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Spatial and temporal patterns of a generalist urban carnivore;
American black bears (*Ursus americanus*) at Lake Tahoe (CA)

By

Jan Mario Kornelis Klip

A dissertation submitted in partial satisfaction of the
requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Justin S. Brashares, Co-Chair
Professor Stephanie M. Carlson, Co-Chair
Professor Eileen A. Lacey

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Spatial and temporal patterns of a generalist urban carnivore;
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By Jan Mario Kornelis Klip

Abstract

Spatial and temporal patterns of a generalist urban carnivore;
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University of California, Berkeley

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Human populations are growing and exert an increasing pressure on remaining wild habitats. Development and encroachment into wild habitats often create a wildland-urban interface. Understanding how and which species are able to persist or even flourish in these shared habitats, is important for conservation purposes and reducing human-wildlife conflict. Human-wildlife conflict may be of particular concern when it involves larger carnivores. Urban wildlife involved in conflict sometimes may be considered to have a lesser ecological value than its wild counterparts. This is particularly the case when animals are thought to be reliant on garbage and other human-provided food sources. However, as wild habitats shrink, wildlife cannot be exclusively preserved in remote wilderness settings. The American black bear (*Ursus americanus*) is a good example of an adaptable animal that is able to thrive in human-modified habitats but consequently is involved in high levels of reported bear-human conflict. Black bears are not endangered in most of their range, but lessons learned from this charismatic animal are likely applicable in deeper conservation contexts. In this dissertation, I attempted to better understand what it means to be classified as an urban animal, how spatial distributions and resource selection might vary between urban and wild areas, how drought might affect distributions, and how bear behavior might be influenced through human induced stimuli.

First, despite its ubiquitous use, the term “urban” was not homogenous throughout the scientific literature and needed to be defined. Spatially defined urban extents have great influence on whether wildlife is deemed urban or not. This was even more important because the prevailing paradigm prior to this study was that black bears observed in urban areas were spending the majority of their time in this habitat. From 2010-2014, I outfitted 27 bears with GPS Iridium radio collars in Lake Tahoe to understand spatial usage. I assessed existing urban definitions and tried to define the most conservative definition that would include human development in the broadest sense. I assessed whether bears were spending 50% or more of their time in urban areas,

if they did I considered them urban. During 2010-2011 no bears spent $\geq 50\%$ of their time in urban areas; during 2012 25% of the bears spent $\geq 50\%$ of their time in urban areas, whereas during 2013, 2014 and 2015 half of the bears spent $\geq 50\%$ or more of their time in urban areas. Additionally, I assessed preference at three different orders (scales). While bears appeared to prefer urban habitats at first order (defined as the study area), they generally did not select urban habitats within their home range (second order).

Further, I evaluated how home range estimates varied as a result of the method used and between urban and wild habitats. My results indicated that different home range tools and methods yielded different home range sizes and configurations. Home range sizes were not consistently statistically different from other published, mostly wild, bear home ranges. Additionally, I tried to illuminate how use of the urban area might increase as a result of drought. The Lake Tahoe region and California as a whole suffered a prolonged drought from 2012-2016. Wildlife were expected to seek out anthropogenic resources in close proximity to human habitation to overcome natural food deficits. An uptick in urban use in 2014 was noted and might be attributable to drought conditions. An effort was made to identify patterns in space use as a result of sex and season, and results indicated that home range sizes for females and females with cubs did not differ in size.

Additionally, I assessed how models might provide different results between urban and wild areas. During the fall season, overlap with the urban portion of the home range was strongest, and use was even more pronounced during the fall of 2014 as a result of drought impacts. The RSF function included roads, roads with speeds greater than 35 mph, hiking trails, wetlands, known bear conflict areas and elevation. Females with cubs selected for areas of known conflict, which is supported anecdotally by the large number of bear-human conflicts reported by a small number of females with cubs.

