertson et al., 2011; Knopff et al., 2014). Although cougars can be found in almost every naturally occurring ecotype, habitat selection models have demonstrated that they do tend to avoid most built environments, including paved roads, urban zones, and areas of intensive agriculture (Beier, 2009; Dickson et al., 2002; LaRue & Nielsen, 2015). Cougars are particularly at risk from habitat fragmentation and rarely attempt large highway crossings, limiting their dispersal in built-up areas like Southern California (Riley et al., 2014). If cougars are to establish breeding populations in the fragmented forests of the Midwest and East, they must adapt their behavior and physiological mechanisms to tolerate even more intensive human disturbance.

The second factor that may limit the cougar's ability to successfully recolonize its historical range is human tolerance of its presence and behavior. Intentional persecution led to the extinction of the eastern cougar a century ago; therefore, cougars have little chance of re-establishing themselves in the eastern US unless attitudes have changed since then. Fortunately, there is evidence to suggest that this is the case. Manfredo et al. (2003) analyzed public values toward wildlife in the US and documented a shift over the last century from majority traditional/utilitarian wildlife orientations toward mutualist/protectionist orientations. Cross-cultural studies suggest that as societies transitions toward urbanization, financial security, and universal education, individuals begin to view wildlife less as a resource to use and more as entities with intrinsic value and rights (Teel et al., 2007). Studies of attitudes toward cougars in the Midwest have found that the public generally approve of cougars returning, although survey and interview respondents expressed distrust in government agencies and concerns about the hazards cougars might present to livestock, game, and people (Davenport et al., 2010; Dodson, 2004).

Any chance of cougars and humans coexisting in the eastern US hinges upon whether people can tolerate the presence of cougars this time around and, in turn, if cougars can adapt to tolerate human activities. What's more, these two factors likely interact to some degree. Adaptability to human-dominated ecosystems might allow cougars to populate land east of the Mississippi, but conflict is always a concern when large carnivores make their home near human development. Although cougars rarely harm people, fear of attacks (often compounded by media coverage), livestock depredation, and pet loss can all damage attitudes toward cougars (Wolch et al., 1997). Human-cougar coexistence therefore demands a difficult balancing act. In effect, cougars must tolerate human activities enough that they are able to live and breed in disrupted landscapes, but not so much that they interfere with human livelihoods and strain public sympathy for their existence.

An additional complication is that the threshold between coexistence and conflict is not fixed. Whether an individual frames a cougar's behavior as problematic depends on their personal values, beliefs, and attitudes toward that animal (Peterson et al., 2010). Some believe cougar populations should be reduced to protect livestock, pets, or wild game; others believe cougars should be controlled only if they directly threaten human safety (See Figure 1.2) (Teel et al., 2002; Zinn et al., 1998). Even when there is relatively high agreement that agencies should control predators, stakeholders disagree about the acceptability of various management tools, and whether those should be lethal or nonlethal (Slagle et al., 2017). When making decisions about predator populations, wildlife managers are charged with the difficult task of predicting cougar behavior, navigating varied social thresholds, and arriving at the most acceptable plan of action.

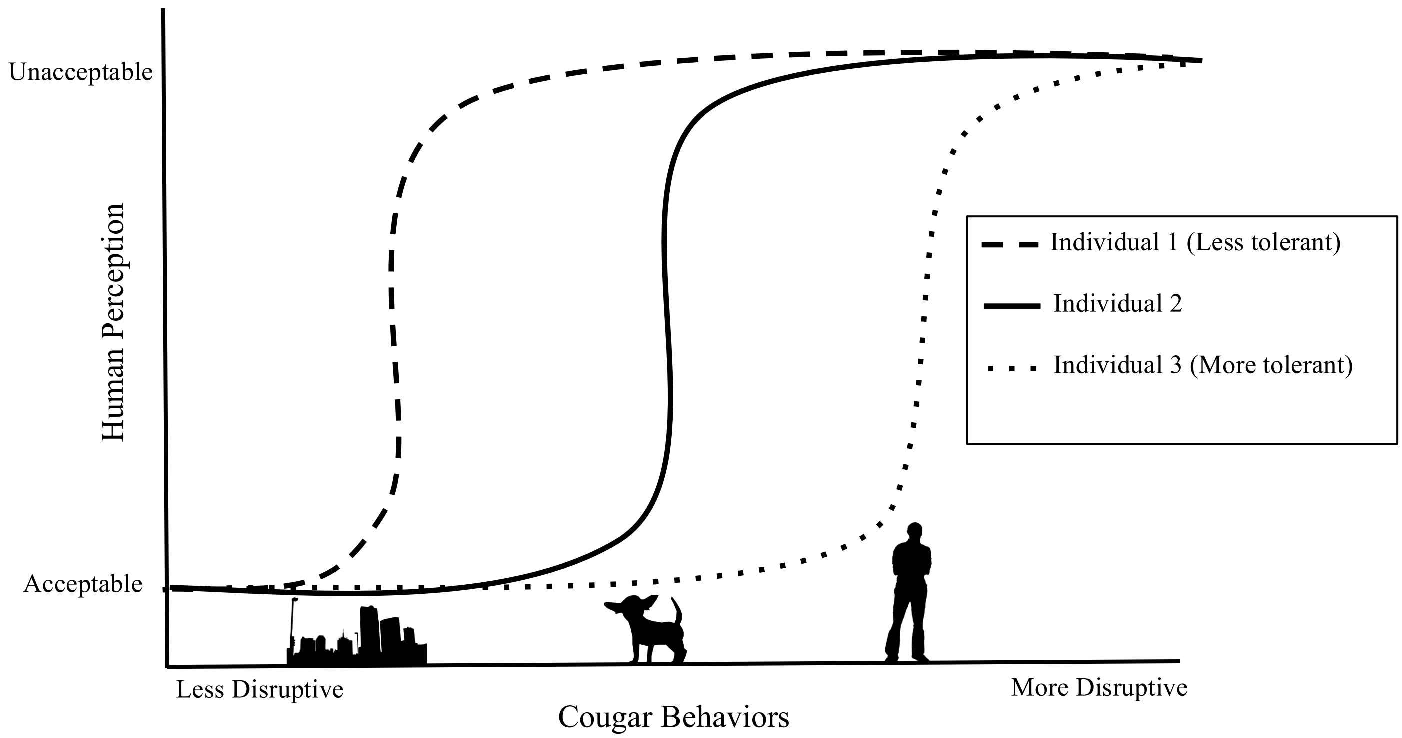


Figure 1.2: Individual human tolerance determines the threshold between coexistence and conflict. Each line represents an individual with a particular threshold for accepting cougar behaviors. **Individual 1** tolerates cougars existing in the wilderness, but believes they should be controlled if they approach human development. **Individual 2** tolerates cougars appearing near human development, but draws the line when pets are attacked. **Individual 3** tolerates almost any cougar behaviors until human lives are put at risk. A population of individuals with different tolerance thresholds is more likely to experience conflict over management decisions.

### Measuring Tolerance

Tolerance, and its relationship to human and cougar behavior, will shape the course of cougar conservation over the next several decades. Although the term "tolerance" is frequently applied in both animal behavior and human dimensions research, there are measurement challenges in both fields that have led to difficulty applying the concept to improve human-wildlife relationships.

**Tolerance in Animal Behavior.** In animal behavior, tolerance is defined as the amount of disturbance that an individual animal can withstand before altering its behavior or physiology (Nisbet, 2000). Tolerance is distinct from habituation in that the former can be considered a distinct threshold while the latter is a process by which an individual shifts their tolerance threshold to accommodate increased disturbance (Bejder, 2009). Measures of wildlife tolerance of anthropogenic disturbance are often attained through behavioral observations (e.g. flight initiation distance), but with large, elusive carnivores these can be difficult to obtain systematically, safely, and unobtrusively. Distribution and abundance models can predict the amount of human disturbance wildlife can tolerate on a landscape level, but provide little insight into variation in tolerance between individuals or meta-populations, which can be significant (Sweanor et al., 2005).

Physiological responses to disturbance often precede observable behavioral change in animals, and are thus of interest to conservation biologists studying wildlife adaptability to anthropogenic change. The vertebrate stress response is a potential pathway through which wildlife might adaptively cope with human-caused perturbation factors (Dantzer et al., 2014). Large carnivores, like all vertebrates, secrete glucocorticoid hormones that induce physiological processes intended to help them maintain homeostasis or escape threats in the face of rapid change. Baseline glucocorticoid levels, a common measure of stress in a population, can be analyzed non-invasively in feces or hair, which is useful for large carnivore applications (Sheriff et al., 2011). Studies in birds have demonstrated that populations established near urban areas developed a dampened behavioral and stress response to human disturbance compared to wild populations, indicating increased tolerance of disturbance (Atwell et al., 2012). Studies of long-term stress in grizzly bears found similar results (Bourbonnais et al., 2013); however, few studies have attempted to examine stress physiology in free-living cougars.

**Tolerance in Human Dimensions of Wildlife.** In the human dimensions realm, tolerance is often used to describe public perceptions of wildlife, but is yet to be consistently defined or operationalized (Bruskotter et al., 2015). Briefly, public tolerance of wildlife has been measured through attitude statements (including perceived risk) (Riley and Decker, 2000), normative beliefs (including acceptable population sizes and acceptability of management actions under different conflict scenarios), behavioral intentions (Naughton-Treves et al., 2003), and even through direct statements such as "How tolerant are you of wolves?" (Lewis et al., 2012). Though each of these discrepant measures of tolerance can be useful, they are difficult to compare and interpret across studies. Despite a lack of a consistent definition for the concept, there seems to be almost universal agreement that human tolerance is vital to wildlife conservation, and indeed may be the last barrier before full recovery of large carnivores (USFWS, 2009; Treves & Bruskotter, 2014). The Iowa Department of Natural Resources exemplified this concern in a brochure aimed at educating the public about cougars, stating that Midwesterners' "tolerance or intolerance … will dictate whether [cougars] will ever be able to get a foothold in the state" (Iowa DNR, 2013).

Because human tolerance is widely considered to be one of the most important factors determining the range and success of recovering carnivores, its application has had real consequences for conservation policy. The US Fish and Wildlife Service cited low public tolerance in their decision to remove the Northern Rocky Mountain wolf from the Endangered Species List, claiming that returning management to the states would bolster public support and improve the wolf's long-term outlook (USFWS, 2009). However, reported intolerance of a community can vary immensely depending on how researchers choose to construct tolerance metrics (Bruskotter et al., 2015). Therefore, it is imperative that human dimensions researchers develop a tolerance scale that is a) reliable, b) consistent, and c) useful to wildlife managers. A robust tolerance metric would allow policymakers to experiment with longitudinal studies and convincingly demonstrate the efficacy (or inefficacy) of tolerance-boosting strategies.

**Cougars as a Case Study**

The tolerance-measuring challenges discussed above are common to large carnivore research around the world. However, *Puma concolor* are an ideal candidate system to address these questions for several reasons. In the US, cougars can be considered a conservation success from a population standpoint; they represent the "other side" (and its attendant conflicts) for highly endangered felids like the Amur leopard (*Panthera pardus orientalis*). Having recuperated major population losses, cougars are now at a critical juncture as they attempt to recolonize a landscape that has changed drastically over a century of absence. Cougars entering eastern ecosystems would fill a currently empty apex predator niche, potentially mitigating an explosion of deer that have degraded forests and spread zoonoses such as Lyme disease (Côté et al., 2004; LaRue et al., 2012). Successful eastward dispersal of mountain lions may also be key to the recovery of the geographically isolated Florida panther (*Puma concolor coryi*), an endangered cougar subspecies that has lost well over half of its genetic diversity from inbreeding depression (Culver et al., 2008). Because eastern ecosystems stand to gain significant biodiversity benefits through the establishment of cougar populations, wildlife managers must work within the limits of human and cougar tolerance by implementing policies that encourage human-cougar coexistence.

**Research Approach**

I will use a social-ecological systems lens to examine the role of tolerance in human-cougar interactions. Through a double-barreled project, I aim to examine a) cougar tolerance of human disturbance through a stress hormone assay and b) human tolerance of cougar conflict through a social survey. In each chapter, I will examine the literature to develop a working definition of tolerance, implement a research methodology intended to operationalize these definitions, and assess the efficacy of each approach. Finally, I will link my findings to potential management applications and interpret their relevancy for cougar recovery and for large carnivore conservation around the world.

**Social-Ecological Systems**

This project employs a social-ecological systems (SES) approach to examine human-cougar conflict from both a sociological and biophysical perspective. Ecologists have long thought of natural systems in terms of inputs, outputs, and interactions between moveable parts, but only recently have researchers begun to include human attributes when depicting these systems (Holling, 1996; Adger, 2000). The SES lens allows wildlife managers to integrate human and biological variables in their adaptive planning while prioritizing resiliency and self-sustainability in a system (Meadows, 2008). Human-cougar interactions can be thought of as a social-ecological system, complete with feedback loops, interdependence of human and biophysical variables, and thresholds for system collapse (Adger, 2000). In this project, I chose a multi-disciplinary approach to understanding tolerance between humans and cougars by adapting methodologies from human dimensions, sociology, animal behavior, and conservation physiology.

**Measuring Human Tolerance through a Social Survey**

To examine human tolerance of cougars, we surveyed communities in the Western US, where cougar populations have grown significantly since the 1960s. Because *Puma concolor* are not federally protected, their management is left up to the states, creating a patchwork of different cougar policies across the region that can serve as a natural experiment testing the effect of policy on tolerance (Hornocker & Negri, 2010). We chose to survey similar communities in three states with widely varying cougar management policy in an attempt to access the full breadth of the tolerance spectrum. Residents of Red Bluff, CA are prohibited from sport hunting cougars; residents of Ellensburg, WA are permitted to hunt cougars in season but may not use hounds to pursue them; and residents of Kalispell, MT are permitted to hunt cougars in season with or without hounds, as per state policy.

We designed and conducted a survey to assess respondents' tolerance of mountain lions near their community, measured through attitudes, behavioral intentions, and acceptability of management actions. We compared each method of measuring tolerance conceptually and tested robustness, reliability and predictive ability. Using a framework adapted from sociological studies of human tolerance, we proposed an integrative definition of tolerance for use in wildlife studies and tested whether the definition fit the survey data. Finally, we applied this novel definition of tolerance to a case study of Red Bluff, California, as an attempt to understand the effect of restrictive hunting policy on human tolerance of large carnivores.

**Measuring Cougar Tolerance through Stress Hormones**

We collaborated with wildlife state agencies and research groups in Montana, Washington, and California to obtain cougar hair samples gathered from animals tranquilized and collared as part of a population study, harvested by hunters, removed by depredation permits, or found dead. We used an analytical chemistry approach to validate a novel procedure to separate, identify, and extract cortisol from cougar hair. We explored relationships between hair cortisol content and anthropogenic variables, while controlling for intrinsic and environmental variables, and used Aikake's Information Criteria to select models that best explained variation in hair cortisol. Finally, we discussed future applications for this technique and management implications, particularly for wildlife managers setting cougar policy for the first time in Midwestern and Eastern states.

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## Chapter 2: Factors Influencing Cougar Stress Hormones in Hair

### Background

Human development is a major threat to wildlife populations worldwide. However, some species have demonstrated a remarkable ability to adapt to anthropogenic activities and land use change. The house sparrow (*Passer domesticus*) and brown rat (*Rattus norvegicus*) are familiar examples of species that tolerate and even benefit from urbanization, but even large carnivores usually associated with wilderness have been known to take advantage of human-dominated landscapes. Increased sightings of predators like cougars (*Puma concolor*) near human communities are due at least in part to patterns of exurban development that are more conducive to wildlife encounters (Hansen et al., 2005). However, there is also evidence that these species have rapidly altered their behavior and physiology to cope with (and in some cases, actively exploit) built ecosystems (Ditchkoff et al., 2006).

Some of the most obvious behavioral changes occur when urban wildlife restrict their movements both temporally and spatially to avoid human activity (Gehrt et al., 2009). Compared to their counterparts in undeveloped areas, urban carnivores are more nocturnal, have smaller home ranges and dispersal distances, and maintain higher population densities (Ditchkoff et al., 2006). These behavioral modifications allow wildlife to maximize the benefits of foraging and reproducing near development while minimizing the likelihood of negative human encounters. Other species, such as sage grouse and wolverines, are sensitive to the novel challenges presented by urbanization and are rarely found near human habitation (Hansen et al., 2005). Cougars may be considered fairly adaptive carnivores that avoid areas of dense urbanization and human activity but are increasingly sighted near the wildland-urban interface, where they take advantage of exurban prey sources such as white-tailed deer (*Odocoileus virginianus*), mesocarnivores, and domestic animals (Smith et al., 2017; Dickson & Beier, 2002; Knopff et al., 2014; Morrison et al., 2014). This adaptability has allowed cougar populations to persist and even grow during periods of intense land-use change, but also brings them into social conflict with humans (Sweanor & Logan, 2010; Kertson et al., 2011).

The emerging field of conservation physiology aims to understand the mechanisms that help wildlife cope with anthropogenic challenges like development and to apply this information toward preventing biodiversity loss (Dantzer et al., 2014). Stress, one possible driver of adaptation to anthropogenic change, is triggered by a suite of highly conserved glucocorticoid hormones (CORT) that can be quantified readily in vertebrate blood and saliva (instantaneous metrics of stress) or in feces, urine, hair, and feathers (longer-term metrics of stress) (Sheriff et al., 2011). CORT levels are influenced not only by unpredictable external perturbations, but also by predictable changes in seasonal food availability and reproduction, as well as by intrinsic factors such as age and sex (Dantzer et al., 2014). Therefore, it is important to take these factors into account when attempting to quantify the effect of additional stressors like land-use change, extreme weather, or human activities.

**The Vertebrate Stress Response.** In vertebrates, the term “stress” encompasses a broad range of physiological processes that allow an individual to maintain homeostasis in the face of environmental perturbation. Stress pathways in mammals are triggered by the hypothalamic-pituitary-adrenal (HPA) axis, which controls CORT secretion. The stress response can refer to the magnitude or the duration of CORT production following a negative stimulus (Sapolsky, 1992). While most CORT is excreted within a few hours of release, a portion is permanently incorporated into the tissue (e.g. hair, feathers), providing a long-term record of an individual's stress response over the past several weeks to months (Sheriff et al., 2011).

In the short term, stress is adaptive. Rapid mobilization of glucose triggered by CORT secretion helps an organism escape an immediate threat to their survival (Sapolsky et al., 2000). However, CORT production has a metabolic cost, and overactivation of the hypothalamic-pituitary-adrenal axis (the neuroendocrine pathway controlling CORT) can have serious deleterious effects on immune function and reproduction (Wingfield & Sapolsky, 2003; Pederson & Grieves, 2007). Therefore, organisms must regulate their stress response to neither under-react to potentially lethal threats nor over-react to non-harmful stimuli. Depending on the demands of the environment, baseline CORT can have a positive, negative, or non-significant relationship to an individual's overall fitness, and the stress response may change based on life-history traits (age, experience) or surrounding conditions (climate, time of year). (Breuner et al., 2008).

Stress also has a genetic component (Evans et al., 2006; Baugh et al., 2012). Heritable phenotypic variation in the stress response is often pronounced enough that individuals may be categorized along a "boldness" continuum, with shyer individuals consistently demonstrating a heightened CORT and behavioral response to unfamiliar stimuli compared to bolder individuals (Darrow & Shivik, 2008; Atwell et al., 2012). Boldness and novelty-seeking behaviors incur tradeoffs between resource gain and predation risk that vary depending on the environment. Therefore, an organism's ability to correctly calibrate its stress response can significantly influence survival in a rapidly changing environment (Bonier et al., 2009).

***Intrinsic factors affecting the stress response.*** The homeostatic set point, or baseline level, for circulating glucocorticoids varies depending on the individual (Williams, 2008). If not controlled for, differences in baseline CORT attributed to intrinsic factors like age and sex may be large enough to conceal the physiological effects of anthropogenic stressors (Ahlering et al., 2013; Bourbonnais et al., 2013). In reproduction and lactation, females mammals produce more prolactin, a peptide hormone that induces parenting behavior and suppresses CORT (Cook, 1997). Sexually dimorphic behavior like dispersal and territorial aggression can systematically expose males and females to different levels of environmental perturbation (Creel et al., 2013; Lafferty et al., 2015).

The aging process can also change an individual's stress response over time. Juveniles often demonstrate a less reactive physiological and behavioral response to novel stimuli compared to adults in the population (Wada, 2008). Conversely, the CORT-reproduction tradeoff hypothesis predicts that older individuals with fewer future opportunities to breed should attempt to do so despite stressful environments (Wingfield & Sapolsky, 2003). Therefore, it may benefit aged individuals to suppress HPA activity in favor of reproduction.

***Environmental factors affecting the stress response.*** Glucocorticoid levels have been shown to fluctuate seasonally in some vertebrates according to climate, food availability, and breeding season (Kitaysky et al., 1999; Lynch et al., 2002; Romero et al., 2008). Cougars have no defined breeding season (although some populations experience a birth pulse in late summer), but the availability and vulnerability of ungulates, their main prey in most systems, changes from summer to winter (Cooley et al., 2008; Jansen & Jenks, 2012). Inclement weather, such as droughts and storms, can also elevate CORT in populations (Romero et al., 2002; Landry et al., 2016). While cougars have adapted to thrive in a huge variety of climates and ecotypes, the effects of climate could still act as an important environmental stressor and should be accounted for.