Finally, human-wildlife conflict has been growing globally and conflicts involving black bears also increased in number and significance throughout the western United States. This trend was particularly evident throughout the Lake Tahoe Basin. After meetings throughout the last decade with many local and regional stakeholders, including the late Senator Dave Cox, the California Department of Fish and Wildlife decided to implement aversive conditioning (AC) in addition to a continued education effort and depredation process allowing lethal removal of nuisance bears. AC was not intended to, nor had it previously been successful in persuading bears to leave urban areas. It had shown success, though, in modifying the behavior of certain bears by scolding bold behavior and rewarding their natural, shy behavior. I studied the effectiveness of using Karelian bear dogs and less-lethal ammunition to condition the behavior of bears. Three protocols were used: soft release, release with dogs, release with dogs and less-lethal ammo. I tested when bears would return to the capture location, reliance on the urban envelope, whether averted bears became more nocturnal, selected a hibernacula further away developed areas, were less winter active, decreased their foraging on anthropogenic resources and usage of known conflict areas. Contrary to expectation, some bears did not return to their capture or release locations. The

majority of these individuals had experienced AC, with AC with Dogs appearing to have the greatest effect. Additionally, the return to patch time (BRP) for bears treated with Karelian bear dogs was greater than bears in the Control group for their return to both capture and release locations. Dogs also had the greatest effect on all behavioral proxies examined and bears treated with Dogs seemed to become more nocturnal, less winter active and spent less time in urban areas. These impacts of bear behavior may ultimately reduce the level of conflict with humans.

The research presented in this dissertation adds to the growing body of literature on wildlife in the wildlife-urban interface and black bears specifically. Black bear behavioral responses to AC and how they may become less likely to engage in conflict showed promising results. My work suggested that a bear's ecology living in the wildlife-urban interface may be more complicated and that mixed space use strategies, using both wild and urban areas, appear to be common.

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1. General Introduction

Wildlife management and ecology has entered a phase where the impacts of humans on wildlife and vice versa are becoming more and more intertwined (McKinney 2008, Ellis et al. 2010, Artinuzzi et al. 2013). This has come as a result of an increasing amount of Wildlife Urban Interface (WUI) around the world (Crooks 2002, Radeloff et al. 2005). Ecological processes may be impacted by the WUI and wildlife that live here often shift their behavior (Riley et al. 2003, Baker and Harris 2007). Additionally, wildlife occupying niches closer to people may have a higher propensity for coming into conflict with humans (Treves et al. 2004, Graham et al. 2005). In some areas this brings forth conservation issues due to retaliatory responses, such as lethal removal of carnivores as a result of livestock depredation (Miller and Hobbs 2002, Treves and Karanth 2003). Some species of wildlife may benefit from living in the WUI. In many cases additional food sources become available due to human activities. For example, irrigated pastures or gardens may attract ungulates (Rondeau and Conrad, Jon 2003), fruit trees may attract various species including stone martens (*Martes fiona*; Hisano et al. 2016), access to garbage may attract raccoons (*Procyon lotor*; Riley et al. 1998), red fox (*Vulpes vulpes*; Harris et al. 1987) and various bear species (*Ursus* sp.; Baruch-Mordo et al. 2008, Coleman et al. 2013). As a result of these additional resources, fecundity may increase and consequently urban densities may become higher than wild densities (Beckmann and Lackey 2008), further increasing human-wildlife conflict.

In this dissertation I seek to advance the understanding of space use by wildlife in the WUI, and how space use may be affected by humans and human-induced stimuli. Specifically, I hope to 1) better understand when wildlife utilizing urban areas should be considered “urban wildlife” and how variation in urban definitions generate different results, 2) test different space use methods and models and their effect on habitat use descriptions, and 3) examine how space use of potential conflict within the WUI can be influenced through aversive conditioning.

Historical Perspective

While public interest in wildlife living within urban areas has endured for centuries (e.g., Rosenzweig and Blackmar 1992), the formal study and active management of urban wildlife is a relatively young pursuit (Ditchkoff et al. 2006). Urban wildlife was recognized early on by leaders in the wildlife profession. Leopold (1933) stated: “a pair of wood thrushes is more valuable to a village than a Saturday evening band concert and costs less”. The first president of the Wildlife Society, R. Bennitt, said in 1946: “I still look forward to the day when we shall hear men discuss the management of songbirds, wildflowers and biota of a city.....” (Adams 2005). Despite this interest, the study of urban wildlife didn’t begin in earnest until the National Wildlife Federation’s “Backyard Wildlife Program” in 1973 (Adams 2005). Other organizations, such as the Humane Society of the United States, supported this program. Later in the 1970s, The Wildlife Society initiated the coordinated study of urban wildlife through what is now called the Urban Wildlife Working Group, which focused on advancing science in urban environments.

The scientific literature on urban wildlife reflects its somewhat recent arrival as a formal area of study: only 2% of wildlife studies were devoted to urban wildlife in 1985 (Adams 2005).

The recent growth in the study of urban wildlife reflects not only scientific acceptance, but also changes in urban planning and management that have created habitat for wildlife within cities or pushed cities into areas that were recently wildlife habitat. People's desire to live in green areas in combination with wildlife laws, particularly the Endangered Species Act of 1973, incentivized land planners to integrate existing vegetation, mature trees, natural bodies of water and riparian corridors into new housing and other developments. In rural areas, large landholdings were subdivided into smaller parcels often to create "ranchettes" or suburban housing developments (Orlando 2008). As a result, the way our living spaces were created and managed changed, and the boundary between rural and urban became blurred. The new reality of wildlife in human-dominated areas challenged historical research focus on animals living in pristine areas (Cohn 2005).

Somewhat predictably, the first major thrust of wildlife research at the WUI focused on species considered aesthetically pleasing to urban dwellers, or at least not in conflict with humans. Even today, projects on urban songbirds and butterflies remain a primary focus of research and of great public interest (DeStefano and DeGraaf 2003). Urban species with the potential to cause extensive damage or that represent dangers to people and their pets traditionally fell outside of research and in the domain of wildlife control efforts. Thus, while millions of dollars a year were spent on control of urban squirrel (Sciuridae family), opossum (*Didelphis virginiana*), raccoon and other populations, surprisingly little formal research studied the ecology of these species in their urban habitat (Adams 2016). As that research has now grown, we have learned that more species are able to live in developed areas than initially thought, a process coined as "synurbanization," or the adjustment of wildlife to developed habitat (Luniak 2004, Adams 2005).

As urban areas became "greener" so too did public attitudes towards wildlife generally (Kellert 1984, Bingham et al. 1995) and urban wildlife specifically (Gilbert 1982, Conover 1997). Changing public attitudes towards wildlife transformed wildlife management policy. For example, a California ban on mountain lion (*Puma concolor*) hunting was enacted in 1990 (Proposition 117). California banned the use of dogs to hunt black bear (*Ursus americanus*) and bobcat (*Lynx rufus*) in 2012 (Senate Bill 1221), and a statewide ban on trapping bobcats was established in 2015. Thus, in California, changes in attitudes about carnivore harvest and possibly optimism for human-wildlife coexistence have created new opportunities for wildlife to utilize urban habitats but also new challenges associated with managing these species. Perhaps no species embodies these changes and challenges in California more than the black bear.

Black bears have been among the greatest beneficiaries of increased environmental legislation and more protective public attitudes towards wildlife. In fact, black bear populations have grown over the last few decades across North America (Garshelis and Hristienko 2006), including in

California. However, this population growth, combined with a renewed popularity of backyard chickens (Matt 2012, Schindler 2012) and ever-increasing access to garbage, has resulted in heightened bear-human conflict. Conflict between bears and humans is not a new phenomenon; the attraction of bears to garbage and other anthropogenic food sources is particularly well-studied (Rogers et al. 1974, Robbins et al. 2004, Matthews et al. 2006, Merkle 2011). Thus, while bear-human conflict is not new, the recent resurgence of black bear populations, both in abundance and distribution, has led to rapidly increasing rates of conflict in urban and peri-urban areas. Conflict in such areas is now so common that an entire sub-field of bear research has developed around their management and ecology in urban areas.

This dissertation aims to add to the growing body of literature in this field with novel approaches to address urban wildlife management challenges. It also attempts to bring forth suggestions which are applicable broadly and may help find management solutions to human-wildlife conflict that have eluded wildlife managers for at least forty years now.