**Human-Induced Stress**. Human development in and around wildlife habitat is one of the most rapid forms of environmental change, and can thus act as a significant source of stress for wildlife. In many species, anthropogenic noise creates difficulties in foraging, mating, and rearing young, and has been associated with increased baseline CORT levels (Kight and Swaddle, 2011). Disturbance in the form of increased human activity and recreation, even when not directly lethal, can serve as a stressor for some species (Dantzer et al., 2014). Studies have found elevated fecal CORT levels among wolves (*Canis lupus*) exposed to snowmobiling activity (Creel et al., 2002) and among wildcats (*Felis silvestris*) inhabiting areas of a natural park with high tourist visitation rates (Piñeiro et al., 2012). Unsurprisingly, direct human predation in the form of harvest can act as a significant source of perturbation for carnivores – for example, cougars pursued with dogs multiple times over the course of a season demonstrated markers of chronic stress upon recapture (Harlow et al., 1992; Bryan et al., 2015).

Some wildlife populations living near human activity have shown a declining response to disturbance over time, indicating some level of habituation to sublethal perturbations like noise or recreation. Romero et al. (2002) found that marine iguanas (*Amblyrhynchus cristatus*) experiencing heavy tourist disturbance in the Galápagos islands had lower baseline and stress-induced plasma CORT levels than did iguanas in protected areas. Similarly, a population of dark-eyed juncos (*Junco hyemalis*) in urban San Diego, CA demonstrated lower CORT response to handling and bolder foraging behaviors compared to a “wild” population unaccustomed to human disturbance. A common garden study showed that these differences endured through generations, suggesting some degree of heritability (Atwell et al., 2012). Modulating the stress response to anthropogenic disturbance may be maladaptive if survival is lower near human development (i.e. an ecological trap); however, as many species gain nutritional and security benefits from cohabiting with humans, “bold” phenotypes may be rewarded over time and persist.

Complete avoidance of human activity can be a liability in an increasingly developed world, and the ability to tolerate human development has been key to the survival and flourishing of many species. People also perceive benefits of coexisting with wildlife, as many exurban residents appreciate viewing semi-habituated animals near their homes (Curtin 2002; König, 2008). However, costs such as property damage and disease transmission also begin to accrue when wildlife use built ecosystems, whether out of necessity or drawn in by attractants. In the case of large carnivores, pet and human safety become a concern. For sensitive and habituated populations alike, stress physiology and the associated glucocorticoid hormones can elucidate the mechanisms behind behavior and conflict, reproduction, and survival under environmental change.

**Hair CORT as a Metric of Long-Term Stress.** While many of the above-cited studies measured stress hormones in plasma or fecal samples, hair as a biological substrate for CORT is a novel and potentially useful metric of long-term stress in mammals (Sheriff et al., 2011; Macbeth et al., 2012). Hair is thought to be an integrated measure of stress reflective of an organism's baseline and stress-induced CORT levels over several weeks as the hair grows. Therefore, transient stress induced during the sampling process is not evident in the current sample, and researchers can theoretically gauge a population's physiological response to environmental or anthropogenic change over an extended period. Hair can be gathered non-invasively if snags are used, and CORT in hair remains stable for up to several decades after sampling (Bechshøft et al., 2012). Hair CORT concentrations can be significantly affected by pelage color, hair type (guard or underfur), and body region (Bennett et al., 2010; Bourbonnais et al., 2013). Nevertheless, animal and human studies have demonstrated that when these factors are controlled for, an individual's total hair CORT is linearly related to plasma and salivary CORT levels and is reflective of environmental stress experienced over the course of the hair growth (Davenport et al., 2006; Kalra et al., 2007).

As the potential applications for conservation physiology are numerous, a large number of hair CORT studies have been conducted in the past decade in a variety of free-living carnivores, including grey wolves (Bryan et al., 2013), grizzly bears (*Ursus arctos*; Macbeth et al., 2010; Bourbonnais et al., 2013) and Canada lynx (*Lynx canadensis*; Terwissen et al., 2013). However, additional validation of this methodology is still needed in several areas. Firstly, the mechanism by which CORT is deposited in hair is not fully understood. Passive diffusion of hormone from capillaries into the shaft was long assumed to be the primary method of delivery; however, radiolabeling studies have found that very little plasma CORT is present in regrown hair (Russell et al., 2012; Keckeis et al., 2012). This finding suggests at least some local production of hormone in the hair follicle and raises questions about the extent to which hair CORT truly represents integrated baseline CORT levels. Secondly, most studies across mammalian taxa have used cortisol assays without validating the specificity of the antibodies used to measure cortisol or even confirming the presence of cortisol in the hair of the species of interest. While HPA axis functioning tends to be evolutionarily conserved, the composition of glucocorticoid hormones in biological substrates can vary significantly between species (Dantzer et al., 2014). Additionally, most commercially available antibodies cross-react with other steroid hormones that might also be present in the hair (Berk et al., 2016). If antibodies used in a cortisol assay in fact bind to some other compound, interpretation of findings can be altered considerably.

**Rationale/Hypotheses**

While hundreds of studies have investigated wildlife stress physiology, few have attempted to quantify CORT in the free-living cougar. Because cougar behavior is difficult to observe in the wild, non-invasive sampling of CORT across populations could address questions about how cougars respond to environmental change and human disturbance. In this study, we will examine long-term stress in cougar populations across the Western US by relating hair CORT levels to human & livestock density, history of conflict, and hunting pressure. To our knowledge, cortisol has never been measured in cougar hair; therefore, preliminary validation of the method was needed. The major goals of this study were to 1) confirm the presence of cortisol in cougar hair; 2) develop a method to extract and specifically measure hair cortisol in a competitive immunoassay; and 3) identify intrinsic, environmental, and anthropogenic factors associated with hair glucocorticoid concentrations in cougars. We tested four hypotheses in our hair cortisol modeling approach to determine whether hair cortisol levels were driven mainly by individual, intrinsic factors (**H1**), environmental factors (**H2**), anthropogenic factors (**H3**), or by some combination of the above three factors (**H4-7**).

## Methods

**Sample Collection.** We collaborated with state wildlife agencies and research groups to collect 214 hair samples from harvested, depredated, captured, or found dead cougars in Northern California, Eastern Washington, and Western Montana. Samples were collected from June 2016 to April 2017. Collaborators and field technicians were instructed to cut or shave 20 mg of guard hairs from the hindlimb of the sedated animal, pelt, or carcass as near to the skin as possible (See Figure 2.1). Samples were then placed in sealed coin envelopes and mailed to our laboratory in Missoula, MT, where we stored them at room temperature in a dry, dark location for up to 3 months prior to extraction.

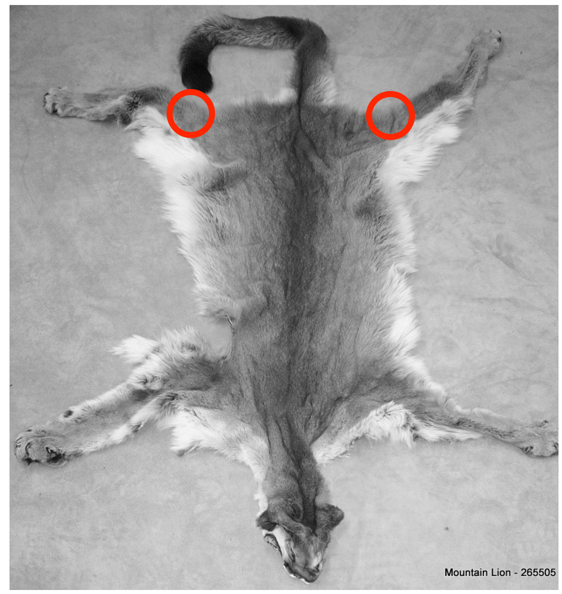

Figure 2.1. Image provided to collaborators indicating correct body location for hair sampling.

**Cortisol Extraction**. Our protocol for extracting CORT from cougar hair was adapted from a procedure developed by Bryan et al., 2013 for use in domestic dogs (*Canus familiarus*). In brief, we weighed out between 15-25 mg of hair from each sample and transferred the weighed portion to an Eppendorf tube. We washed samples twice with distilled water and twice with isopropanol for 1 min per wash. Hair was thoroughly dried after each wash, then we added two 4.67 mm diameter stainless steel ball bearings (BC Precision, Chattanooga, TN) to the tubes. Hair samples were ground into a powder using an ad-hoc tissue homogenizer fashioned from a paint can shaker. We weighed out 10 mg of hair powder and transferred the portion to a test tube with 500 μl HPLC-grade methanol. Samples were sonicated for 30 minutes and incubated in a hot water bath at 50° C for 24 hours. We centrifuged samples, then aliquotted the supernatant into a fresh test tube. For measurement with enzyme immunoassay, methanol was evaporated under a nitrogen stream and samples were reconstituted with assay buffer.

**Cortisol Separation with HPLC.** We used an Agilent 1260 Infinity high performance liquid chromatography (HPLC) instrument equipped with a degasser, quaternary pump, autosampler and diode array detector (Agilent, Santa Clara, CA) to separate compounds in a pooled cougar hair sample (n=3) and compared the resulting chromatogram to a chromatogram of known hormone standards purchased from Steraloids (Wilton, NH) & Sigma-Aldrich (St. Louis, MO). We identified compounds of interest from a literature review of relevant corticoids and other steroid hormones, and selected 4-pregnen-11β-17, 21-triol-3,20,dione (cortisol); 4-pregnen-11β,21-diol-3,20-dione (corticosterone); 17α,21-dihydroxypregn-4-ene-3,11,20-trione (cortisone); 4-pregnen-11β,21-diol-3,18,20-trione (progesterone metabolite); 4-pregnen-20β,21-diol-3,11-dione (progesterone metabolite); 4-pregnen-11β,20β,21-triol-3-one (20β-dihydrocorticosterone); 5α-androstan-3α,11β-diol-one (testosterone metabolite); 1,3,5(10)-estratrien-3,17β-diol (estradiol); 5β-pregnan-3α,21-diol-11,20-dione (tetra-hydro-11-dehydrocorticosterone); 5β-pregnan-3α,20β,21- triol-11-one (progesterone metabolite); and 4-pregnen-21-ol-3,20-dione hemisuccinate (deoxycorticosterone) for comparison. Chromatographic separations were conducted using a Restek Ultra Biphenyl column (2.1 mm x 100 mm x 5 μm; Restek, State College, PA). Samples were eluted in a gradient between mobile phase A (0.1% formic acid in water) and mobile phase B (0.1% formic acid in acetonitrile). The gradient started at 35% B and went to 90% B over 10 minutes, and the flow rate was 0.4 mL/min. We collected fractions based on observed peaks in the chromatogram and assessed the presence of cortisol in each fraction using a commercially available cortisol enzyme immunoassay kit (Enzo Life Sciences, Farmingdale, NY).

As per the manufacturer's note, cross-reactivity of the antibody used to analyze cortisol was as follows: cortisol (100%), prednisolone (122.35%), corticosterone (27.68%), 11-deoxycortisol (4.0%), progesterone (3.64%), prednisone (0.85%), testosterone (0.12%) and <0.10%: androstenedione, cortisone, estradiol. We also used this kit to assess cortisol levels in triplicate in individual hair samples. We read plates using a Multiskan Ascent spectrophotometer from Thermo Fisher Scientific (Waltham, MA) and assessed coefficients of variation (CVs) using their proprietary software. We re-ran samples with CVs >15% for improved accuracy. Intra-assay coefficient of variation (CV) was 4.44% ± .38% (n=12), while inter-assay CV was 2.31% ± .82% (n=8).

**Statistical Analysis.** We used an exploratory approach to identify potential variables of interest associated with variation in CORT levels. We employed a manual stepwise model-building method in which linear regression with backwards elimination of covariates was used to construct top models for each hypothesis, assessing initial model fit using significance of variables and Pearson's $r^2$. We assessed model performance using an information theoretic framework with Aikake's Information Criterion adjusted for small sample sizes (AICc). Intrinsic variables set as fixed effects included Sex (a categorical variable with two levels; "male" and "female"), AgeClass (categorical with three levels: “kitten,” “subadult,” and “adult”), Source (a categorical variable reflecting sample source with four levels: “harvest,” “depredation,” “capture,” and “found dead”), and HairColor (a qualitatively scored categorical variable with three levels; “white”, “light brown” and “dark brown”). Environmental variables set as fixed effects included MeanPrecip (a continuous variable reflecting daily average precipitation in mm) and Season (categorical with three levels; “spring/summer”, representing April-August, “fall”, representing September- November, and “winter”, representing December-March). Anthropogenic variables set as fixed effects included “PopDensity” (a continuous variable reflecting average number of people/$km^2$), “SheepGoats” (a continuous variable reflecting total number of sheep and goats per county) and “Hunted” (categorical with two levels; “yes” and “no”, based on whether cougar hunting was allowed in that state). We conducted analysis at the county level, and all models included “County” as a random effect in an effort to account for reduced variance between samples from the same geographic region.

We obtained Anthropogenic data from US Census Bureau and Department of Agriculture records, while environmental data was obtained from the University of Idaho’s METDATA dataset (available at http://metdata.northwestknowledge.net/) and the University of Montana’s Numerical Terradynamic Simulation Group (available http://www.ntsg.umt.edu/project/default.php). We extracted environmental data at the county level using ArcGIS v 10.5 (Esri, Redlands, CA).

Cortisol levels were natural log-transformed to improve normality of residuals. We removed CORT levels greater than three standard deviations above the mean from analysis as outliers. We assessed collinearity of covariates using a Pearson’s $R^2$ threshold of < 0.6 and Variance Inflation Factor (VIF) threshold < 2.0. If variables were found to be collinear, the covariate with the best explanatory power was selected and implemented in models going forward. We conducted statistical analyses in R v 3.4.1 with packages lme4 and MuMIn (the R Foundation, https://www.r-project.org/).

**Results**

**Sample Composition**. Of the 214 hair samples received, 25 were less than 15 mg in total weight and were not assayed, leaving 189 usable samples. Forty-nine percent of samples came from cougars in Western Montana, 37% from Eastern Washington, and 14% from Northern California (See Figure 2.2). Sex distribution of samples was 47.1% female and 52.9% male, with two individuals of unidentified sex. Adult animals (>2 years) provided the majority of the samples (58.7%), followed by 24.9% subadults (between 1 and 2 years) and 5.3% kittens (<1 year). Age class data was not recorded for 21 individuals. Most samples (67.2%) came from cougars harvested during the general season in Montana and Washington. Thirty-eight samples (20.1%) came from "problem" cougars removed by landowners or state agencies for livestock depredation and/or public safety. Most cougars associated with a depredation or public safety event were male (65.8%). Sixteen samples (8.5%) were collected from tranquilized animals by teams of researchers as part of ongoing cougar collaring studies in Siskiyou County, CA and Ravalli County, MT. Seven samples (3.7%)

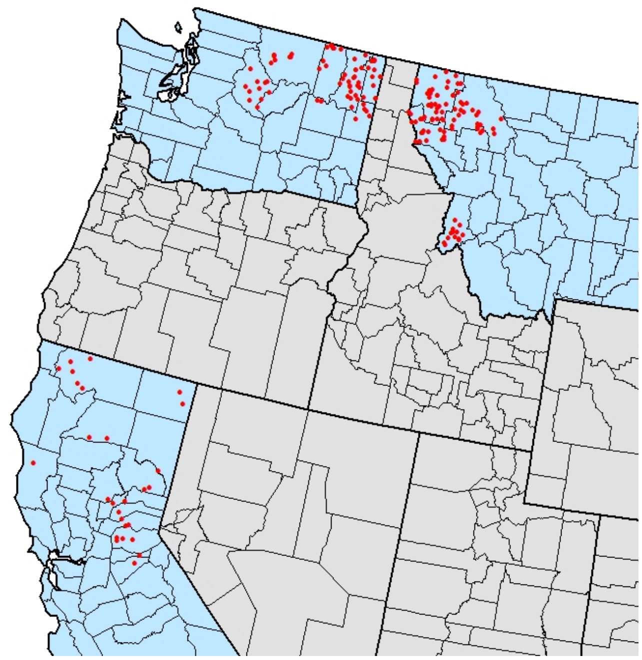

Figure 2.2. A map displaying sample locations. Red points indicate GPS coordinates or closest known location of sampling.

came from animals found dead (due to road accidents, intraspecific conflict, or poaching) and one sample was collected from a cougar with an injured foot that was euthanized by the state.

**Cortisol Assay Validation**. We analyzed a pooled sample of cougar hair extract using HPLC and collected fractions corresponding to each major peak in the resulting chromatogram. We found that fraction 3, which eluted 1.8 minutes into separation, produced the strongest cortisol signal following EIA (See Fig. 2.3). Fraction 3 had the same retention time as the known cortisol standard, providing strong evidence that the EIA cortisol antibody was indeed reacting to cortisol extracted from the hair sample rather than cross-reacting with another steroid hormone.

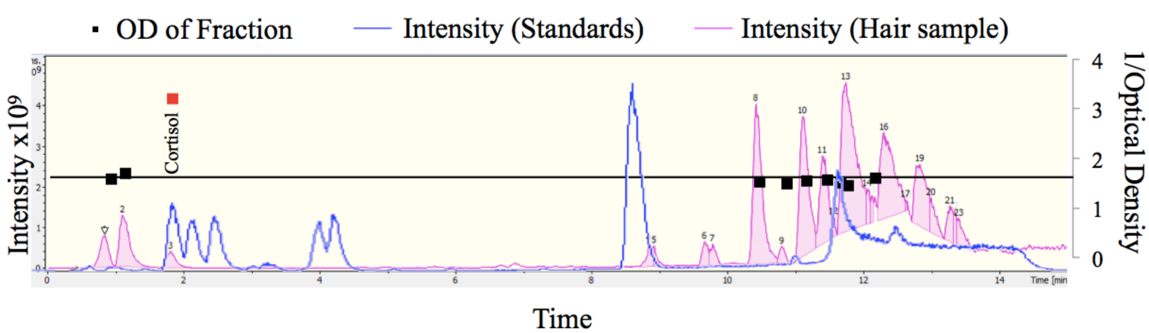


Figure 2.3. Chromatograms of known steroid hormone samples (blue) and compounds in a pooled cougar hair sample (pink). Square points represent the inverse of the optical density of each fraction as measured by spectrophotometry, with the red square representing the fraction that bound most strongly to the cortisol antibody in EIA. The horizontal line represents the spectrophotometer's limit of cortisol detectability; points below the line represent fractions containing a less than detectable amount of cortisol.

We assessed parallelism by serially diluting a pooled cougar hair extract (n=2) and a cortisol standard and comparing the resulting optical densities at each relative concentration (Figure 2.4). The sample curve closely mirrored that of the cortisol standard, demonstrating acceptable parallelism ($r^2$ = .99), and providing strong support that further measurements using this method would not be biased by dilution.

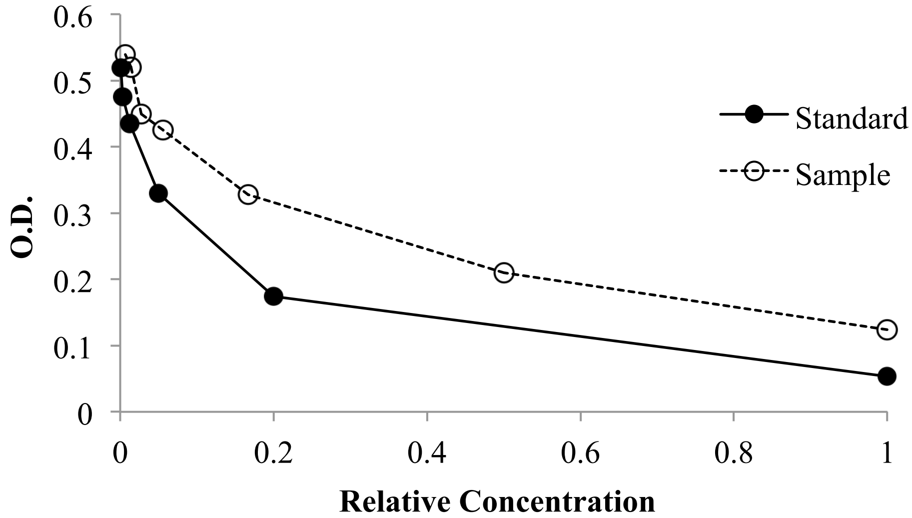


Figure 2.4. Parallelism of a serially diluted hair sample compared to a cortisol standard. Optical density, a measure of cortisol concentration, is plotted against relative concentration of the sample and standard.