Study System

I conducted my field studies in the western portion of Lake Tahoe stretching along the highway 89 corridor to Truckee (CA). This covers El Dorado, Placer and Nevada counties in California and is an 850 km² area. Elevation within the study area ranged from 1897m at lake level to 3317m. The Lake Tahoe ecosystem supports a variety of wildlife including mountain lions, coyotes (*Canis latrans*), bobcats, beaver (*Castor canadensis*) and mule deer (*Odocoileus hemionus*). Vegetation in this area was dominated by a mixed conifer forest of white fir (*Abies concolor*), Jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*Pinus contorta*), and red fir (*Abies magnifica*; Roth et al. 2004). The area is an important tourist destination during both the summer and winter seasons. During the summer, over a million tourists vacation here, and in winter well over 2.5 million visit the area for skiing and other winter sports activities. Wildlife in the area overlap dramatically with humans, with black bears, coyotes, and beavers often linked to high levels of human-wildlife conflict each year. Beavers dam small streams and cause flooding that damages homes and gardens or build lodges underneath floating piers, impairing their function. Coyotes attack pets and bears break into vacation homes and cars and rummage through people's belongings in campgrounds in search of food. While these issues are not new, the many people who visit the area are unprepared to avoid wildlife conflict because they come from locations where they do not cohabitate with bears, such as the San Francisco Bay Area or the Sacramento Area. Consequently, their awareness of bear-human conflict may be limited, and once they undergo the learning experience they are "replaced" with a fresh "crop" of naïve tourists.

Dissertation Outline

In chapter 2, I sought to understand how the ecology and behavior of black bears in human-dominated areas might be interpreted differently because of the definition of "urban" used in spatial analyses. I used four definitions of the urban extent to quantify usage of urban areas by

radio collared black bears, and I tried to understand whether urban versus wild is truly a binary classification or whether bears employed mixed space strategies. I also quantified several aspects of habitat use and behavior of bears fitted with GPS collars as they moved across gradients of human settlement to better understand when and what habitats are used in the urban and wild interface. I looked at how use of the urban interface changed during the day, month, season and year, and I compared the influence of sex class to illuminate patterns. I concluded the analysis by assessing three orders (scales) of habitat preference. My results send a cautionary signal regarding imprecise definitions for urban areas, as different definitions generated vastly different results regarding patterns of bear activity. Additionally, considering bears in a binary fashion, defining them either as urban or wild, seems to oversimplify the complex ecology of bears utilizing urban areas. Many of the bears I studied employed a dominant mixed space strategy. Additionally, when assessing habitat use in urban areas, bears appeared to select for vestiges of natural habitat. Patterns of habitat selection appeared to illustrate resource partitioning between the sexes, especially between males and females with cubs. Finally, habitat selection varied between the three spatial scales assessed and demonstrated how preference for certain habitats was scale dependent.

In chapter 3, I evaluated three different home range methods and compared results from this study to close to 80 previously reported home ranges. Furthermore, I assessed how sex and season affects home range size and examined the dependency of bears on the urban envelope by assessing seasonal home range overlap with the urban areas. I assessed the effect of drought on home range overlap and modeled habitat selection within the home range through a resource selection function (RSF). These efforts revealed several patterns that have direct relevance for understanding the ecology and management of black bears that live in and around urban areas. My results indicated that different home range tools and methods yielded different home range sizes and configurations. Home range sizes were not uniformly statistically different from other published, mostly wild, estimates of bear home ranges. Furthermore, females' and females with cubs' home range sizes did not differ from each other. Home range overlap indicated that the urban area is of disproportionate importance to these bears, further supported by the fact that the overlap of the core home range was greater than 95% of locations. Additionally, the increase in home range overlap within the urban area in the fall of 2014 was likely attributable to the impacts of drought. Finally, the RSF indicated that males unexpectedly selected for roads and that females with cubs selected areas of known bear conflict the strongest.

In chapter 4, I assessed the efficacy of using aversive conditioning (AC) on American black bears. Previous studies generally focused on whether animals return to the area where they were a nuisance, I looked further into how behavioral proxies and AC with Karelian bear dogs (KBD) might influence spatial patterns. Specifically, I tested if the AC treatment was predictive of bears a) changing their daily activity patterns to become more nocturnal, b) spending less time in urban areas, c) selecting hibernacula further from roads and homes, d) becoming less active in the winter, and e) becoming less reliant on food-waste dumpsters. By measuring these various

aspects of bear behavior, I hoped to gain a deeper insight on the efficacy and sustainability of commonly used AC methods. Contrary to expectation, some bears did not return to their capture or release locations. The majority of these individuals had experienced AC, with AC with Dogs appearing to have the greatest effect. Additionally, the number of days before bears returned to the capture and release location was greater for bears treated with KBDs. Dogs also had the greatest effect on most bear behavioral proxies examined and bears treated with Dogs seemed to be more nocturnal, less winter active and spent less time in urban areas. These impacts on bear behavior may reduce their level of conflict with humans. Based on these findings, I conclude that Karelian bear dog programs are a valuable addition to programs focused on dealing with bears in the wildlife urban interface.

In the final chapter of this dissertation, I draw general conclusions and summarize key findings of the dissertation and provide recommendations and direction for future research in human-wildlife conflict. These recommendations and reflections are based on my dissertation research and my nine years working as a wildlife professional with the California Department of Fish and Wildlife.

2. What makes an urban bear urban?

Introduction

The human population in the United States is growing, and wildlife habitat is being lost at an alarming rate (Mckee et al. 2003, Ellis et al. 2010, Artinuzzi et al. 2013). As a result, the interface between urban areas and wildlife, i.e., the Wildlife Urban Interface (WUI), is growing (Radeloff et al. 2005). Wildlife is affected by living in the WUI or in closer proximity to humans in part because their habitats are lost, developed, and homogenized (McKinney 2006). Many animals change their behavior when in close proximity to people (Frid and Dill 2002, Riley et al. 2003, Rondeau and Conrad, Jon 2003, Baker and Harris 2007). Additionally, living in and near human-dominated areas can affect the life histories and population trends of wild animals (DeStefano and DeGraaf 2003, Ditchkoff et al. 2006, Gehrt, Stanley and Riley 2010). Not surprisingly, wildlife living in proximity to developed areas frequently come into conflict with people. Conflicts affect their conservation (Miller and Hobbs 2002), especially when wild animals attack people, their pets (Graham et al. 2005, Grubbs and Krausman 2009), or cause monetary damage (Conover 1997, Decker and Chase 1997, Merkle 2011).

Initially, research at the WUI did not focus on human-wildlife conflict but on species considered aesthetically pleasing to urban dwellers (Adams 2005). As that research has now grown, we have learned that more species are able to live in developed areas than was initially thought, a phenomenon termed “synurbanization,” defined as the adjustment of wildlife to developed habitat (Luniak 2004). Some generalist species benefit from WUI while excluding many specialists (Crooks 2002). These ecological “winners” of human development included wild boars (*Sus scrofa*) in Berlin, Germany (Jansen et al. 2007), white tailed deer (*Odocoileus virginianus*) in the Eastern United States (Kilpatrick et al. 2004), bobcats (*Felis rufus*) in the Western U.S. (Ruell et al. 2009), and bears (*Ursus sp.*) in North America (Beckmann and Berger 2003b). In fact, black bear (*Ursus americanus*) populations have grown over the last few decades across North America (Garshelis and Noyce 2006, Scheick and McCown 2014), including in California. Perhaps no species has benefitted from utilizing the California WUI as much as the black bear.

Studying bears in the WUI requires clear definitions for what is considered urban, particularly because many wildlife species may deploy a mixed space strategy, including use of both wild and urban areas. The rapid growth of research in this area has been confounded by the lack of a clear definition of “urban.” According to the U.S. Census Bureau (2010), the term “urban” refers to areas with more than 1000 people per square mile. However, this is seldom the definition employed in studies of urban wildlife. For example, The Wildlife Society’s Urban Wildlife Working Group defines urban wildlife as “species that utilize human dominated landscapes” (Wildlife Society 2012). To further complicate matters, the term “human-dominated” is also vague and lacks a precise definition. Previously published work on urban bears have defined “urban” in various ways including a) areas within officially designated city limits (Lyons 2005, Beckmann and Lackey 2008), b) areas exceeding a threshold housing density (Luke 2013), or c) with no explicit definition of this criterion (Baruch-Mordo et al. 2008). This inconsistency has created an “apples to oranges” challenge when comparing studies of urban wildlife broadly and

urban bears specifically. Without a precise spatial delineation of urban, results vary in space and time, often in the same regions.