**Exploratory Data Analysis.** Mean cortisol levels for all individuals was 236.71 ± 269.99 pg/mg. Four outliers with cortisol levels greater than three standard deviations above the mean (i.e. >2143.95 pg/mg) were removed from analysis. Although body condition for most individuals was not known, two of the four individuals removed as outliers were specially noted by field technicians to be "emaciated," while the other two samples had been contaminated with blood in the sampling process. Cortisol concentration in this population was right-skewed and was natural log transformed in models to improve normality of residuals.

***Intrinsic Factors.*** Hair color and sample source (harvest, depredation, capture, or found dead) appeared to have no influence on cortisol content ($p=0.764$ and $p = 0.242$) and was thus excluded as a factor in further analysis. Hair from female cougars had slightly higher cortisol content (259.87 ± 263.37 pg/mg) than hair from male cougars (212.85 ± 275.62 pg/mg; $p < .05$). Kittens in the sample demonstrated higher mean cortisol content (579.33 ± 643.88 pg/mg) compared to subadults (245.99 ± 294.56 pg/mg) and adults (209.12 ± 192.05 pg/mg; $p < .05$). See Figure 2.5 for graphical displays of the data.

***Environmental Factors***. We assessed relationships between hair cortisol and a number of environmental/meteorological variables, including average temperature (degree Celsius/year), standard deviation of average temperature, mean precipitation (mm/day), total precipitation (mm/year), and mean net primary productivity (kg carbon/year). These environmental covariates were all highly collinear and all but standard deviation of temperature demonstrated inverse relationships with hair cortisol, so we selected mean precipitation (MeanPrecip) as a representative variable based on strength of correlation with the dependent variable ($r^2 = -.30$). In the variable "Season", spring and summer were collapsed into a single level (spring/summer) due to insufficient data from spring alone. We found that cougar hair cortisol content was higher in samples collected during winter (273.95 ± 269.27 pg/mg) compared to fall (186.01 ± 249.62 pg/mg) and spring/summer (199.54 ± 318.83 pg/mg; $p < .01$). See Figure 2.6 for graphical displays of the data.

***Anthropogenic Factors***. We found no evidence of a relationship between hair cortisol content and cattle density on the landscape ($p = .32$). Nor did we see any difference in hair cortisol between harvested, depredated, captured, and found dead cougars ($p = .242$). We did identify weak relationships between cortisol and human population density (PopDensity) as well as number of sheep and goats (SheepGoats) in the county ($r^2 = -.26$ and $-.22$ respectively). Ultimately, the inclusion of SheepGoats did not improve explanatory power of models (possibly due to collinearity with PopDensity), so it was not selected for further analysis. "Hunted" cougars in Montana and Washington had higher hair cortisol (256.33 ± 284.21 pg/mg) than did non-hunted cougars in California (115.70 ± 89.02 pg/mg). See Figure 2.7 for graphical displays of the data.

**Model Selection**. Seven candidate linear mixed effects models were developed based on our initial hypotheses and compared using an AIC selection framework (Table 2.1). We then computed model-averaged estimates, back-transformed estimates, and confidence intervals for each proposed effect (Table 2.2).

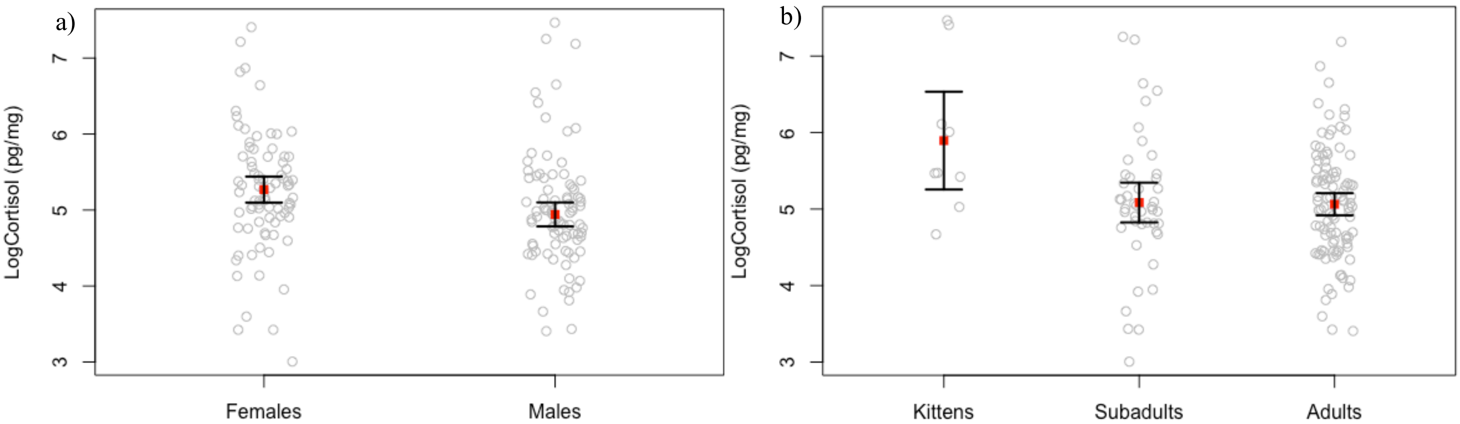


Figure 2.5. Charts demonstrating differences in hair cortisol concentration by a) sex and b) age class. Light grey circles represent actual data points, red squares are the mean for each factor, and error bars represent a 95% confidence interval for the mean. Kittens are defined as individuals <1 year old, while subadults are between 1-2 years and adults are >2 years old.

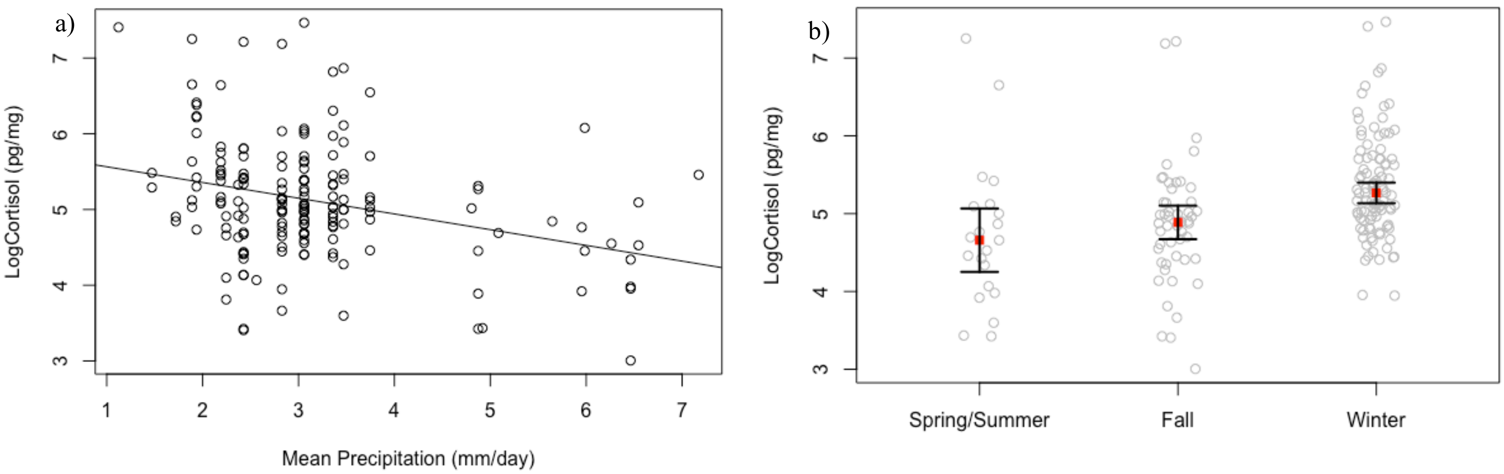


Figure 2.6. Charts demonstrating a) the relationship between hair cortisol and mean precipitation and b) differences in mean cortisol by season. Unfilled circles represent actual data points, red squares are the mean for each factor, and error bars represent a 95% confidence interval for the mean. The trendline ($r^2 = -0.30$) represents the univariate linear relationship between hair cortisol and precipitation.

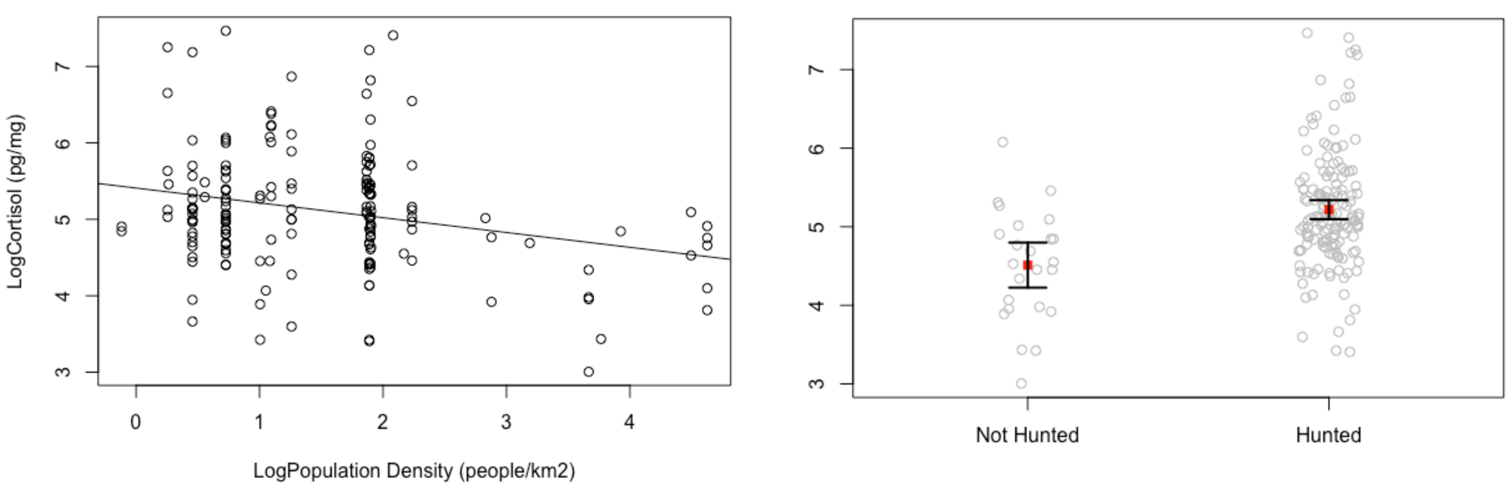


Figure 2.7. Charts demonstrating a) the relationship between hair cortisol and population density and b) differences in mean cortisol in states with and without hunting. Unfilled circles represent actual data points, red squares are the mean for each factor, and error bars represent a 95% confidence interval for the mean. The trendline ($r^2 = -0.26$) represents the univariate linear relationship between hair cortisol and precipitation.

| Hypothesis | Fixed Effects in Top Model | AICc | ΔAICc | $w_i$ |
|---|---|---|---|---|
| **Model 7: Intrinsic/Environmental/Anthropogenic** | **AgeClass + Season + Hunted + PopDensity** | **341.6** | **0.0** | **.625** |
| **Model 4: Intrinsic/Environmental** | **AgeClass + Season + MeanPrecip** | **343.2** | **1.62** | **.903** |
| Model 6: Intrinsic/Anthropogenic | Sex + AgeClass + Hunted + PopDensity | 345.3 | 3.73 | 1.00 |
| Model 1: Intrinsic | Sex + AgeClass | 356.9 | 15.3 | |
| Model 5: Environmental/Anthropogenic | Season + MeanPrecip + PopDensity | 373.8 | 32.2 | |
| Model 2: Environmental | Season + MeanPrecip | 376.2 | 34.6 | |
| Model 3: Anthropogenic | Hunted + PopDensity | 387.4 | 45.8 | |

Table 2.1. Candidate linear mixed-effects models for intrinsic, anthropogenic, and environmental effects on cougar hair cortisol (natural log transformed). All models contained County as a random intercept. Models with ΔAICc < 2 are in bold. $W_i$ refers to cumulative Aikake weights, or the cumulative probability that the models are the best fit of the available data. Clarification of fixed effects names provided in Methods section.

| Model Parameter | | Model-averaged Estimate | Back-transformed Estimate | 95%CI |
|---|---|---|---|---|
| AgeClass | Adult | -0.63 | 0.53 | (0.33, 0.87) |
| | Subadult | -0.55 | 0.58 | (0.34, 0.97) |
| Season | Spring/Summer | -0.38 | 0.68 | (0.46, 1.01) |
| | Fall | -0.68 | 0.51 | (0.50, 0.87) |
| logPopDensity | | -0.15 | 0.86 | (0.75, 0.97) |
| Hunted | | 0.43 | 1.54 | (1.06, 2.24) |
| MeanPrecip | | -0.16 | 0.85 | (0.77, 0.94) |

Table 2.2. Model-averaged parameter estimates and 95% confidence intervals for top models with ΔAICc < 2. Back-transformation was conducted by raising $e$ to the power of each estimate. Back-transformed estimates <1.0 indicate a negative effect while values >1.0 indicate a positive effect on hair cortisol content. A back-transformed estimate of 1.0 indicates no effect. For AgeClass, "kitten" was held constant, while for Season, "winter" was held constant. A confidence interval overlapping 1 indicates a non-significant effect.

## Discussion

Measuring stress-related cortisol in wild carnivore hair is a promising new application for conservation physiology, but validation of the method has been lacking. Here, we used HPLC to demonstrate that cortisol was present in measurable amounts in cougar hair and bound specifically to the cortisol antibody in our kit. This form of validation is not commonly employed in the hair cortisol literature, but we recommend that future studies, especially those involving hair from previously untested species or antibodies, employ an analytical chemistry approach to identifying and separating compounds in hair before interpreting results.

Mean hair cortisol content in cougars was higher than reported for other carnivores (Bryan et al., 2015; Bourbonnais et al., 2013). Although cougar hair cortisol has never been measured, and thus cannot be directly compared to other studies, Harlow et al. (1992) found that plasma cortisol was also elevated in cougars compared to other vertebrates, and proposed that high cortisol levels in felids may be an adaptation to reliance on protein catabolism.

The best supported model explaining variation in cortisol corresponded to the global model (Model 7), suggesting that intrinsic, environmental, and anthropogenic factors all contribute to the cougar stress response. While female cougars had slightly higher hair cortisol content than males, this effect was ultimately not supported in our top models. In some wildlife, cortisol levels are sexually dimorphic, and can be particularly high in lactating females or dominant males of social species (Koren et al., 2008; Maestripieri et al., 2008). However, several studies in carnivores have found no difference in hair cortisol content between sexes (Macbeth, 2010; Terwissen et al., 2013).

Considering that harvest of females with dependent young is illegal in both Montana and Washington, we assume that most of our samples came from non-lactating animals. Males demonstrated more variation in cortisol than females, and the four samples with most cortisol that were excluded from analysis as outliers all came from male cougars. When these outliers were included, mean cortisol levels became higher in males than females. Bourbonnais et al. (2013) found that stressors were not evenly distributed throughout the landscape and that males and female grizzly bears tended to encounter them at different rates. Male cougars tend to have larger home ranges than females and may therefore experience more variation in stressors in the landscape as well as more intraspecific conflict (Grigione et al., 2002).

Age class was one of the strongest predictors in the two top models, with kitten hair containing higher cortisol content than hair from subadults and adults. Mammalian young normally demonstrate a hyporesponsive HPA axis, so this finding was contrary to expectations (Wada, 2008). Of our 10 kitten samples, 60% came from harvested individuals, 30% from depredation removals, and one was found dead from "presumed intraspecific conflict". Montana and Washington state wildlife agencies prohibit the harvest of spotted kittens, so our sample was likely skewed toward older kittens close to 1 year of age, when markings are no longer visible (Sunquist & Sunquist, 2002). Upon reaching 12-18 months of age, juveniles are abandoned by their mother and must disperse from their natal range, entering a period of immense challenges that only 20-30% survive (Beier, 1995; Sweanor et al., 2000; Lambert et al., 2006). Elevated systemic cortisol in these individuals may help them cope with environmental perturbations associated with the onset of independence in late kittenhood.

Cougar hair clipped in winter had significantly higher cortisol content than hair clipped in fall. Though hair removed in the spring and summer also had lower mean cortisol than winter hair, the effect was not significant, possibly due to smaller sample size (CI = 0.46 - 1.01, n=21). Cougars in northern latitudes grow a dense winter coat that is shed in late spring, so cortisol in winter hair should be mostly incorporated during the late fall/early winter period (Currier, 1983). Seasonal prey availability can influence cortisol levels, and Knopff et al. (2010) found that cougar kill rates were higher in the summer, during the peak of ungulate births. However, other studies have found no seasonal difference in cougar kill rates, instead hypothesizing that increased availability of adult prey in poor health and at lower elevations may compensate for lack of neonatal prey during the winter (Cooley et al., 2008; Elbroch et al., 2013). Photoperiod alone is known to influence glucocorticoid levels in laboratory settings, suggesting the presence of endogenous circannual rhythms independent of environmental events, and increased metabolic expenditure during cold weather could also account for higher cortisol content in cougar hair (Dalmau et al., 2000; Romero et al., 2007). Wild ungulates often show a peak in cortisol production during winter months, but this is thought to be a response to caloric restriction rather than temperature or inclement weather (Huber et al., 2003).

Accounting for a few weeks of lag time as the hair grows in, the winter cortisol spike also corresponds to the duration of big game hunting seasons in all three states. A Florida study found that cougars avoided roads and heavily visited areas during fall/winter deer hunting season, demonstrating that cougars perceived hunters as a threat regardless of whether the cougars themselves were a direct target (Janis & Clark, 2002). Increased human activity associated with hunting, like snowmobiles and vehicular traffic, has been linked to elevated fecal cortisol in elk (*Cervus elaphus*) and wolves (Millspaugh et al., 2001; Creel et al., 2002). Cougar hunting season also occurs during this period of higher cortisol, but is unlikely to be the sole cause of the seasonal spike as this pattern was observed in California, where cougar hunting is prohibited, as well as in Montana and Washington.

Mean daily precipitation was a significant factor in the model with the second-best AIC and in our averaged model, signifying that a 1% increase in mean daily precipitation (mm) resulted in a 14.8% decrease in cortisol levels. Precipitation is correlated with net primary productivity (NPP), a direct measure of the rate at which an ecosystem stores carbon as plant biomass and a proxy measure of food web complexity (Clark et al., 2001). We might tentatively conclude that counties with higher mean precipitation provide more forage for primary consumers, allowing the ecosystem to support more prey and reducing stress from food limitation in apex predators. NPP is a coarse metric of biodiversity that subsumes many ecological variables, but Herfindal et al. (2005) did find an inverse relationship between NPP and home range size in Eurasian lynx (*Lynx lynx*), demonstrating that apex predators can respond behaviorally to bottom-up trophic level changes. Precipitation is also related to snow depth, and there is a well-documented relationship between snow accumulation and predation success in wolves (Nelson & Mech, 1986) and lynx (Murray, 1991). However, it is not clear whether snow depth affects kill rates for cougars, who stalk rather than chase their prey (as wolves do) and are not specially adapted for snowy environs (as lynx are).

We also found a significant inverse relationship between human population density and cougar hair cortisol content, indicating that a 1% increase in human density (people/km$^2$) resulted in a .15% decrease in cortisol levels. Several explanations for this relationship present themselves. First, it is possible that cougars inhabiting areas of dense human settlement are chronically stressed and have developed adrenal insensitivity/exhaustion, a condition paradoxically marked by lower baseline and stress-induced cortisol levels (Fink, 2009). Adrenal exhaustion is the final stage of chronic stress and is associated with extreme neuroendocrine dysfunction, disease, and poor body condition (Boonstra et al., 1998). Cougars are known to spatially and temporally avoid human activity on a fine scale, suggesting that they certainly perceive people as a perturbation factor in their environment (Sweanor and Logan, 2010; Morrison et al., 2014). However, chronic stress resulting in observable pathology is thought to occur rarely in nature and then only in response to intense predation pressure or severe food limitation (Boonstra, 2012). For context, cougars demonstrated a suppressed response to an adrenal challenge after being chased with hounds, treed, and anaesthetized five times over the course of a 2-month period, a highly manipulated situation that they would not regularly experience in nature (Harlow et al., 1992). We are skeptical that cougars in our sample are chronically stressed, especially considering that 11 out of 12 Californian cougars in counties with relatively high human density (15-90 people/km$^2$) were found to be in "ideal" body condition (unpublished data).

Secondly, it could be that there is an inverse association between cougar density and human density, resulting in lower cortisol levels due to less intraspecific conflict among those cougars that do inhabit populous regions. Unfortunately, cougar abundance data was not available for the broad spatial scale we examined, so we were unable to directly test this hypothesis. We do know from a study by Riley and Malecki (2001) that, provided prey and habitat requirements are met, human density has no effect on cougar abundance in Montana. In more populous regions, such as Southern California, cougar density is actually higher than expected as highways and human development block subadult dispersal from source habitat (Riley et al., 2014). However, this population is considered to be a unique example of cougars persisting within the bounds of a metropolis, and is accordingly subject to high levels of discord and inbreeding. A much more typical example can be found in Eastern Washington, where there is a decreasing gradient of cougar use as housing densities increase and a distinct threshold of housing densities beyond which cougars will not penetrate (Maletzke et al., 2017). Moshkin et al. (2001) propose that solitary, territorial species (such as cougars) should theoretically demonstrate higher HPA reactivity to social conflict compared to colonial species, but more empirical study is needed to understand the role of glucocorticoids in intraspecific strife in solitary species.

Another potential rationale for declining cortisol levels at higher human densities is that cougars inhabiting urbanized counties are habituated to human activities and have downregulated their HPA pathways as a response to frequent disturbance. This finding is not unprecedented – Walker et al. (2005) found that Magellanic penguins (*Spheniscus magellanicus*) habituated quickly to human presence, and that penguins exposed to heavy tourist pressure demonstrated a decreased glucocorticoid response compared to individuals from a pristine site. Romero et al. (2007) found that tourist exposure had a similar effect on the stress response of Galápagos marine iguanas, suggesting that the process of habituation occurs across taxa. Both studies were quick to point out that a depressed stress response is not necessarily beneficial, and may in fact reduce the animal's ability to cope with other deleterious environmental stressors when they occur.

Habituation involves a declining response to negative stimuli over time, and as we only have a single data point for each individual we cannot say for certain that habituation has occurred (Bejder, 2009). Another possibility is that cougars living in more populous areas are a self-selecting group of "bolder" individuals with an innately lower stress response. Avian studies have found that not only do urban-dwelling songbirds show a lower physiological and behavioral response to human disturbance than their sylvan counterparts, but that this difference may also be due in part to an "immigrant effect" in which a combination of selection and drift favored bolder phenotypes over time (Partecke et al., 2006; Atwell et al., 2012). Burdett et al. (2010) showed that while most cougars avoided exurban development in a natural area around San Diego, a few individuals appeared to actively prefer exurban habitat, selecting it more often than predicted. While there are definite benefits to sharing the landscape with humans (including the presence of alternative prey sources and less competition), there are also risks that could deter all but the boldest, least reactive individuals. In Burdett et al.'s study, cougars that selected exurban habitat had higher mortality from road accidents and human depredation than did individuals that avoided these areas, demonstrating that boldness may not be an adaptive trait in all environments. The boldness hypothesis does not preclude the habituation hypothesis, and in most scenarios some combination of both is likely to occur.

Finally, we found that even after controlling for climate and human population differences, cougars in California had significantly lower hair cortisol content than cougars in Montana and Washington. This difference was hypothesized to be due to the prohibition of cougar hunting in the state of California since 1990. Studies in wolves (Bryan et al., 2015), spider monkeys (*Ateles hybridus*; Rimbach et al., 2013), and mourning doves (*Zenaida macroura*; Roy & Woolf, 2001) have demonstrated that glucocorticoid levels can be elevated in more heavily hunted wildlife populations. Considering that Harlow et al. (1992) found markers of chronic stress among cougars pursued by dogs, we expected cougars in Washington, where hound hunting is banned, to demonstrate lower hair cortisol than cougars in Montana. However, initial exploratory data analysis suggested that mean cortisol levels were similar regardless of whether hound hunting was allowed. Bryan et al. (2015) hypothesized that hunting-induced stress in Canadian wolves came not only from intensity and type of harvest but also from social disruption following removal of dominant individuals by harvest. Cougars are solitary animals, but Elbroch (2017) described a network of cougar interactions in the Grand Tetons that included cooperative feeding between unrelated individuals and frequent communication via calls and scrapes that reinforce territorial boundaries. Hunting changes the age structure of cougar populations by selectively removing older males and has been shown to create social disorder as surviving individuals struggle over sudden territorial voids (Robinson et al., 2008; Maletzke et al., 2014). This spatial instability would be expected to occur regardless of whether dogs were used and could be a driving factor behind increased hair cortisol in Montana/Washington.

Other rationales for the effect of state on hair cortisol content present themselves. Genetic drift alone could explain why cougars in California have lower integrated cortisol levels than geographically distant populations in the inland Northwest. Alternatively, grey wolves are only just beginning to colonize northern California, while packs have been present for a decade or more in Eastern Washington and Montana. Intraguild conflict could be a source of stress for cougars, although little is known about how wolves and cougars interact and compete. Most research along these lines has been conducted in national parks, where apex predator diversity is highest. A study in Banff, Canada found evidence of prey switching, spatial avoidance, and interference competition between cougars and wolves after the latter recolonized the park (Kortello et al., 2007). However, a similar study in Yellowstone National Park found that wolf presence was not an important predictor of cougar survival compared to intrinsic and topographic factors, as well as anthropogenic mortality due to hunting (Ruth et al., 2011). An independent-samples t-test demonstrated no significant difference in cougar hair cortisol levels between Washington counties with resident wolf packs and counties without known wolves (data from WDFW). However, more fine-scale wolf density data was not available for MT and WA, making it difficult to ascertain whether intraguild competition could be a factor in state cortisol differences.

**Management Implications.** In this study, we determined that the cougar stress response is affected by a number of intrinsic, environmental, and anthropogenic factors that may be relevant to wildlife managers, both in states with extant cougar populations and in states expecting cougar recolonization in the near future. We developed and validated a method for measuring cortisol in cougar hair that could be used to measure the physiological effect of future management actions, such as altering cougar hunting regulations. Managers should be aware that cougar hunting with or without dogs can create social instability that may be reflected in long-term cortisol levels. We found that living in regions of high human density (i.e. wildland-urban interface) was not in itself a source of physiological stress for cougars, but was in fact associated with a small decrease in hair cortisol. The finding that cougars living in urbanized counties demonstrate lower hair cortisol content does not necessarily imply increased conflict potential, as cortisol levels were not associated with involvement in depredation or public safety removals in our sample. The ability to modulate HPA reactivity in response to human development supports the hypothesis that cougars will be able to adapt to more populous regions east of the Mississippi river as they continue to disperse into their historic range (LaRue et al., 2012). However, reducing the stress response in urbanized environments could prove deleterious if cougar mortality remains high due to human conflict. Whether the cougar's adaptability will be its downfall will ultimately depend on human tolerance of its presence in the wildland-urban interface.

**Limitations and Future Directions.** A limitation of this study, and of many like it, is that it is difficult to ascertain the behavioral and pathological implications of varied cortisol production in free-living vertebrates. We found that cougars involved in a depredation or public safety event did not differ in cortisol content from harvested, captured, or found dead cougars, so it remains unclear whether hair cortisol can be predictive of conflict-prone behaviors. Body condition was known for only a handful of individuals and did not vary enough for us to develop any relationship between cortisol and health. Therefore, while we found that cougars do respond physiologically to anthropogenic factors like hunting and human density, it is difficult to predict how and when these changes will manifest in the population. In the interest of obtaining a large sample from a broad geographic region, we chose to obtain hair opportunistically from ongoing collection efforts rather than randomly sample individuals in the region, so the data here is likely not representative of the general population.

The goal of this study was to identify hormones in cougar hair, conduct a large-scale survey of cougar cortisol levels across the Western US, and identify variables of interest for further investigation. Future studies should aim to conduct longitudinal research on GPS collared cougars subject to differing levels of hunting pressure and anthropogenic disturbance to obtain more granular and representative data about their environment, health, and behavior that can be linked to variation in hair cortisol content.

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## Chapter 3: Operationalizing Human Tolerance of Wildlife

### Background

**Tolerance and the Cognitive Hierarchy.** Tolerance is considered the foundation of human-wildlife coexistence (Lotz et al., 2017; Frank, 2015). Wildlife researchers and managers are especially interested in policies and outreach that could improve tolerance of large carnivores like cougars (*Puma concolor*), a species that provides important ecosystem benefits but has had a fraught relationship with people. Because of the perceived importance of tolerance, there is a demand for research that provides meaningful data concerning the limits of public tolerance of wildlife. In the Human Dimensions of Wildlife (HDW) literature, tolerance is widely employed as a holistic psychological measure that encompasses a broad range of feelings and behaviors toward wildlife (Treves & Bruskotter, 2014). However, the literature has long suffered from definitional ambiguity and unexamined assumptions, and the relationship between tolerance and other more well-defined socio-psychological constructs remains unclear (Bruskotter et al., 2015). In this study, we will develop an integrated metric of tolerance that clarifies extant definitions, then test the validity of this framework on data collected from a survey of human attitudes, beliefs, and behavioral intentions toward cougars in the Western US.

In the current HDW literature, tolerance studies seldom clearly define the concept at hand, instead relying on an unspoken or intuitive understanding that in reality differs depending on the study. When tolerance *was* explicitly defined, definitions provided were either vague enough to encompass a broad range of concepts or bore only a passing resemblance to other definitions found in the literature. Tolerance was alternately considered to be “passive acceptance of a wildlife population” (Bruskotter & Fulton, 2012); “individual-level judgments… (such as attitudes and perceptions), as well as individual behaviors” (Treves and Bruskotter, 2014); “beliefs, emotions, attitudes, and inclinations to act” (Treves et al., 2013) and “an ability to accept damage from wildlife” (Kansky et al., 2014). Outside of HDW, tolerance has been more consistently operationalized; in animal behavior disciplines, tolerance is a clear threshold defined as “the intensity of disturbance that an individual accepts without responding in a defined way” (Nisbet, 2000), while in sociology, tolerance is simply “putting up with something you do not like” (Vogt, 1997).

Definitional uncertainty around the term tolerance in HDW has led to the development of multiple different metrics used to assess what is purportedly the same concept (Bruskotter et al., 2012). Below is a brief review and comparison of the various constructs that have been used thus far to measure human tolerance of wildlife in HDW, followed by a distillation of the major points of contention and agreement among researchers.

***Tolerance as an attitude.*** In a wildlife context, attitudes are defined as cognitive or affective judgments about animals and their impacts (Fulton et al., 1996). Attitude statements can take on a variety of forms (including the desirability of maintaining the species on the landscape, whether the species is generally liked or disliked, perceptions of risk posed by the species, concerns about the future of the species, concerns about conflict, etc.), but must elicit either positive or negative views toward wildlife (Riley and Decker, 2000; Zimmerman et al., 2005). Attitudes toward wildlife have been linked to value orientations, demographic factors (age, sex, education level, and income), social group identity, normative and descriptive beliefs, experiences with wildlife, and behavioral intentions (Kellert & Berry, 1980; Koval & Mertig, 2004; Davenport et al. 2010; Slagle et al., 2017). Measuring tolerance as an attitude is useful not only because attitudes are the direct antecedents of behavioral intentions, but also because understanding salient attitudes can guide wildlife educators and policymakers toward specific areas of concern, such as disease transmission or livestock depredation (Azjen & Fishbein, 1975; Vaske & Needham, 2007).

As an attitude, tolerance has been variously operationalized as a tendency to report positive, neutral, or negative judgments of wildlife (Bruskotter et al., 2015; Lewis et al., 2012; Kansky et al., 2014). In a meta-study, Kansky et al. defined tolerance as "the proportion of individuals who have a *positive* attitude toward a species group despite suffering damage by that species group." Similarly, other HDW studies have conceived of tolerance as an attitudinal scale ranging from "very intolerant" (a negative attitude) to "very tolerant" (presumably a positive attitude) (Lewis et al., 2012). However, the traditional sociological definition of tolerance ("putting up with something you do not like") presupposes prejudice and *negative* attitudes. Finally, Bruskotter & Fulton (2012) characterized tolerance as a disposition toward inaction and passivity toward wildlife, a neutral point on a scale from active intolerance to active stewardship. Whether tolerance is constructed as an ideal end-state or merely an indifferent midpoint can fundamentally change the interpretation of the scale employed to measure the concept. As Bruskotter et al. (2015) point out, alternative conceptualizations of tolerance can also have very real impacts on conservation policy, as when uncertainty over the role of human intolerance in the recovery of the grey wolf (*Canis lupus*) contributed to protracted legal battles over its status as an protected species.

Given that attitudes are value-driven and difficult to change later in life, experts agree that a conservation campaign that improves the attitudes of even 5% of the intended audience can be considered a success (Manfredo et al., 1995). Therefore, measuring tolerance by examining attitudes can give the impression that tolerance is fairly fixed (Agarwala et al., 2010; Naughton-Treves et al., 2003). For example, Lewis et al. (2012) concluded that implementing a wolf hunting season had had no effect on tolerance of wolves, but conceded that the attitudes measured may be resistant to change.

Additionally, because attitude statements about wildlife can be fairly general (e.g. “Do you like or dislike mountain lions?”) and do not ask respondents to place themselves in a specific context with an animal, they demand little elaboration, or “thoughtful consideration of arguments central to the issue” (Petty & Cacioppo, 1986; Davenport et al., 2010; Gore et al., 2008; Morgan and Gramann, 1989). Rather than carefully evaluating each attitude statement, individuals may instead fall back on well-worn heuristics favored by their social group. For example, among hunters and ranchers, low-elaboration attitude statements can elicit overwhelmingly hostile perspective toward large carnivores (see Lewis et al., 2012, in which nearly 70% of deer hunters reported negative attitudes toward wolves). In contrast, among the general public, low elaboration often manifests as a surprisingly rosy picture of human attitudes toward charismatic predators (see Duda et al., 1998, in which over 85% of New Englanders reported positive attitudes toward wolves; see also George et al., 2014). Unspecific attitude statements may therefore obscure the complex and shifting relationships between humans and wildlife.

***Tolerance as a normative belief (acceptance/acceptability).*** Normative beliefs are value-driven social cognitions about the appropriateness or acceptability of an action, situation, or behavior (Zinn et al., 1998). Formal rules (policies, laws, regulations) and informal rules (social compacts, observed public behavior, expectations) all influence normative beliefs. Normative beliefs may differ substantially between social groups, as individuals rely on cues from others like them to determine the acceptability of an action or situation (Manfredo et al., 1995). Studies have linked normative beliefs about wildlife to individual value orientations, emotions, social group identity, attitudes, perceived risk, and behavioral intentions (Loker et al., 1999; Wald & Jacobson, 2013; Vaske et al., 2013; Zinn et al., 1998; Zinn et al., 2000). Preliminary evidence suggests that normative beliefs may be more pliable than attitudes, making them a potential target for future policy interventions (Rohan, 2000; Karlsson & Sjöström, 2011).

Wildlife acceptance capacity (WAC) is one of the most commonly used normative tolerance metrics. Wildlife acceptance capacity, or the "cultural carrying capacity" of a community, emerged from the observation that just as natural resources regulate the biological carrying capacity of an environment, societal expectations can regulate the distribution of wildlife on the landscape (Decker & Purdy, 1988; Organ and Ellingwood, 2000). Wildlife acceptance capacity as a tolerance metric usually manifests as a survey item asking respondents whether they believe a wildlife population should increase, decrease, or remain the same size (Riley & Decker, 2000; Slagle et al., 2013). Researchers have occasionally conceived of WAC as an attitude rather than a normative belief (Kansky et al., 2014; Karlsson & Sjöström, 2011). However, from a social-psychological perspective, Zinn et al. (2000) argue that the normative approach is a more fitting theoretical framework when WAC is intended to measure societal-level acceptability of wildlife populations.

Another normative tolerance metric examines human ability to tolerate hazardous wildlife behavior by measuring situation-specific beliefs about acceptability of management actions in response to different wildlife conflict scenarios that usually increase in severity (Decker et al., 2006; Zinn et al., 1998). The output from this measurement is known as a reaction norm, a visual representation that displays acceptability/tolerance thresholds for the human population in question (see Figure 3.1). Like WAC, reaction norms can predict controversy when stakeholders disagree about appropriateness of wildlife populations and their behaviors (Metcalf et al., 2015). Reaction norms also reveal public expectations under specific conditions, information that can be of additional use to wildlife managers when planning for wildlife conflict. It is important to note, however, that normative beliefs merely reveal appropriateness of a behavior, while attitudinal statements have the added benefit of eliciting the rationale and motivations behind behavioral intent.

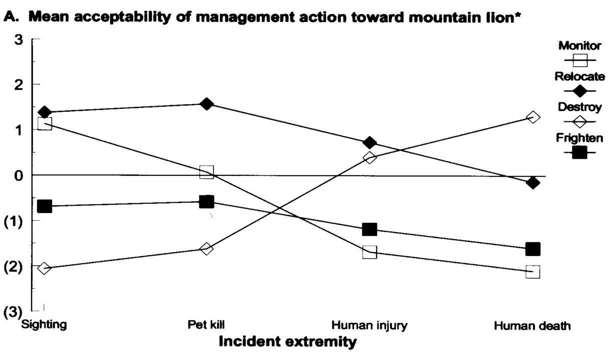

Figure 3.1. From Zinn et al. 1998

***Tolerance as behavioral intent.*** Unlike attitudes and beliefs, human behavior directly influences the success and persistence of wildlife populations. For this reason, some have considered tolerance mainly in the context of associated behaviors. In Bruskotter's (2012) conceptual model, tolerance and acceptance comprise the middle region in a behavioral spectrum that ranges from intolerance (engaging or planning to engage in anti-conservation behaviors) to stewardship (engaging or planning to engage in pro-conservation behaviors). Under this model, tolerance is defined by inaction, passivity, and/or restraint in interactions with wildlife (Figure 3.2). An important contribution of this model is the acknowledgement of a realm beyond mere tolerance ("stewardship") that represents actively positive interactions with and emotions toward wildlife.

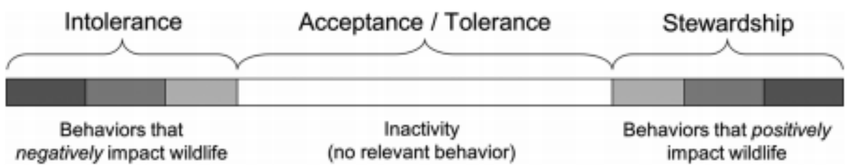


Figure 3.2. From Bruskotter & Fulton, 2012

Others have created latent tolerance metrics that combine attitude and belief statements with reported behavioral intentions. For example, one social survey asked hunters about their intentions to poach wolves as part of a multi-item tolerance scale that also included belief and attitude statements (Treves et al., 2013). Similarly, Morzillo and Needham (2015) measured tolerance holistically by asking landowners about both their intentions to conserve beavers (*Castor canadensis*) on their property and their normative beliefs about acceptability of beaver behavior. Conservation campaigns sometimes choose to target behaviors because intentions, unlike attitudes, are relatively malleable.

Because behavioral intentions are the highest-order cognitive construct, they are the most circumstance-specific and least universal element of the cognitive hierarchy (Fulton et al., 1996). Targeting a specific negative action or intent does not approach the lower-order cognitions (attitudes, beliefs, and values) that ultimately determine behaviors of interest. Identifying the normative and attitudinal antecedents of behaviors can be useful in drawing broader conclusions about a population while overcoming difficulties associated with measuring behavior (particularly illegal ones like poaching). The specificity of behavioral intent also presents a problem for those wishing to apply results across studies of different systems. Bruskotter et al. (2015) found that depending on the measured behavior, anywhere from 4% to 26% of a surveyed population could be coded as intolerant of wolves.

**Integrating the Constructs.** Broadly, the various HDW tolerance metrics discussed above fit under three higher-level cognitive constructs: attitudes, normative beliefs, and behavioral intentions (Table 3.1). Tolerance is sometimes conceived of as a latent psychological variable encompassing some or all of the cognitive constructs (see Treves et al., 2013), and Bruskotter et al. (2015) demonstrated that both normative beliefs and attitudes adequately predict behavioral intentions toward wolves ($r = >.70$), suggesting that either metric could be of practical use to wildlife managers. However, as detailed above, attitudes and acceptability measure different cognitions and cannot be substituted for one another, so the theoretical rationale for combining these constructs warrants further examination.

| Cognitive Construct | Specific Metric | Examples |
|---|---|---|
| Normative Beliefs | Wildlife Acceptance Capacity | Karlsson & Sjöström, 2011<br>Riley & Decker, 2000<br>Organ & Ellingwood, 2000<br>Wald & Jacobson, 2013 |
| | Acceptability of Management Actions | Morzillo & Needham, 2015<br>Decker, Jacobson, & Brown, 2006 |
| Attitudes | | Treves et al., 2013<br>Kansky, Kidd, & Knight, 2014<br>Lewis et al., 2012 |
| Behavioral Intentions | Stewardship Intentions | Morzillo & Needham, 2015 |
| | Intolerant Intentions | Treves et al., 2013<br>Naughton-Treves et al., 2003 |
| | Intolerant Intentions | Treves et al., 2013<br>Naughton-Treves et al., 2003 |

Table 3.1. Tolerance metrics commonly used in the human dimensions of wildlife literature.

Despite definitional uncertainty, is clear from the literature that tolerance is a psychological construct closely tied to elements of the cognitive hierarchy. Therefore, it may be possible to reconcile these definitions and methodologies into an overarching construct that captures the various aspects of tolerance intuitively understood in the HDW field. To incorporate the various scales used in prior studies while remaining relevant to wildlife management objectives, an appropriate tolerance metric should a) integrate attitudes and normative beliefs, b) predict behavioral intentions, and c) present clear management applications. Drawing from the sociological literature, I propose that tolerance be defined as **acceptance of wildlife and wildlife behaviors that one dislikes** **(**Vogt, 1997; van Doorn, 2014). This seemingly paradoxical definition incorporates two cognitive axes: attitudes toward an object or situation and acceptability of the same. Importantly, this definition of tolerance presupposes negative attitudes, creating a distinction between those who actively *enjoy* wildlife and those who merely *put up with* wildlife.