An additional challenge is that urban wildlife is often approached in a binary fashion, i.e., a bear is considered either urban or wild (Lyons 2005, Beckmann and Lackey 2008), with urban bears being those that spend the majority of their time in urban areas (Beckmann and Lackey 2008). But what percentage of time is sufficient for a bear to be considered urban? Prior research suggests that bears utilize the urban landscape because of the availability of anthropogenic food sources (Rogers et al. 1974, Robbins et al. 2004, Peirce and Van Daele 2006, Merkle 2011). Moreover, bears are expected to use urban areas mostly at night (Lyons 2005, Matthews et al. 2006). Finally, bears are expected to use urban areas relatively more during the spring and fall when additional calories are required (Lewis et al. 2015). In spring, bears are just waking up from hibernation, and in the fall bears in hyperphagia are preparing for hibernation.

Beyond the challenge of defining whether bears are wild or urban, there are also many knowledge gaps related to bear habitat use in urban areas. For example, when bears use urban areas, do bears use areas that are vestiges of the “original” native habitat, similar to other wildlife? (McKinney 2002). Anecdotal evidence suggests that riparian areas are used extensively by bears in Lake Tahoe’s urban habitats (Klip, unpublished). Habitat use of urban bears, however, has not been studied widely, although Tri (2016) found that WUI bears did not differ much in habitat use from wild bears. Understanding habitat use and preferences may help understand how the behavior of urban bears differs from wild bears and potentially help mitigate bear-human conflict in urban areas.

In this study, I show how our understanding of the ecology, behavior, and management of black bears in human-dominated areas has been influenced by the definition of “urban” used in analyses. Specifically, I tested if a) different definitions for the urban extent generated different estimates of resource selection and different conclusions regarding whether urban bears used the urban envelope exclusively or employed mixed space use strategies (hereafter; Urban extents and mixed space use), b) described time allocation of bears spent in urban areas and how this varied temporally and by sex (hereafter; Temporal variation), and c) assessed the habitat usage of bears captured in urban environments and characterized the habitats preferred at three orders of habitat preference (hereafter; Habitat use and preference). By providing one of the first detailed characterizations of the urban extent and space use by bears in urban habitats, my analyses contributes to improved management of bears living in close proximity to people or in the WUI.

Methods

I collected bear movement data from Spring 2011 to Spring 2015. During this period, 27 bears were captured, including 12 females, 10 males, and five females with cubs.

Study area

This study was conducted in the western portion of the Tahoe Basin (hereafter; Basin), in El Dorado, Placer and Nevada counties, California (Figure 1). The outer extent for analysis was defined by enclosing all bear GPS locations with a 500m buffer. The full study area

encompassed approximately 850 km², consisting of both private and public property. Elevation within the study area ranged from 1897m at lake level to 3317m. Vegetation in this area was dominated by a mixed conifer forest of white fir (*Abies concolor*), Jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*Pinus contorta*), and red fir (*Abies magnifica*; Roth et al. 2004). California Wildlife Habitat Relationships (CWHR) plant communities present in the study area included montane hardwood, montane hardwood-conifer, riparian, chaparral, wet meadow, and barren (Mayer and Laudenslayer 1988).

Capture methods

Trapping locations for black bears were selected based on the following criteria: safety, ability to monitor the trap, limited opportunity for trap tampering, recent bear activity, and opportunity to obscure the trap from the road. Coordination with local businesses, homeowners, and governmental organizations such as California State Parks helped me secure trapping locations. No trapping occurred in areas where bears were causing damage to homes and vehicles. Trapping in these areas commenced either once the offending bear had been euthanized or until no new damage had been detected for at least two weeks (no damage for two weeks was considered indicative that the offending bear had left the area).