In theory, the truly tolerant accept some amount of unfavorable wildlife/wildlife conflict. Why would someone accept something they dislike? In 2007 study, urban residents indicated tolerating nuisance wildlife either due to overriding personal values ("I don't kill [possums] because they are God's creatures") or because of a perceived lack of personal efficacy to change their situation, obliging them to simply put up with it (van Velsor & Nilon, 2006). In effect, tolerance emerges when individuals are willing (or compelled) to accept disagreeable wildlife qualities for the sake of coexistence. Top-down regulations may influence tolerance by altering injunctive social norms in favor of accepting wildlife, although changing attitudes through regulations can be more difficult (Rohan, 2000; Ostrom, 1999). Tolerance is a fragile virtue that is particularly strained when peaceful coexistence requires a tradeoff with higher-ranking values, like security, self-efficacy, or stability (Sullivan, 1979; van Doorn, 2014; Peffley et al., 2001).

The two axes of tolerance (attitudes and normative beliefs about acceptability) are related, but ultimately measure different constructs. Therefore, we posit the existence of four distinct typologies defined by their position on the two axes: the "enthusiastic", the "pragmatic", the "intolerant", and the "tolerant" (See Table 3.2). This construction limits the bounds of tolerance to a single quadrant.

| Attitude | | |
|---|---|---|
| | Positive Attitude/Low Acceptability<br>(+ -)<br>“PRAGMATIC” | Positive Attitude/High Acceptability<br>(+ +)<br>“ENTHUSIASTIC” |
| | Negative Attitude/Low Acceptability<br>(- -)<br>“INTOLERANT” | Negative Attitude/High Acceptability<br>(- +)<br>“TOLERANT” |
| | **Acceptability** | |

Table 3.2 should be considered both situation and individual-specific. A survey respondent may tolerate cougars existing in the wilderness, but regress into intolerance when presented with a more intrusive situation, such as cougars living near human communities (Casey et al., 2005; Manfredo et al. 1998; Metcalf et al., 2015; Sponarski et al., 2015).

**Rationale/Research Questions**

We tested the applicability of this novel tolerance metric to a dataset collected from surveying members of three rural communities in the Western US. We aimed to address the following research questions:

1. What are the antecedents of attitudes, normative beliefs about acceptability, and behavioral intentions toward cougars in the Western US?
2. Can the four proposed typologies be identified among survey respondents?
3. If the data fit the proposed framework, what demographic variables and behavioral intentions are associated with each typology?

**Methods**

**Study Species.** The cougar is a large carnivore that was once persecuted to near extinction in the Western US, but has since made a significant recovery and is even returning to parts of its historic eastern range (LaRue et al., 2012). Unlike wolves, cougars in the Rocky Mountain West were not reintroduced but are "naturally" regaining ground, aided by careful conservation in many states over the last several decades. Nevertheless, cougar management has been a source of controversy, particularly surrounding the ethics and legality of hunting and trapping (see Chapter 4 for more direct discussion of cougar hunting policy in the West). Concurrent with the spread of both cougar populations and exurban development has been an increase in human-cougar conflict (Thompson, 2010). Although direct attacks on humans are still rare, cougars are known to prey on livestock and domestic pets in rural communities and along the wildland-urban interface (WUI). Cougars were chosen as the subject of this study because, as is the case with many large carnivores, value-laden conflicts over their management have generated a broad range of attitudes and beliefs about the degree to which society should tolerate their presence and behaviors.

**Study Sites.** The selected study sites (Red Bluff, CA, Ellensburg, WA, and Kalispell, MT; See Figure 3.3) are Western communities of below 20,000 people living in the WUI, with cougar populations inhabiting nearby protected areas. The three communities are predominately white (80-94%) and the majority of residents voted for the Republican presidential candidate in 2012. In Red Bluff, citizens are subject to California state law, which prohibits hunting cougars. Although residents of Ellensburg are permitted to hunt cougars in season, a 1996 ballot initiative in Washington banned the traditional method of using dogs to pursue and tree cougars. Finally, in Kalispell, cougar hunting with or without dogs is permitted and regulated during an

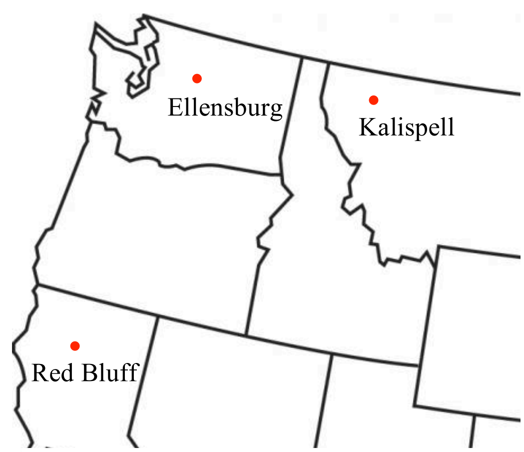

Figure 3.3: Map of Study Sites

annual season as per Montana state regulations. These three communities were selected for a) their proximity to cougar habitat and thus susceptibility to human-cougar conflict; b) their reasonably similar demographics; and c) varying cougar protection policies in place in each state, theoretically providing access to a wide swath of the tolerance spectrum.

**Survey Sampling.** We distributed a web-based social survey to members of the general public residing in Red Bluff, Ellensburg, and Kalispell (N=3137). We purchased an address list from Survey Sampling International (SSI), a social data company that used a combination of U.S. postal service delivery points and commercial databases to generate a simple random sample of households in the three communities. Address-based sampling promises 95% coverage of postal households and is now preferable to telephone surveys as many homes no longer have an associated landline (Dillman et al., 2014). Although we addressed letters and postcards to respondents by name whenever possible, the survey itself was designed to be anonymous.

Before distribution, the survey was pretested with an initial sample of 20 respondents representing the general public. Following feedback from the survey pretest, questions were rewritten for clarity and brevity, resulting in a final survey time of around 13 minutes in duration and between 23-31 questions in length, depending on responses. Because *Puma concolor* is known by many common names (e.g. cougar, mountain lion, puma) in the Western U.S., we included a neutral photo of a cougar at the opening of the survey to ensure that all respondents recognized the animal referred to in the survey items.

We employed a tailored-design method as developed by Dillman et al. (2014) to maximize survey response rates while operating under the constraints of the budget and the need for respondent anonymity. A brief cover letter explained the purpose of the research and provided instructions for accessing the online survey through a Qualtrics-embedded website. The letter was mailed to just over 1000 addresses per community and included a decorative sticker in each envelope as an incentive to complete the survey. The incentive was intended to activate social exchange theory, which posits that individuals are more likely to accept a cost to them (e.g. the effort of responding to a survey) when a rewarding relationship has been established (Dillman et al., 2014). At 10 and 20 days after mailing the cover letter, we distributed reminder postcards urging those who had not yet completed the survey to do so. Ultimately, 507 letters were returned as undeliverable, 547 surveys were attempted and 520 were completed (20.8% response rate, 95.1% completion rate). The number of completed surveys was large enough to ensure with 95% confidence that our estimates would be within 5 percentage points of the population parameters.

**Survey Instrument.**

***Attitudes.*** We measured attitudes with a series of Likert-type items presenting positive or negative judgments about cougars. Respondents selected a score from 1 (Strongly Disagree) to 7 (Strongly Agree) that most corresponded to their position on the statement. One question ("Indicate the extent to which you like or dislike cougars") was measured on a scale from 1 (Strongly Dislike) to 7 (Strongly Like). For more examples of attitude statements used in the survey, see Table 3.3.

***Normative beliefs about acceptability***. To measure normative beliefs, we presented survey respondents with three cougar conflict scenarios occurring in their community. The first scenario involved a cougar sighting, the second involved a cougar killing pets, and the third involved a cougar attacking a person. For each scenario, respondents were asked to rate the acceptability of different management actions (do nothing, frighten the cougar away, capture and relocate the cougar, shoot and kill the cougar) on a scale from 1 (highly unacceptable) to 5 (highly acceptable).

***Behavioral intention*.** Behavioral intentions were measured with two Likert-type items asking about intentions to vote for increased cougar protection or for increased cougar hunting opportunities. Respondents selected the score from 1 (Very Unlikely) to 7 (Very Likely) that corresponded to their likelihood to engage in the stated behavior.

***Demographic/Social Data and Beliefs*.** In order to link tolerance to individual traits, we included a series of optional items eliciting demographic data about respondents (educational level, total household income, age, gender, and the length of residence in their current state). We also asked respondents if they identified as a hunter, a livestock owner, or if they were currently a member of any conservation organizations. To gauge history of prior experience with cougars, we asked respondents whether they had ever seen a cougar or signs of a cougar either in the wilderness or near their community, and if so, approximately how often. We included a statement assessing respondents' risk perception of cougars (measured from 1 (Strongly Disagree) to 7 (Strongly Agree)), as a previous study by Riley and Decker (2000) showed that risk perception moderated the effect of attitudes on acceptability of cougars in Montana. Finally, we asked respondents whether they believed the number of cougars in their area was increasing, measured on the same 1 through 7 Likert-type scale. For the survey instrument, please see the Appendix.

**Statistical Analysis.** We used ordinary least squares regression to test for effects of covariates of interest on three dependent variables: attitudes, acceptability, and behavioral intention. We evaluated significance at the 95% confidence level, and variables with p-values $<.05$ were considered statistically significant. We assessed normality using histograms and normal probability plots. To address multicollinearity of the independent variables, we removed variables with a Variance Inflation Factor $> 2$ (Vaske, 2008). For other dichotomous comparisons, we used independent sample t-tests, assuming equal variances if the p-value from Levene's Test was $>.05$. All data was analyzed using IBM's Statistical Package for the Social Sciences v. 23 (IBM, Armonk, NY).

## Results

**Demographic Data.** Fifty-nine percent of respondents were male, and the average age of respondents was 54. Just over half of respondents had received a bachelor's degree or higher, and the median household income was $60-80,000 USD per year. Respondents were generally long-time state residents; 78% had lived in their current state for over 20 years. Respondents typically reported at least some previous experience with cougars - a substantial majority (88%) reported having seen either cougars or cougar signs (tracks, scat, etc.) in the past, 55.4% said they had seen signs of a cougar in their community, and 31% of respondents reported having previously seen an actual cougar in their community.

Thirty-nine percent of respondents self-identified as hunters, but of those hunters only 19% had purchased a cougar tag in any state. Of those hunters who had purchased a cougar tag in their lifetime, 28% had gone cougar hunting in the past year (n=9) and 15% had ever used dogs to hunt cougars (n=6). Livestock owners made up 23% of the respondents, and among livestock owners 28% reported that their livestock had been threatened or attacked by cougars at least once in the past. Twenty-one percent of respondents reportedly belonged to conservation groups. Among these members, group type was equally split between hunting-oriented groups (e.g. Ducks Unlimited, Rocky Mountain Elk Foundation, National Rifle Association) and non-hunting-oriented groups (e.g. Audubon Society, World Wildlife Fund, Sierra Club)

**Attitudes.** Respondents agreed the most strongly that “cougars were an important part of the ecosystem” ($\bar{x} = 6.03$) and disagreed the most strongly that “cougars should be treated as a nuisance animal” ($\bar{x} = 3.02$). Most respondents indicated liking cougars ($\bar{x} = 5.51$). “It is unethical to kill a cougar” was one of the most controversial statements, with a middling average ($\bar{x} = 4.04$) but a high standard deviation (SD = 2.02). In general, attitudes toward cougars skewed positive among the sample population. Based on the high Cronbach’s alpha reliability score ($\alpha = .87$), we combined the attitudinal items into a single variate (“Attitudes”) by reverse-coding negative statements and taking the average of the total scores on each item. The resulting scale ranged from 1 (highly negative attitudes, indicated by a score of 1 on each item) to 7 (highly positive attitudes, indicated by a score of 7 on each item) and skewed slightly high with a mean score of 4.77. See Table 3.3 for full attitude statements.

| Attitude Statements | Reliability (Cronbach's α) | $\bar{x} \pm SD$ |
|---|---|---|
| Cougars have the right to exist wherever they are found | .87 | 4.65 ± 1.87 |
| It is unethical to kill a cougar | | 4.04 ± 2.02 |
| Humans should manage cougar populations so that humans benefit | | 3.73 ± 1.70 |
| The needs of people are always more important than any rights that cougars might have | | 3.67 ± 1.80 |
| Cougars should be treated as a nuisance animal in my area | | 3.02 ± 1.73 |
| Cougars are an important part of the ecosystem | | 6.03 ± 1.11 |
| I take pride in the amount of cougars in my area, even if they cause some problems | | 4.40 ± 1.66 |
| Indicate the extent to which you like or dislike cougars | | 5.51 ± 1.36 |

Table 3.3. Respondents were asked to rate their agreement with each attitude statement on a scale from 1 (Strongly Disagree) to 7 (Strongly Agree). The final question was rated on a scale from 1 (Strongly Dislike) to 7 (Strongly Like).

After combining the attitudinal items into a single scale, we used ordinary least squares regression to identify the most important predictors of attitudes in the sample (See Table 3.4).

**OLS Regression of Demographic Variables on Attitudes toward Cougars**

| Variable | Standardized β | Std. Error | Sig. |
|---|---|---|---|
| (Constant) | 6.365 | .472 | .000 |
| Education | .148 | .030 | .000 |
| Income | -.070 | .027 | .088 |
| Gender | .085 | .100 | .042 |
| Age | -.012 | .003 | .761 |
| Hunting Participation | -.170 | .111 | .000 |
| Livestock Ownership | .007 | .120 | .875 |
| Conservation Group Membership | -.060 | .119 | .137 |
| Cougar Experience | .013 | .010 | .770 |
| Risk Perception | -.323 | .028 | .000 |
| Population Perception | -.283 | .036 | .000 |

Table 3.4. $r = .624$, $r^2 = .389$

Ordinary least-squares regression on Attitudes demonstrated that risk perception (β = -.323, $p<.001$), population trend perception (β = -.283, $p<.001$), and self-identification as a hunter (β = -.170, $p<.001$) were the strongest negative predictors in the model, meaning that those who believed themselves to be personally at risk from cougars, those who believed cougar populations were growing, and hunters had the most negative attitudes toward cougars. Education (β = .148, $p<.001$) was the strongest positive predictor in the model, meaning that as education level increased, attitudes toward cougars became more positive. Gender (with female as the reference category) was also weakly associated with attitudes (β =.085, $p <.05$), meaning that women had more positive attitudes toward cougars than men. Income, age, livestock ownership, conservation group membership, and prior experience with cougars were not significant predictors of attitudes at the 95% confidence level. The overall Pearson's $R^2$ for the model was .389.

Through independent-sample t-tests, we found that among livestock owners, those whose animals had been threatened by cougars had significantly lower attitudes (mean difference = -.76, $p<.01$), while among hunters, those who had purchased a cougar tag in the past did not have significantly different attitudes toward cougars ($p = .090$).

**Acceptability.** Capturing and relocating the cougar was the most acceptable course of action in all situations but human injury, at which point relocation was slightly overtaken in acceptability by destroying the cougar. Lethal management crossed the threshold of acceptability (represented by the horizontal line in Fig. 3.4) only when human life was directly threatened. Not intervening was borderline unacceptable in the case of a cougar sighting, and became less acceptable as situational severity increased.

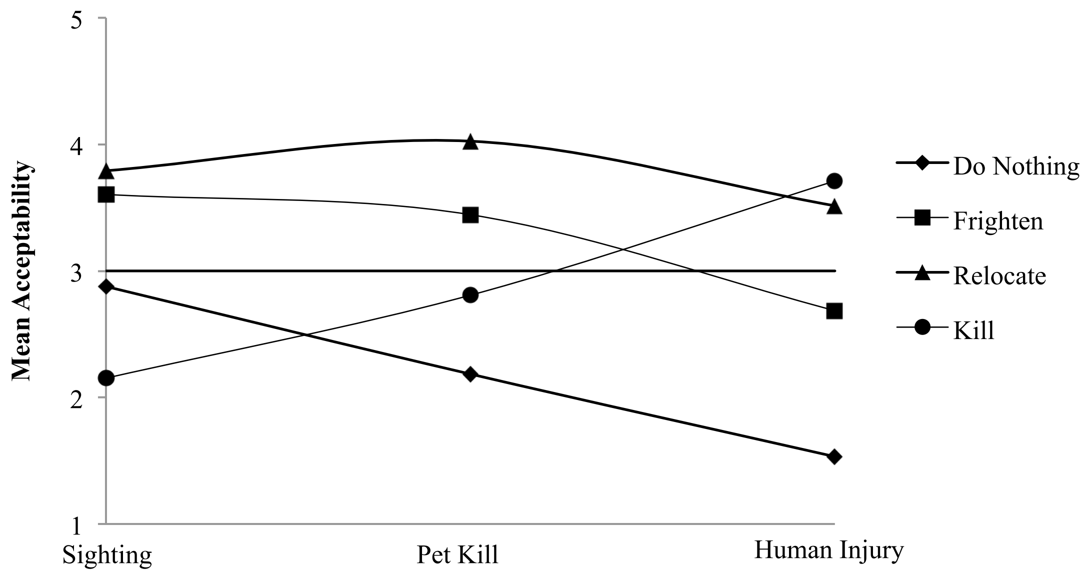


Figure 3.4. Mean acceptability of management actions under three conflict scenarios: a cougar is seen in your community, a cougar has killed several pets in your community, and a cougar has attacked and injury a person in your community. Respondents rated four possible management actions ("Do Nothing," "Frighten the Cougar Away," "Relocate the Cougar," and "Shoot and Kill the Cougar") on a scale from 1 (Highly Unacceptable) to 5 (Highly Acceptable).

Based on the construction of the survey items, there were two potential thresholds of interest: the inaction/action threshold (doing nothing vs. frightening, relocating, or killing the cougar) and the nonlethal/lethal threshold (doing nothing, frightening, or relocating the cougar vs. killing the cougar). For the purposes of this analysis, we chose the former threshold for a few reasons. First, we found that attitudes and acceptability of lethal management were collinear (VIF > 2), making it difficult to include both variables in further models. Strong collinearity of the two factors suggested to us that individuals responding to the proposition of lethal management were drawing on their attitudes toward cougars and toward killing cougars rather than considering the acceptability of the cougar's actual behavior in the scenario. Therefore, we operationalized acceptability as an individual's ability to accept cougar behavior without expecting management to intervene (See Table 3.5).

| Acceptability | Reliability (Cronbach's α) | x̄ ± SD |
|---|---|---|
| **Cougar sighted in neighborhood** | .77 | 2.87 ± 1.29 |
| **Cougar has killed several pets** | | 2.18 ± 1.14 |
| **Cougar has attacked and injured a human** | | 1.53 ± 0.88 |

Table 3.5. Respondents were asked to rate the acceptability of wildlife managers doing nothing under each scenario on a scale from 1 (Highly Unacceptable) to 5 (Highly Acceptable).

Based on the high Cronbach's alpha reliability score ($\alpha = .77$), the acceptability items were combined into a single variate ("Acceptability") by taking the average of the total scores on each item. The resulting scale ranged from 1 (highly unacceptable, indicated by a score of 1 on each item) to 5 (highly acceptable, indicated by a score of 5 on each item) and skewed slightly low with a mean score of 2.22. After combining the three items into a single scale, we used ordinary least squares regression to identify the most important predictors of acceptability.

Ordinary least-squares regression on Acceptability demonstrated that risk perception ($\beta = -.196$, $p<.001$), self-identification as a hunter ($\beta = -.182$, $p=.001$) and population growth perception ($\beta = -.152$, $p<.01$) were significant negative predictors in the model, meaning that those who perceived more risk from cougars, hunters, and those who believed cougar populations are growing were less accepting of cougar conflict. Conservation membership was weakly associated with lower acceptability ($\beta = -.096$, $p<.05$), possibly because at least half of the conservation organizations in the sample were hunting-related. Prior experience with cougars ($\beta = .123$, $p<.05$) was a positive predictor of acceptability, meaning that those who had seen cougars or cougar sign before were more accepting of cougar conflict. Education, income, gender, age, and livestock ownership were not significant predictors in the model. The overall Pearson's $R^2$ for the model was .210.

**OLS Regression of Demographic Variables on Acceptability**

| Variable | Standardized β | Std. Error | Sig. |
|---|---|---|---|
| (Constant) | 3.093 | .438 | .000 |
| Education | .066 | .028 | .183 |
| Income | .028 | .025 | .567 |
| Gender | .061 | .094 | .217 |
| Age | .011 | .003 | .805 |
| Hunting Participation | -.182 | .103 | .001 |
| Livestock Ownership | -.039 | .112 | .423 |
| Conservation Membership | -.096 | .110 | .045 |
| Cougar Experience | .123 | .009 | .023 |
| Risk Perception | -.196 | .026 | .000 |
| Population Perception | -.152 | .034 | .003 |

Table 3.6. R = .458, $R^2$ = .210

**Behavioral Intentions.** Respondents were more likely to vote to increase cougar protections ($\bar{x}$ = 3.97) than they were to vote to increase cougar hunting opportunities ($\bar{x}$ = 3.50). We reverse coded the cougar hunting statement and found that the Cronbach's alpha reliability score for the two statements was α = .80. The voting intention items were combined into a single variate ("Behavioral Intention") by taking the mean of individual scores on each item. The resulting scale ranged from 1 (highly unlikely to vote for cougar protection, indicated by a score of 1 on each item) to 7 (highly likely to vote for cougar protection, indicated by a score of 7 on each item).

| Behavioral Intention | Reliability (Cronbach's α) | x̄ ± SD |
|---|---|---|
| Vote to increase cougar protection | .80 | 3.97 ± 2.04 |
| Vote to increase cougar hunting opportunities | | 3.50 ± 1.98 |

Table 3.7. Respondents were asked to rate their likelihood of voting for each policy on a scale from 1 (Highly Unlikely) to 7 (Highly Likely).

After combining the behavioral intention items into a single scale, we used ordinary least squares regression to identify the most important predictors of behavioral intention and to determine if attitudes and acceptability each uniquely contributed to explaining variation in behavioral intent.

**OLS Regression of Attitudes, Acceptability, & Demographics on Behavioral Intent**

| Variable | Standardized β | Std. Error | Sig. |
|---|---|---|---|
| (Constant) | 1.039 | .685 | .130 |
| Attitude | .552 | .061 | .000 |
| Acceptability | .089 | .066 | .010 |
| Education | .020 | .036 | .554 |
| Income | -.046 | .032 | .141 |
| Gender | .040 | .118 | .822 |
| Age | .047 | .003 | .117 |
| Hunting Participation | -.188 | .132 | .000 |
| Livestock Ownership | .006 | .145 | .856 |
| Conservation Membership | -.014 | .145 | .668 |
| Cougar Experience | -.135 | .011 | .000 |
| Risk Perception | .012 | .036 | .728 |
| Population Perception | -.192 | .045 | .000 |

Table 3.8. R = .846, $R^2$ = .715

Ordinary least-squares regression on Behavioral Intentions demonstrated that attitudes (β = .552, p<.001) and acceptability (β = .089, p=.01) were significant positive predictors in the model of behavioral intentions, meaning that those with high attitudes and acceptability were more likely to vote for cougar protection. Self-identification as a hunter (β = -.188, p<.001), cougar experience (β = -.135, p<.001) and population perception (β = -.192, p<.001) were significant negative predictors in the model, meaning that hunters, those with prior cougar experience, and those who believed cougar populations are growing were less likely to vote for cougar conservation. The overall Pearson's $R^2$ for the model was .715.

Through independent-sample t-tests, we found that among livestock owners, those whose animals had been threatened by cougars were no less likely to vote for cougar protection (p = .397), while among hunters, those who had purchased a cougar tag in the past were significantly less likely to vote for cougar protection than those who had not (mean difference = 1.79, p<.001)

**Tolerance Typologies.** To test for the presence of the four typologies proposed in Fig. 3.3, scores on the latent cougar acceptability scale were plotted against scores on the latent attitudinal scale for each conflict scenario. A score of 3 on the acceptability scale represented an individual who, on average, reported that not intervening was neither acceptable nor unacceptable for the particular conflict scenario. We fit a framework to the data that divided the points into four segments based on position a) to the left or the right of the neutral acceptability line (x=3) and b) above or below the neutral Attitude line (y = 4.5). See Figure 3.5.

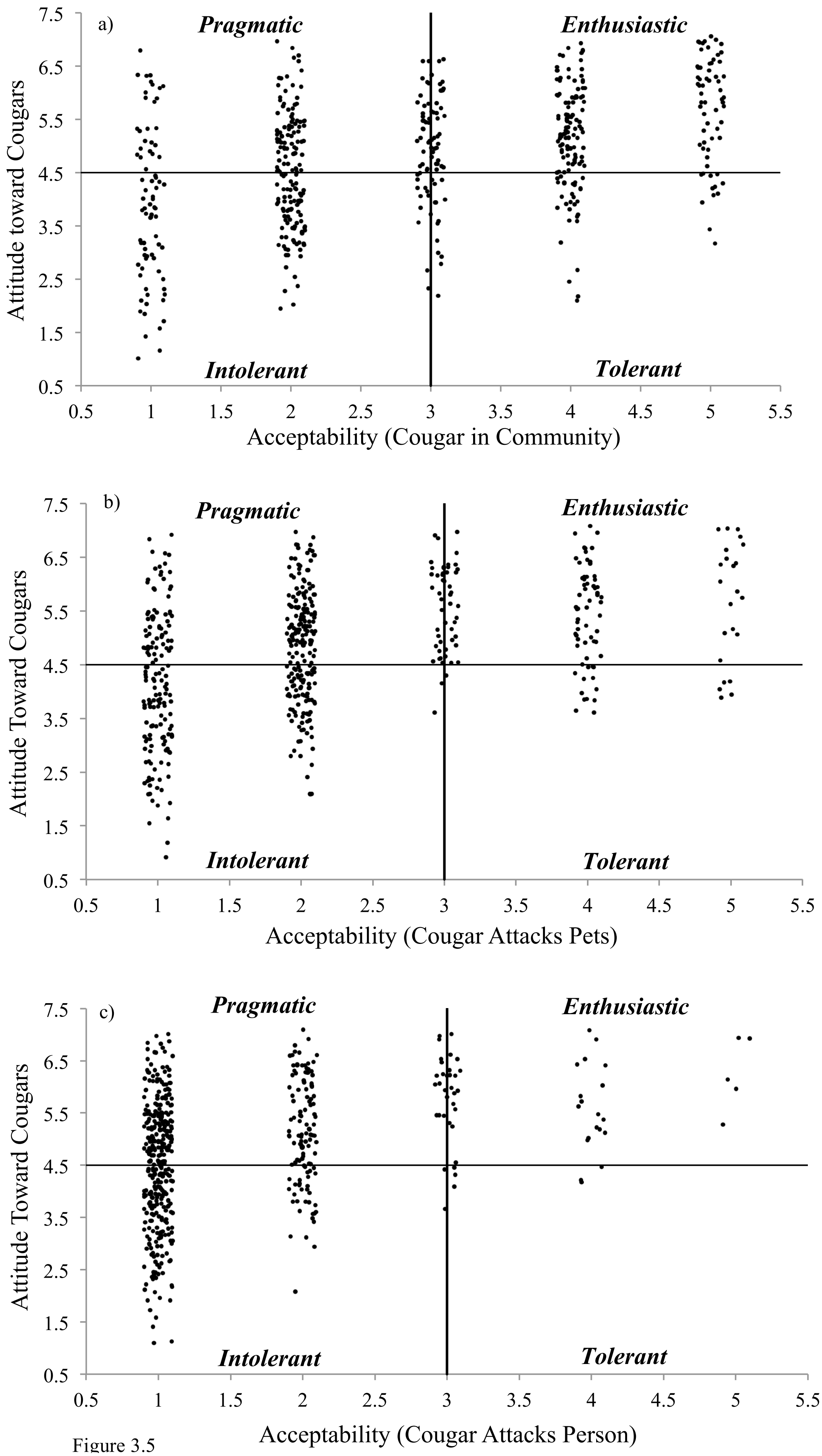
a)
Pragmatic
Enthusiastic
Intolerant
Tolerant
Attitude toward Cougars
Acceptability (Cougar in Community)
7.5
6.5
5.5
4.5
3.5
2.5
1.5
0.5
0.5 1 1.5 2 2.5 3 3.5 4 4.5 5 5.5
b)
Pragmatic
Enthusiastic
Intolerant
Tolerant
Attitude Toward Cougars
Acceptability (Cougar Attacks Pets)
7.5
6.5
5.5
4.5
3.5
2.5
1.5
0.5
0.5 1 1.5 2 2.5 3 3.5 4 4.5 5 5.5
c)
Pragmatic
Enthusiastic
Intolerant
Tolerant
Attitude Toward Cougars
Acceptability (Cougar Attacks Person)
7.5
6.5
5.5
4.5
3.5
2.5
1.5
0.5
0.5 1 1.5 2 2.5 3 3.5 4 4.5 5 5.5

Figure 3.5

In Fig. 3.5a, Attitudes vs. Acceptability (Cougar in Community), responses were fairly evenly distributed in the scatterplot, and significant variation was present ($R^2$ = .19). Enthusiastic (n=205), Pragmatic (n=102), Intolerant (n=138), and Tolerant (n=71) individuals could all be identified. In Fig. 3.5b, Attitudes vs. Acceptability (Cougar Attacks Pets), acceptability declined along with membership in the "Enthusiastic" and "Tolerant" typology groups. In Fig 3.5c, Attitudes vs. Acceptability (Cougar Attacks Person), membership in the "Tolerant" group declined almost to zero.

Because the most variation was present in Fig 3.5a, we selected this first scenario for futher analysis of the variables associated with tolerating cougar conflict. We used Pearson's chi-square test of independence to assess the categorical variables associated with typology. We found significant differences in typology membership between non-hunters and hunters, men and women, livestock owners and non-livestock owners, those with no experience with cougars in the community and those with some experience, and voting intentions (Table 3.9)

| | **Typology** | | | |
|---|---|---|---|---|
| **Group Membership** | Pragmatic | Enthusiastic | Tolerant | Intolerant |
| Female | 39.8% | 52.0% | 31.9% | 28.5% |
| Male | 60.2% | 48.0% | 66.7% | 70.8% |
| Livestock | 14.9% | 20.0% | 31.0% | 28.5% |
| No Livestock | 85.1% | 80.0% | 69.0% | 71.5% |
| Hunter | 37.6% | 24.9% | 52.1% | 54.0% |
| Non-Hunter | 62.4% | 75.1% | 47.9% | 46.0% |
| < Bachelors Degree | 17.8% | 29.2% | 18.3% | 34.7% |
| > Bachelors Degree | 17.8% | 41.6% | 16.7% | 23.8% |
| Experience | 52.0% | 52.7% | 70.4% | 63.8% |
| No Experience | 48.0% | 47.3% | 29.6% | 36.2% |
| Vote For | 58.4% | 65.2% | 21.1% | 14.6% |
| Vote Against | 24.8% | 18.1% | 66.2% | 76.6% |
| Neither | 16.8% | 16.7% | 12.7% | 8.8% |

Table 3.9. Percentages are distributed by column and should be read as "52% of Enthusiasts were female."

**Discussion**

In general, attitudes toward cougars skewed positive ($\bar{x}$ = 4.77, SD = 1.22). This finding aligns with results from prior surveys of the general public, who tend to report a positive outlook on wildlife when presented with low-elaboration attitudinal statements (George et al., 2014). Hunting participation was one of the strongest negative predictors of cougar attitudes, demonstrating how social group identity can influence the heuristics used to rapidly process attitude statements. Cougars, like many predators, have come to symbolize other human conflicts (economic insecurity, environmental destruction, unwanted government intervention) and values (living in harmony with nature, self-determination, security & protection) that may come to the forefront when individuals are presented with low-elaboration attitude statements (Manfredo & Dayer, 2010). In contrast, respondents may consider hypothetical conflict scenarios taking place in their own community more carefully, accessing their prior experience and knowledge rather than using heuristic cues to respond quickly (Petty & Cacioppo, 1986).

Prior interactions with cougars were associated with higher acceptability, more negative behavioral intentions, and no differences in attitudes. Previous studies have found that more experience with predators was associated with negative attitudes, implying that as cougar populations recover and encounters become more common, tolerance for them may decrease (Davenport et al., 2010). In contrast, the majority (69%) of respondents in our sample considered their prior interactions with cougars to be neutral to very positive (Data not shown). Riley & Decker (2000) found that members of the public tended to overestimate the level of risk cougars presented; it could be that some familiarity with cougars actually reduces fears about their presence and increases their acceptability (Johansson et al., 2016). The finding that factors like prior experience interact differently with attitudes, acceptability, and behavioral intentions emphasizes the complexity of these constructs and provides evidence that they may not be substitutable in management implications.

Attitudes and acceptability were weakly correlated, but with significant variation in responses, particularly when respondents were presented with the least severe (and most common) conflict scenario in which a cougar was seen in the community. In contrast, Wildlife Acceptance Capacity (WAC), another frequently used measure of acceptability, is typically found to be strongly correlated with attitudes, leading some to suggest that normative beliefs and attitudinal beliefs may be close to interchangeable (Riley & Decker, 2000; Bruskotter et al. 2015). We found that for borderline conflict scenarios, attitudes and acceptability became unyoked, creating a wide distribution of responses that allowed us to apply our framework and identify four distinct typologies among respondents. For conflict situations that do not directly involve human or pet injury, an individual or social group's reported attitudes toward a species may not align with their expectations for management action. As scenarios became more serious, tolerance of cougar behavior declined and agreement that intervention would be necessary increased.

` The framework presented here is intended merely as a conceptual aid for understanding the complex and scenario-specific relationships between attitudes and normative beliefs toward wildlife. Boundaries for the four proposed typologies should be considered context-dependent and could be aligned in any number of ways, including based on midpoints for the scales, averages of scores, or predicted responses. Our data do provide some theoretical contributions, including the finding that although true tolerance toward cougars does exist, it is relatively rare (~14% of respondents) compared to other groups. The frequency of tolerance toward cougars aligns with sociological findings about the low prevalence of tolerance between human social groups in the US (Sullivan et al. 1979). These results also present a significant cohort of people who were intolerant of cougars and cougar conflict (~27% of respondents). Nearly 20% of respondents were classified as "Pragmatic", reporting positive attitudes toward cougars and intending to vote for cougar protection but remaining wary of cougars in their community. Although tolerance was relatively rare, it is important to note that "Enthusiasts," those reporting high attitudes and high acceptability, were the largest group in our sample.

**Management Implications.** Our findings suggest that tolerance need not be the ultimate object of predator conservation. In fact, "putting up with something you do not like" does not accurately describe how the majority of people feel about cougars – active enjoyment or consistent antipathy are much more common views. However, considering that individual attitudes are resistant to improvement via campaign, tolerance-boosting strategies that target *acceptability* could potentially shift "intolerant" and "pragmatic" people into the "tolerant" and "enthusiastic" domains. The results of our OLS regression suggest that educational interventions focusing on accurate risk and population trend perceptions could influence acceptability of cougars. Besides education, conflict prevention should be emphasized, as we found that when cougars threaten or attack livestock, attitudes are damaged significantly. Interestingly, acceptability was higher among respondents who had prior experience with cougars, indicating that managers need not focus on preventing all cougar encounters. Tolerance of cougar conflict dropped dramatically once pet safety was compromised; managers could therefore focus on rewarding responsible pet ownership among residents of the WUI.

**Limitations and Future Directions.** Men (59%), older people ($\bar{x}$ = 54 years), and hunters (39%) were overrepresented in the sample compared to their true prevalence in the populations of interest. Because of potential bias, caution should be used when applying these results to larger populations. However, this sample could be considered a self-selecting group representative of those in rural communities most disposed to participate in wildlife decision-making.

Wildlife managers and conservationists are set a problematic task when confronting human-predator conflict. Controversy is to some degree inevitable when attitudes and acceptability vary as much as they do in the populations examined here. Over half of respondents believed no intervention would be necessary if a cougar were seen in their community; however, behavioral escalation is always a possibility, and waiting for an incident to occur before acting may do more harm to attitudes and beliefs than good. The route to coexistence with wildlife can be murky, as interventions that improve acceptability may not necessarily affect behavioral intentions, and vice versa. In future, it could be beneficial to examine the relationship between attitudes and acceptability for more benign scenarios (predators existing in the wilderness, predators acting as a non-destructive nuisance, predators damaging human property) to understand further patterns of tolerance. Future research should also focus on pre- and post-testing attitudes, acceptability, and behavioral intentions after implementing strategies (such as compensation, providing predator-proof fencing, permitting sport hunting or farming, education) intended to improve tolerance of wildlife.

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## Chapter 4: Testing the Tolerance Metric Across Communities and Social Groups

### Background

Large carnivores are a source of fascination to people. Conservationists have long recognized that charismatic predators like polar bears (*Ursus maritimus*) seem to galvanize the public to act and contribute to conservation campaigns (Slocum, 2004). Apex predators also serve an important ecological role – they exert landscape-level effects disproportionate to their biomass by controlling non-native species invasion, disease, herbivory, and other processes (Fortin et al., 2005; Rizzari et al., 2014; Wallach et al., 2010). As public values toward wildlife shift toward protection, a growing number of people around the world expect wildlife managers to maintain ecosystem health by supporting recovering carnivore populations (Manfredo et al., 2011).

However, wildlife value shift has not been complete, and instead proceeds slowly across generations and regions. Mutualist wildlife value orientations, or beliefs that wildlife are inherently valuable and should be protected rather than used, are associated with financial security, urbanization, and education. In contrast, utilitarian wildlife orientations, or beliefs that the value of wildlife comes mainly from its utility to people, are associated with financial instability, less formal education, and rural dwelling (Manfredo et al., 2011). This rural-urban cleavage in value orientations means that those who live closest to large carnivore populations are both the least willing to protect them and the most likely to bear the costs of doing so.

While large carnivores provide ecosystem benefits, these societal costs are neither insignificant nor equally distributed. In 2015, the U.S. Fish & Wildlife Services made available over $450,000 in reimbursement to farmers and ranchers who had lost livestock to wild animals. However, many viewed the program as inadequate compensation for their actual losses (USFWS, 2015; Naughton-Treves, 2003; Karanth, 2013). Hunters regard predators as competitors for game species, while predators regard pets and livestock of rural and suburban residents as prey. Although incidents are relatively rare, human safety is also a concern when coexisting with large carnivores (Breitenmoser, 1998; Quigley & Herrero, 2005). While cultivating tolerance is crucial to carnivore conservation, putting up with problematic predator behaviors can be a tall order for those experiencing the brunt of conflict. Attitudes are further damaged when a species takes on a symbolic significance for other societal conflicts and concerns, such as unwanted government intervention or loss of economic opportunity (see Bangs et al., 2005 on grey wolves in the Western US, or Kittinger et al., 2012 on Hawaiian monk seals).

To reduce conflict and environmental injustice, it is important that communities in the wildland-urban interface perceive some net benefit from tolerating the presence of large carnivores. Ecosystem benefits, while encouraging, may not always appeal to hunters, farmers, and ranchers concerned about their immediate livelihoods. Some pragmatic conservationists have proposed that regulated consumptive use of large carnivores through sport hunting or farming could serve as an incentive for rural communities to conserve more conflict-prone species (Leader-Williams & Hutton, 2005; Lindsay et al., 2006). By providing revenue and a measure of control over wildlife populations, consumptive use imparts benefits to local communities that could theoretically offset the costs of living with large carnivores (Lindsey et al., 2007; Creel & Rotella, 2010). For example, regulated farming has been credited with improving stewardship toward crocodilians in the United States, Zimbabwe, and Australia (Thorbjarnarson, 1999).

Sport (or trophy) hunting has been offered as another economic rationale for conserving carnivores. In Sub-Saharan Africa, sport hunting is a major source of revenue for local communities, with higher per-person fees than other forms of tourism in the region (Lindsey et al., 2007). In the United States, hunters spend considerable time and funds lobbying for the conservation of species of interest, and have historically formed one of the strongest coalitions in favor of sustainable game management (Dunlap, 1988). Conservationists continue to debate whether sport hunting of large carnivores can be sustainable or if the risks imparted to threatened populations outweigh potential benefits (Cooley et al., 2008; Packer et al 2009; Peebles et al., 2013; Robinson et al., 2008). In the Human Dimensions of Wildlife literature, a similar dispute exists concerning whether permitting sport hunting improves tolerance of large carnivores or if it encourages undesirable attitudes, or behaviors such as poaching (Lindsey et al. 2007; Loveridge et al. 2006; Leader-Williams and Hutton, 2005; Treves and Bruskotter, 2014). In 2010, Creel & Rotella noted that "sport hunting [is a] well-established tool to manage large carnivores and broaden societal acceptance." However, this is far from the case, as few studies have attempted to directly examine this proposed relationship between sport hunting and tolerance (but see Treves et al., 2013).

The lack of scholarship concerning the social effects of sport hunting is likely due in part to uncertainty surrounding how best to measure human tolerance of wildlife. Prior studies have conceived of tolerance as a set of attitudes (Treves et al., 2013; Kansky et al., 2014; Lewis et al., 2015), normative beliefs about acceptability (Karlsson &

Sjöström, 2011; Wald & Jacobson, 2013; Decker et al. 2006), or behavioral intentions toward wildlife (Morzillo & Needham, 2015; Treves et al., 2013). In sociology, tolerance is defined as "putting up with something you do not like," a framework that incorporates both an attitudinal and an acceptability component (van Doorn, 2014) (for more information about wildlife tolerance metrics, see Chapter 3). The checkered history of cougar (*Puma concolor*) sport hunting in the Western US presents a unique opportunity to test the suitability of these metrics in a setting where tolerance is likely to vary considerably.

**Cougar Sport Hunting in the US.** In the North America, human attitudes have had a direct influence on cougar sport hunting policies, as well as on the distribution of this large carnivore. Historically, many states and provinces encouraged the removal of cougars and other predators through unregulated or bounty harvest systems (Sunquist & Sunquist 2002). Unrestricted killing and habitat loss eventually led to the extirpation of cougars in the eastern US, although isolated pockets remained in the West and in the Florida Everglades. In the 1960s and '70s, most states with extant cougar populations implemented a regulated harvest season, and managed cougars began to recover (Riley & Malecki, 2001). A few decades later, wildlife managers confirmed the existence of a breeding population in the Black Hills of South Dakota, the first known instance of natural cougar recolonization in the US (Fecske, 2003). Increased sightings of individual cougars in the Midwestern and Eastern US suggest that this recolonization event is ongoing (LaRue et al., 2012).

In the 1990s, a series of ballot initiatives changed the cougar policy landscape in the Western US. First, California residents voted to reclassify cougars as "specially protected mammals" and banned sport hunting outright while allocating $30 million annually to cougar habitat conservation (CA Proposition 117, 1990). A few years later, residents of Oregon and Washington voted to ban hound hunting, the traditional method of pursuing and treeing cougars for harvest (OR Measure 18, 1994; WA Initiative-655, 1996). Since the 1990s, cougar management in the Western US has been characterized by a patchwork of hunting policy that is just as much a product of public attitudes as of management needs or cougar population ecology (see Fig 4.1). State regulations range from Texas, where cougars are classified as nuisance animals, to Oregon and Washington, where hound hunting is banned, to California, where cougar sport hunting of any kind is prohibited. This variation in hunting regulations forms a natural quasi-experiment that could be exploited to better understand the downstream effects of sport hunting policy on human tolerance of cougars, with a particular focus on rural areas where the costs and benefits of cougars/cougar hunting are concentrated.

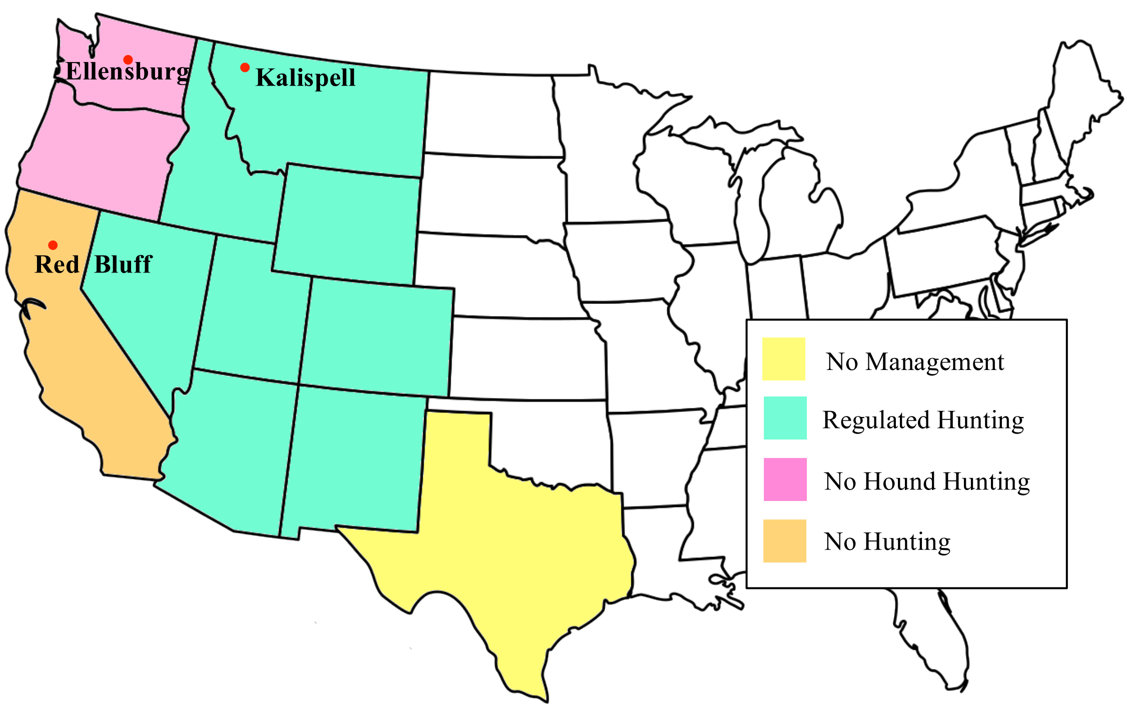


Figure 4.1: A map displaying cougar hunting policies in the Western US. Points in red show the approximate location of the three sites in this study.

Hunting intensity has a perceptible effect on cougar abundance, age class structure, and sex ratios (Robinson et al., 2008; Lambert et al. 2006). However, the social effects of cougar hunting are not well understood. While ballot initiatives such as California's Prop 117 provide an opportunity for the public to directly participate in wildlife policymaking, the urban voting bloc can overwhelm the preferences of rural communities in the wildland-urban interface, where utilitarian value orientations prevail and changes to wildlife management are most keenly felt. Voting trends from Washington Ballot Initiative 655 and California Proposition 117 clearly demonstrate a rural/urban political cleavage, as counties with smaller populations tended to vote against restricting hunting opportunities while larger, more urbanized counties tended to vote in favor of the initiatives (Figures 4.2 & 4.3.). The urban bloc voting effect is particularly evident in California, which possesses multiple large metropolitan centers.

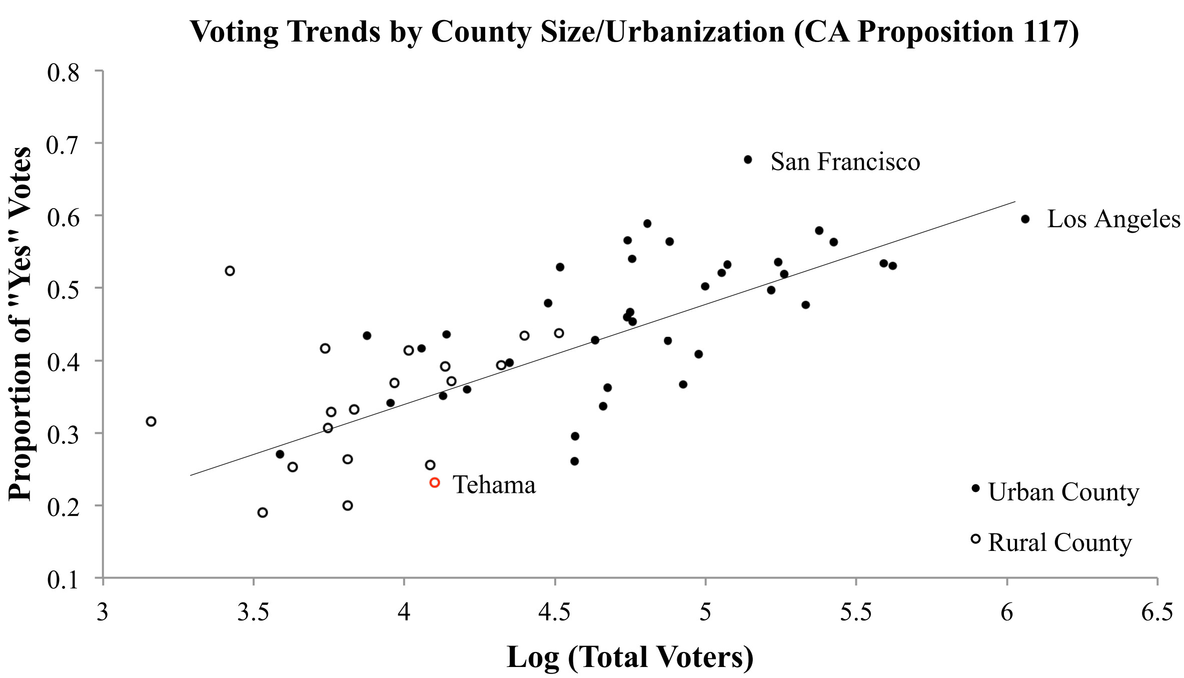


Figure 4.2: A scatterplot displaying the proportion of "Yes" votes by the total number of voters per county for California Proposition 117. Prop 117 banned cougar hunting and allocated $30 million/annum for habitat conservation. Our California study site, Red Bluff, is the largest city and administrative seat of Tehama county (shown in red). Trend line is an OLS regression ($r^2$ = .71) Filled in circles represent counties that are <33.3% rural; unfilled circles are counties >33.3% rural. Data retrieved from the California Secretary of State – Elections Division and the US Census Bureau.

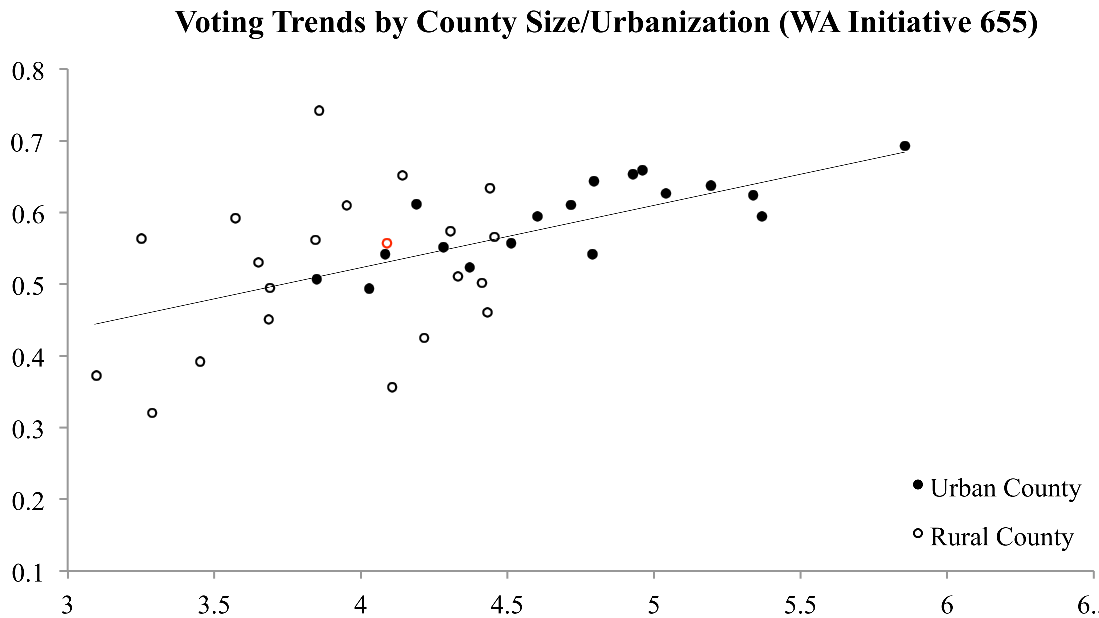


Figure 4.3: A scatterplot displaying the proportion of "Yes" votes by the total number of voters per county for Washington Initiative 655. Initiative 655 banned hound hunting of cougars and black bears. Our Washington study site, Ellensburg, is the largest city and administrative seat of Kittitas county (shown in red). Trend line is an OLS regression ($r^2$ = .58). Filled in circles represent coutnies that are <33.3% rural; unfilled circles are counties > 33.3% rural. Data retrieved from the Washington Secretary of State – Elections & Voting (https://www.sos.wa.gov/elections/) and the US Census Bureau.

## Research Questions

1. Does tolerance (attitudes and acceptability) of cougars differ between Red Bluff, CA, Ellensburg, WA, and Kalispell, MT, three communities subject to differing cougar policy?
2. Do attitudes toward cougar hunting and the use of hounds differ between these three communities?
3. Since 1990, have attitudes toward California Proposition 117 changed among Red Bluff residents?

## Methods

**Sampling.** We used data gathered from a 2017 web-based survey (Qualtrics, N = 3137) that measured attitudes, acceptability, and behavioral intentions regarding cougars and cougar hunting among residents of Red Bluff, CA (Tehama County), Kalispell, MT (Flathead County), and Ellensburg, WA (Kittitas County). These mid-sized (population <20,000) rural communities were chosen for their proximity to abundant cougar habitat and, in the cases of Red Bluff and Ellensburg, for their susceptibility to the urban voting bloc effect in regards to cougar policy. The survey was anonymous but solicited optional demographic information about respondents including age, gender, total household income, education, and length of residency. To identify relevant social groups, respondents were asked the following binary questions: 1) Do you own livestock? and 2) Are you a hunter (any game)? We included a series of items measuring attitudes toward cougars, acceptability of cougars, and attitudes toward cougar hunting and combined related items into three summated scales. Residents of Red Bluff were provided with information about California Proposition 117 (Department of Elections, CA Secretary of State) and asked whether, given the chance today, they would vote to keep or repeal the law. We received 520 completed surveys for a final response rate of 20.9%. For more detailed survey methods, please see Chapter 3, and for the survey instrument please see the Appendix.

**Statistical Analysis.** Categorical differences across communities were assessed using Pearson's chi-squared test. Two-way analysis of covariance (ANCOVA) was used to assess differences between communities and hunters/non-hunters on four dependent variables: attitudes toward cougars, acceptability of cougars, attitudes toward cougar hunting with and without hounds, and acceptability of lethal cougar management. Homogeneity was assessed with Levene's test of Equality of Error Variances. For the interaction terms, post-hoc tests for significance were conducted using the Bonferonni adjustment to correct for multiple pairwise comparisons. IBM SPSS Statistics (v. 24) was used for all analysis.

## Results

**Demographic Data.** Of the respondents, 110 (21%) lived in Red Bluff, 203 (39.2%) lived in Kalispell, and 205 (39.6%) lived in Ellensburg. Across the three communities, there were no significant differences in hunting participation, conservation group membership, gender, or income level of respondents. Respondents from all three communities also reported similar amounts of previous exposure to cougars and/or cougar sign. However, significant differences in education level, length of residence in the current state, and livestock ownership were noted between communities. Only 42.1% of Red Bluff respondents had received a Bachelor's degree or higher, compared to 57.7% of Kalispell residents and 61.8% of Ellensburg residents. Red Bluff respondents were long-time residents of their state: 48.1 years residency on average compared to Kalispell's 31.8 years and Ellensburg's 42.3 years. Finally, 30.9% of Ellensburg respondents reported owning livestock compared to 22.0% of Red Bluff respondents and only 15.3% of Kalispell respondents. To control for variation between states, these three factors (Education, Livestock, and Residency) were included as covariates in our final two-way ANCOVA models.

**Comparing Tolerance between Communities.** After controlling for education level, length of residency, and livestock ownership, there was no significant main effect of Community on any of the dependent variables measured (attitudes toward cougars, acceptability of cougars, or attitudes toward cougar hunting). However, there was a significant interaction between Community and Hunter. Irrespective of community, hunters demonstrated lower attitudes toward cougars than non-hunters. However, hunters in Red Bluff demonstrated significantly lower cougar attitudes than did hunters in Ellensburg (Fig 4.4a**)**. In Kalispell and Ellensburg, hunters were just as accepting of cougars in their community as non-hunters were, but there was a significant divide between hunters and non-hunters in Red Bluff (Fig 4.4b). In general, non-hunters reported more negative attitudes toward cougar hunting than hunters, but non-hunters in Red Bluff held significantly more negative attitudes than did their non-hunting peers in Ellensburg and Kalispell (Fig 4.4c). There were also inter-community differences in attitudes toward specific types of cougar hunting (Fig 4.4d). Red Bluff respondents had more negative attitudes toward cougar hunting than Kalipsell respondents, but made no distinction between hunting with or without dogs in their attitudes. Conversely, Ellensburg residents had much lower attitudes toward hunting with dogs than hunting without dogs. Kalispell residents also had lower attitudes toward hunting with dogs, but their attitudes toward hunting in general were higher than in either Red Bluff or Ellensburg. For full ANCOVA tables, please see the Appendix.

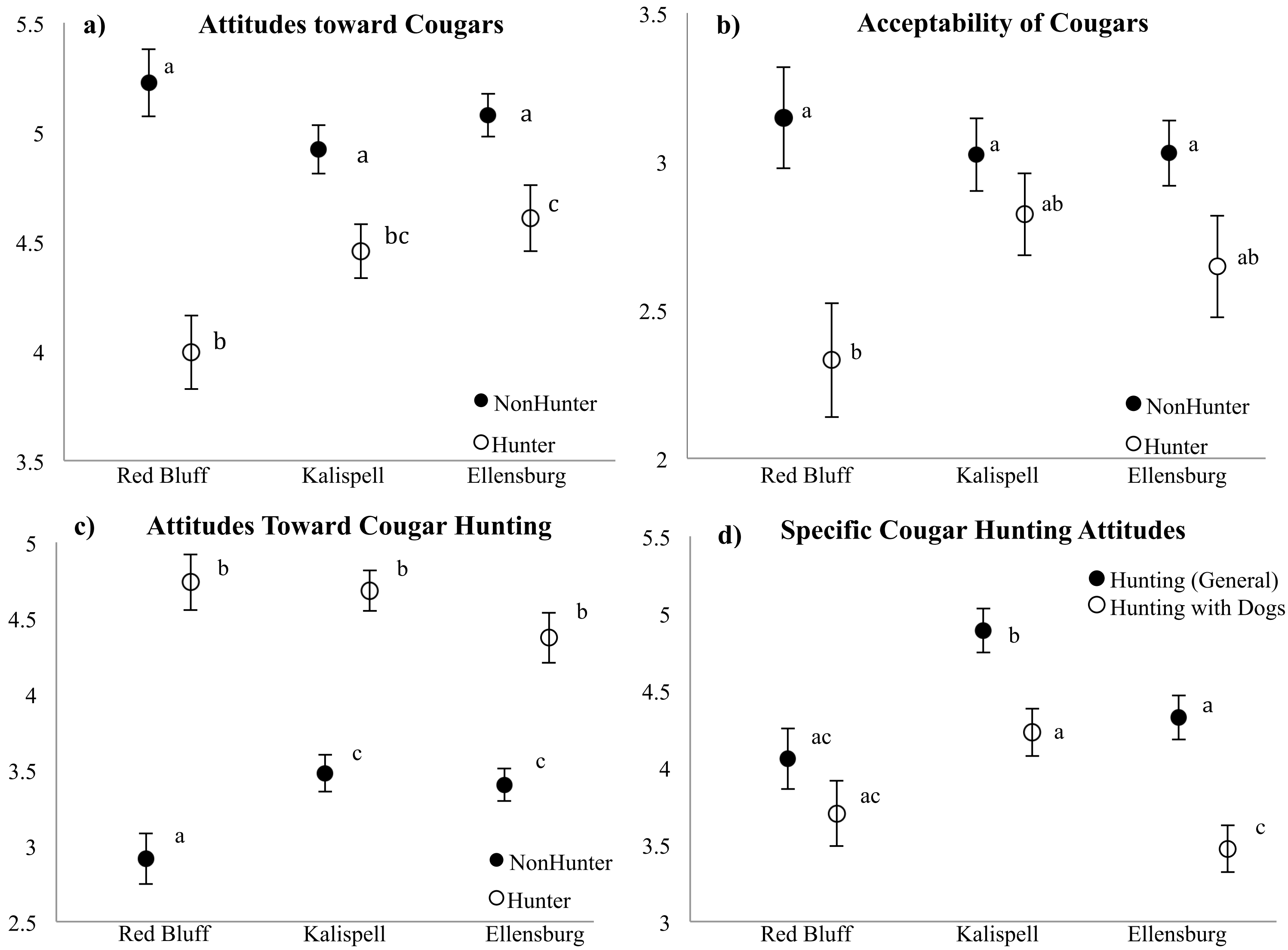


Figure 4.4. Charts displaying a) attitudes toward cougars by hunters and non-hunters in each community; b) acceptability of cougars by hunters and non-hunters in each community; c) attitudes toward cougar hunting by hunters and non-hunters in each community; and d) specific attitudes toward hunting with and without dogs in each community. Points represent mean values for each group and community. Error bars are standard error. Letters represent significant differences between groups.

In order to examine change over time as well as difference between states, we presented Red Bluff respondents with the choice to keep or repeal the cougar sport hunting ban (Proposition 117). If they had the option to vote today, 52% of Red Bluff respondents stated that they would keep Proposition 117, 45% said they would repeal it, and 3% said they would abstain from voting. This overall tendency to maintain the law stands in contrast to actual voting trends from 1990, when only 26% of Red Bluff voters were in favor of the sport hunting ban (see Fig 4.5).

**Proposition 117: Voting Behavior/Intention of Red Bluff Residents 1990 vs 2017**

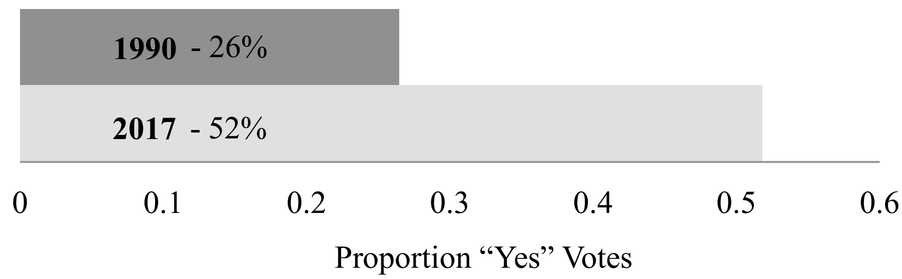


Figure 4.5

**Discussion**

We found little evidence that banning or restricting sport hunting affected tolerance of cougars among the general populace in the three study sites. However, we did identify an interaction between social group identity and community that influenced tolerance. Hunters in Red Bluff were more intolerant of cougars than were hunters in the other communities where some form of cougar hunting was permitted. Despite the ban on hound hunting in the state of Washington, hunters in Ellensburg reported similar levels of tolerance to hunters in Montana, where hound hunting is legal. Only 1% of respondents in all states reported having ever used hounds to hunt cougars, so it's likely that the outcome of Ballot Initiative 655 did not personally hinder the activities of most Washington hunters, who can still readily purchase cougar hunting licenses.

Non-hunters in Red Bluff had more negative attitudes toward cougar hunting than did non-hunters in the other two communities. In addition, attitudes toward specific cougar policies (the legality of hunting with or without hounds) were more negative in the states where those policies were banned. These results align with social norm theory, which predicts that top-down rules and regulations can influence cognition differentially across social groups (Rohan, 2000; Zinn et al., 1998). Wildlife decision-makers and managers should be aware of likely long-term backlash among hunters if sport hunting of large carnivores is prohibited outright, as in California. However, managers may be able to mitigate backlash by providing alternative opportunities for big-game hunters, as Washington state agencies did when they increased the total number of available cougar permits following the passage of Initiative 655 (Doughton, 2008).

Regardless of their severity, cougar sport hunting regulations appear to have had little enduring effect on attitudes toward carnivores among non-hunting members of the general public. Instead, the concept of sport hunting may grow more distasteful to the public once it has been banned, deepening the cognitive divide between hunters and non-hunters. Despite the relative intolerance of Red Bluff hunters toward cougars, results of this survey suggest that attitudes toward the cougar hunting ban may have improved in the past decades, with 52% of respondents indicating that they would vote for Proposition 117 if it were on the ballot in 2017 compared to only 26% who actually voted for the law in 1990. Although our sample may not represent actual voters, this difference in voting intention is striking even factoring in a large margin of error.

These findings highlight the importance of including both attitudinal and acceptability metrics when measuring tolerance of large carnivores. Despite reporting more negative attitudes toward cougars, hunters in Ellensburg and Kalispell were just as accepting of cougar presence in their community as non-hunters, thereby demonstrating true “tolerance” (operationalized in Chapter 3 as “putting up with something you do not like”). The distinction between attitudes and acceptability is an important one to make – when attempting to improve tolerance among social groups with fairly entrenched attitudes toward carnivores, managers and conservationists may achieve better results by instead targeting fluid normative beliefs about acceptability, which can be more transient than attitudes (Nie, 2001).

**Management Implications.** As cougars continue to expand into their historical range, wildlife managers in Midwestern and Eastern states will shortly be called upon to set management goals that foster tolerance, promote healthy cougar populations, and reflect the needs of their constituents, both rural and urban. Results presented here suggest that for the majority of people in rural communities, hunting policy does not significantly influence attitudes toward or acceptability of cougars. However, managers should be aware that regulations set early on could have a lasting, top-down effect on attitudes toward hunting, and that hunters are likely to chafe under restricted cougar take. Depending on the makeup of their constituency, managers and conservationists should reach out to hunters early on and assess their concerns about burgeoning cougar populations before policy is established. Although hunters are a minority in the general public, they contribute a disproportionate amount of funding to wildlife conservation and management. Their cooperation will be necessary if cougars are to re-establish themselves east of the continental divide.

**Limitations and Future Directions.** The results presented here are the product of an observational study. Therefore, it cannot be stated with certainty that cougar policy directly influenced any of the state-by-state differences observed above. In the future, longitudinal studies of public attitudes following major wildlife policy changes could provide additional supporting information. Repeated surveys of wildlife stakeholders attitudes and normative beliefs about a species immediately before, immediately after, and several years after new wildlife policy goes into effect could provide stronger evidence to support results found here. In addition to longitudinal research, cross-sectional research across a variety of study areas, regulations, and species could reveal further patterns elucidating the relationship between wildlife policy and tolerance.

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Appendix

**Survey Instrument**

Introduction

You are invited to share your thoughts and opinions about cougars in your community. We are conducting this research to learn more about human attitudes toward cougars. The questions should take no more than 10 minutes to complete.

All of the information we collect will be confidential and at no time will your name or address be linked to the results. The survey is completely voluntary: you may stop the survey at any time and are free to withdraw from the study. Submitting the survey will be considered your consent to participate in the study.

If you have questions about your rights as a research participant, you may contact the University of Montana Institutional Review Board at (406) 243-6672 or irb@umontana.edu.

If you have questions about the project, you may contact:
Lara Brenner
MSc Candidate in Wildlife Biology at the University of Montana
lara.brenner@umontana.edu
or
Dr. Elizabeth Metcalf
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Please click the "Next" button in the bottom right-hand corner of the screen to continue.

Most of the following questions ask about your thoughts on cougars. The cougar is a species of wild cat known by many different names, including mountain lion, puma, catamount, and panther. For the purposes of this survey, we will use the common name **cougar** to refer to the animal known by those names.

A cougar (*Puma concolor*) on a rock.

Q1 Which state do you live in?

- California
- Montana
- Washington

**Cougar Attitudes**

Q2 Please select the number between 1 (Strongly Dislike) and 7 (Strongly Like) that indicates the extent to which you like or dislike cougars.

- Strongly Dislike **1**
- Dislike **2**
- Somewhat Dislike **3**
- Neither Like nor Dislike **4**
- Somewhat Like **5**
- Like **6**
- Strongly Like **7**

Q3 The following statements reflect different beliefs people have about **cougars**. Please select the number between **1** (Strongly Disagree) and **7** (Strongly Agree) that indicates the extent to which you agree or disagree with each belief.

| | Strongly Disagree **1** | Disagree **2** | Slightly Disagree **3** | Neither Agree nor Disagree **4** | Slightly Agree **5** | Agree **6** | Strongly Agree **7** |
|---|---|---|---|---|---|---|---|
| Cougars should be treated as nuisance animals in my area | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Cougars are an important part of the ecosystem | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Cougars have the right to exist wherever they are found | ○ | ○ | ○ | ○ | ○ | ○ | ○ |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| It is unethical to kill a cougar | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Humans should manage cougar populations so that humans benefit | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| I take pride in the amount of cougars in my area, even if they cause some problems | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| The possibility of encountering a cougar is a positive aspect of living in my area | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| The number of cougars in my area is increasing | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| I feel personally at risk from cougars in my area | ○ | ○ | ○ | ○ | ○ | ○ | ○ |

**Cougar Hunting Attitudes**

Q5 The following statements reflect different beliefs people have **cougar hunting**. Please select the number between 1 (Strongly Disagree) and 7 (Strongly Agree) that indicates the extent to which you agree or disagree with each belief.

| | Strongly Disagree **1** | Disagree **2** | Slightly Disagree **3** | Neither Agree nor Disagree **4** | Slightly Agree **5** | Agree **6** | Strongly Agree **7** |
|---|---|---|---|---|---|---|---|
| Hunting cougars is cruel and inhumane | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Hunting cougars is necessary to control their populations | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Using dogs to hunt cougars is cruel and inhumane | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Hunting cougars is necessary to teach them to fear humans | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| I would feel safer if more cougar hunting was allowed in my area | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Hunting cougars increases the chance of conflict with humans | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Hunting cougars improves deer hunting opportunities | ○ | ○ | ○ | ○ | ○ | ○ | ○ |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Hunting cougars reduces the chance of conflict with livestock | ○ | ○ | ○ | ○ | ○ | ○ | ○ |

**Cougar Behavioral Intentions**

*Display This Question:*
*If Which state do you live in? Montana Is Selected*
*Or Which state do you live in? Washington Is Selected*

Q6.1 The following statements present different types of hypothetical cougar policy. Please select the number between 1 (Very Unlikely) and 7 (Very Likely) that indicates the extent to which you would be likely or unlikely to vote for each cougar policy.

If you had to vote today, how likely is it that you would vote to...

| | Very Unlikely **1** | Unlikely **2** | Slightly Unlikely **3** | Neither Likely nor Unlikely **4** | Slightly Likely **5** | Likely **6** | Very likely **7** |
|---|---|---|---|---|---|---|---|
| ...increase cougar protections in your state | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| ...increase cougar hunting opportunities in your state | ○ | ○ | ○ | ○ | ○ | ○ | ○ |

*Display This Question:*
*If Which state do you live in? California Is Selected*

Q6.2 In the year 1990, California voters passed Proposition 117, which prohibited the sport hunting of cougars in the state and allocated $30 million per year for habitat protection.

If you were voting on Proposition 117 today, how would you vote?

○ Yes (Keep the Law)

○ No (Repeal the Law)

○ Neither (Would Not Vote)

**Cougar Experiences**

Q7 The following 4 questions refer to any experiences you have had with cougars over your lifetime. For each question, please select the response that best describes your experience.

Some of the questions ask you about encountering *signs* of a cougar. *Signs* of a cougar could include footprints, scat, claw marks, kill sites, sounds, scent, or anything that might indicate the presence of a cougar.

| | 0 times | 1 time | 2 times | 3-4 times | 5-10 times | 10-20 times | 20+ times |
|---|---|---|---|---|---|---|---|
| Approximately how often in your life have you encountered *signs* of a cougar in its natural habitat? | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Approximately how often in your life have you encountered *signs* of a cougar in your community? | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Approximately how often in your life have you encountered an *actual* cougar in its natural habitat? | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Approximately how often in your life have you encountered an *actual* cougar in your community? | ○ | ○ | ○ | ○ | ○ | ○ | ○ |

**Hypothetical Scenarios (Acceptability)**

Q8 The following questions present imaginary cougar-human interactions occurring in your community. These scenarios are **hypothetical**, meaning that they are situations that have not necessarily happened.

For each interaction scenario, please rate on a scale of **1** (Highly Unacceptable) to **5** (Highly Acceptable) the acceptability of management actions that could be used to address the situation by selecting the response that best describes your opinion.

**Scenario 1:** Residents of your community report sightings of a cougar. Although there have not been any direct negative encounters between humans and the cougar, people are concerned about its presence.

How acceptable or unacceptable would it be for wildlife authorities to take the following actions?

| | Highly Unacceptable 1 | Unacceptable 2 | Neither Acceptable nor Unacceptable 3 | Acceptable 4 | Highly Acceptable 5 |
|---|---|---|---|---|---|
| Do Nothing | ○ | ○ | ○ | ○ | ○ |
| Frighten the cougar away | ○ | ○ | ○ | ○ | ○ |
| Capture and relocate the cougar | ○ | ○ | ○ | ○ | ○ |
| Shoot and kill the cougar | ○ | ○ | ○ | ○ | ○ |

**Scenario 2:** A cougar has killed several pets in your community .

How acceptable or unacceptable would it be for wildlife authorities to take the following actions?

| | Highly Unacceptable 1 | Unacceptable 2 | Neither Acceptable nor Unacceptable 3 | Acceptable 4 | Highly Acceptable 5 |
|---|---|---|---|---|---|
| Do Nothing | ○ | ○ | ○ | ○ | ○ |
| Frighten the cougar away | ○ | ○ | ○ | ○ | ○ |
| Capture and relocate the cougar | ○ | ○ | ○ | ○ | ○ |
| Shoot and kill the cougar | ○ | ○ | ○ | ○ | ○ |

**Scenario 3:** A cougar has attacked and injured someone in your community.

How acceptable or unacceptable would it be for wildlife authorities to take the following actions?

| | Highly Unacceptable 1 | Unacceptable 2 | Neither Acceptable nor Unacceptable 3 | Acceptable 4 | Highly Acceptable 5 |
|---|---|---|---|---|---|
| Do Nothing | ○ | ○ | ○ | ○ | ○ |
| Frighten the cougar away | ○ | ○ | ○ | ○ | ○ |
| Capture and relocate the cougar | ○ | ○ | ○ | ○ | ○ |
| Shoot and kill the cougar | ○ | ○ | ○ | ○ | ○ |

**Social Group Identification**

Q9 Are you a hunter?

○ Yes

○ No

*Display This Question:*
*If Are you a hunter? Yes Is Selected*

Q9.1 Approximately how many days did you hunt (any game) in the past 12 months? Please enter a number in the box below.

*Display This Question:*
*If Are you a hunter? Yes Is Selected*

Q9.2 Have you ever purchased a cougar tag in any state?

○ Yes

○ No

*Display This Question:*
*If Have you hunted or do you hunt mountain lions? Yes Is Selected*

Q9.2.1 Have you ever used dogs to hunt cougars?

◯ Yes

◯ No

*Display This Question:*
*If Have you ever or do you currently hunt mountain lions? Yes Is Selected*

Q9.2.2 Approximately how many days did you hunt cougars in the last 12 months? Please enter a number in the box below.

Q10 Do you own livestock?

◯ Yes

◯ No

*Display This Question:*
*If Do you own livestock? Yes Is Selected*

Q10.1. What type of livestock do you own?

Please indicate the number and type of livestock that you own. Select one or more of the options by checking the box in the second column that corresponds to the type of livestock you own. Then, enter the approximate number you own in the box to the right of each selected option.

| | Select if owned | Approximate Number |
|---|---|---|
| Horses | ☐ | |
| Cattle | ☐ | |
| Poultry (Chickens, ducks, geese, turkeys, etc.) | ☐ | |
| Sheep | ☐ | |
| Goats | ☐ | |
| Pigs | ☐ | |
| Llamas or alpacas | ☐ | |

Other

*Display This Question:*
*If Do you own livestock? Yes Is Selected*

Q10.3 Have your livestock ever been threatened or attacked by a mountain lion?

- ○ Yes
- ○ No

Q11 Do you belong to any conservation-oriented groups/organizations?

- ○ Yes
- ○ No

*Display This Question:*
*If Do you belong to any environmental groups/organizations? Yes Is Selected*

Q11.1 Please list the conservation-oriented groups/organizations that you belong to below.

**Demographic Information**

This final section asks for some background information about you. The questions are optional and will be used for statistical purposes only.

Q12 What year were you born?
*Please enter a year in the box below.*

Q13 What is your gender?

- ○ Male
- ○ Female
- ○ Other ________________________________________________

Q14 How many years have you lived in the state that you currently reside in?
*Please enter a number in the box below.*

Q15 What is the highest level of education you have completed?

○ Some high school

○ High School or GED

○ Some college, but no degree

○ Business or trade school (Associates)

○ College (Bachelors)

○ Some graduate school, but no graduate degree

○ Masters, PhD, or professional degree

Q16 What was your total **household** income (before taxes) in the last calendar year?

○ 1 - Less than $20,000

○ 2 - $20,000 to $39,999

○ 3 - $40,000 to $59,999

○ 4 - $60,000 to $79,999

○ 5 - $80,000 to $99,999

○ 6 - $100,000 to $119,999

○ 7 - $120,000 or more

**ANCOVA tables for Community Differences**

**Tests of Between-Subjects Effects**

Dependent Variable: Cougar Attitudes

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. |
|---|---|---|---|---|---|
| Corrected Model | 96.530[a] | 8 | 12.066 | 9.508 | .000 |
| Intercept | 237.635 | 1 | 237.635 | 187.245 | .000 |
| Education | 11.082 | 1 | 11.082 | 8.732 | .003 |
| Livestock Owner | 3.197 | 1 | 3.197 | 2.519 | .113 |
| Length of Residence | 2.271 | 1 | 2.271 | 1.789 | .182 |
| Community | 3.725 | 2 | 1.862 | 1.467 | .232 |
| Hunter | 52.936 | 1 | 52.936 | 41.711 | .000 |
| Community * Hunter | 11.356 | 2 | 5.678 | 4.474 | .012 |
| Error | 611.711 | 482 | 1.269 | | |
| Total | 11982.034 | 491 | | | |
| Corrected Total | 708.241 | 490 | | | |

a. R Squared = .136 (Adjusted R Squared = .122)

**Tests of Between-Subjects Effects**

Dependent Variable: Acceptability of Cougars

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. |
|---|---|---|---|---|---|
| Corrected Model | 47.442[a] | 8 | 5.930 | 3.746 | .000 |
| Intercept | 130.985 | 1 | 130.985 | 82.748 | .000 |
| Education | 11.785 | 1 | 11.785 | 7.445 | .007 |
| Livestock Owner | 8.102 | 1 | 8.102 | 5.118 | .024 |
| Length of Residence | .412 | 1 | .412 | .261 | .610 |
| Community | 2.037 | 2 | 1.018 | .643 | .526 |
| Hunter | 21.743 | 1 | 21.743 | 13.736 | .000 |
| Community * Hunter | 6.141 | 2 | 3.071 | 1.940 | .145 |

| | | | | | |
|---|---|---|---|---|---|
| Error | 758.228 | 479 | 1.583 | | |
| Total | 4897.000 | 488 | | | |
| Corrected Total | 805.670 | 487 | | | |

a. R Squared = .059 (Adjusted R Squared = .043)

**Tests of Between-Subjects Effects**

Dependent Variable: Cougar Hunting Attitudes

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. |
|---|---|---|---|---|---|
| Corrected Model | 266.113[a] | 8 | 33.264 | 22.021 | .000 |
| Intercept | 310.722 | 1 | 310.722 | 205.697 | .000 |
| Education | 12.496 | 1 | 12.496 | 8.272 | .004 |
| Livestock Owner | 7.248 | 1 | 7.248 | 4.798 | .029 |
| Length of Residence | 11.816 | 1 | 11.816 | 7.822 | .005 |
| Community | 4.862 | 2 | 2.431 | 1.609 | .201 |
| Hunter | 180.114 | 1 | 180.114 | 119.235 | .000 |
| Community * Hunter | 11.478 | 2 | 5.739 | 3.799 | .023 |
| Error | 728.099 | 482 | 1.511 | | |
| Total | 8199.184 | 491 | | | |
| Corrected Total | 994.212 | 490 | | | |

a. R Squared = .268 (Adjusted R Squared = .256)

**Tests of Between-Subjects Effects**

Dependent Variable: Acceptability of Lethal Management

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. |
|---|---|---|---|---|---|
| Corrected Model | 106.505[a] | 8 | 13.313 | 10.942 | .000 |
| Intercept | 139.405 | 1 | 139.405 | 114.581 | .000 |
| Edu | 4.230 | 1 | 4.230 | 3.477 | .063 |
| Livestock Owner | .378 | 1 | .378 | .310 | .578 |
| Residence | 7.444 | 1 | 7.444 | 6.118 | .014 |
| Community | .714 | 2 | .357 | .294 | .746 |
| Hunter | 74.646 | 1 | 74.646 | 61.353 | .000 |

| | | | | | |
|---|---|---|---|---|---|
| Community * Hunter | 4.016 | 2 | 2.008 | 1.650 | .193 |
| Error | 586.429 | 482 | 1.217 | | |
| Total | 4729.583 | 491 | | | |
| Corrected Total | 692.934 | 490 | | | |

a. R Squared = .154 (Adjusted R Squared = .140)

**Tests of Between-Subjects Effects**

Dependent Variable: Hunting cougars is cruel and inhumane

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. |
|---|---|---|---|---|---|
| Corrected Model | 513.986[a] | 6 | 85.664 | 29.306 | .000 |
| Intercept | 226.012 | 1 | 226.012 | 77.320 | .000 |
| Edu | 7.749 | 1 | 7.749 | 2.651 | .104 |
| Livestock | 1.083 | 1 | 1.083 | .370 | .543 |
| Residence | 15.150 | 1 | 15.150 | 5.183 | .023 |
| State | 32.935 | 2 | 16.468 | 5.634 | .004 |
| Hunter | 403.046 | 1 | 403.046 | 137.885 | .000 |
| Error | 1414.763 | 484 | 2.923 | | |
| Total | 7947.000 | 491 | | | |
| Corrected Total | 1928.749 | 490 | | | |

a. R Squared = .266 (Adjusted R Squared = .257)

**Tests of Between-Subjects Effects**

Dependent Variable: Using dogs to hunt cougars is cruel and inhumane

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. |
|---|---|---|---|---|---|
| Corrected Model | 385.532[a] | 6 | 64.255 | 17.018 | .000 |
| Intercept | 256.697 | 1 | 256.697 | 67.988 | .000 |
| Edu | 8.125 | 1 | 8.125 | 2.152 | .143 |
| Livestock | 4.595 | 1 | 4.595 | 1.217 | .270 |
| Residence | 16.936 | 1 | 16.936 | 4.485 | .035 |
| State | 23.734 | 2 | 11.867 | 3.143 | .044 |
| Hunter | 264.904 | 1 | 264.904 | 70.161 | .000 |

| | | | | | |
|---|---|---|---|---|---|
| Error | 1827.405 | 484 | 3.776 | | |
| Total | 10772.000 | 491 | | | |
| Corrected Total | 2212.937 | 490 | | | |

a. R Squared = .174 (Adjusted R Squared = .164)