Bears were captured between May and November of 2011 to 2014 using a heavy-duty box trap mounted on a trailer (Figure 2). Trapped bears were chemically immobilized using Telazol (Fort Dodge Laboratories Inc., Fort Dodge, IA) following the California Department of Fish and Wildlife (CDFW) Capture and Restraint Manual (Jessup et al. 2001). UC Berkeley's Institutional Animal Care and Use Committee (IACUC) approved all animal handling procedures (IACUC: R358-0315, Sikes 2016).

Adult bears were outfitted with ATS Iridium collars (model G2110E, Advanced Telemetry Systems, Isanti, MN) in 2011 and 2012. During later years, Vectronic Iridium collars (Model GPS PLUS Vectronic Aerospace GmbH Carl-Scheele-Str. 12D-12489 Berlin Germany) were used. Sub-adults were not included in the study to avoid complications resulting from embedding of the collar in the neck as young individuals grow. During the first six weeks of deployment, collars were programmed to gather locations every 20 minutes to monitor for post-capture mortality. After six weeks, positions were gathered every two hours to conserve battery life. All collars were also equipped with VHF transmitters to facilitate location on the ground in real time. In addition to remote drop off mechanisms, cotton spacers that degrade over time were bolted on all collars (Hellgren et al. 1988, Garshelis and McLaughlin 1995); both procedures ensured that animals would not permanently have the collar around their neck. All bears handled were permanently marked with an ear tag (Allflex International, Dallas, TX, 75261) for recognition during future captures or sightings. Bears captured during the hunting season (August - December) were outfitted with an ear tag containing a warning to contact CDFW prior to consuming the animal due to potential drug residue. Preventive measures were taken to avoid infection at the injection site; penicillin and Blu-kote® (H.W. Naylor Co. Inc. Morris, N.Y.) were applied to areas where skin perforation had occurred due to the application of ear tags and injections. Bears were allowed to recover for a minimum of six hours in a quiet location prior to release. The animals had access to clean drinking water upon waking up and recovered without disturbance.

Three sex classes were defined: (1) females, (2) females with cubs, and (3) males. I assigned all individuals to one of the following age classes: cubs less than one year of age and accompanied by a sow, sub-adults over one year old and not accompanied by a sow (40 and 100kg), and adults (> 100kg). Captured bears also participated in an Aversive Conditioning (AC) study, with three treatment groups (control, AC with dogs, and AC with dogs and less-lethal ammo). The effects of AC are reported in chapter 4.

Data layers and software utilized

Three pre-existing spatial definitions of “urban” and a combination of the three definitions were used to classify bears as wild or urban. The overarching objective was to generate a spatial definition that would encompass most developed areas, thereby preventing the erroneous assignment of GPS locations as wild.

The four different spatial extents used to define urban were City Limits, Remote Sensing Data (a.k.a. eVeg), U.S. Census (2010), and the aggregation of the aforementioned (hereafter; Combined). City Limits data were collected from the Tahoe Regional Planning Agency (TRPA) and identified town and city boundaries (<http://www.trpa.org/gis/>). The second urban extent, “eVeg”, was obtained from Forest Service Tiles 17Am 17B, 21A, 21B at a scale of 1:24,000 or 1:100,000 (1:24,000 was not available for tiles 17B and 21A). eVeg classified major ground cover types (USDA Forest Service Pacific Southwest Region 2010); roads and buildings were the main spatial elements defining this urban extent. The third urban extent was Census, which considered all homes in the Basin regardless of whether they were occupied seasonally or year-round. Finally, the fourth spatial extent, Combined, aggregated the previous three spatial criteria and perhaps not surprisingly resulted in the largest urban spatial extent.

All spatial data layers downloaded were re-projected from their native projection to WGS-84 UTM Zone 10. Spatial analyses were completed in ArcGIS 10.2 (ESRI 2015, ArcGIS Desktop, Redlands, CA, Environmental Systems Research Institute) and R (version 3.1.3 R Core Team 2014, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>). Graphs were made in GGPLOT2 (Wickham 2009) or base R and tables were produced in kableExtra (Zhu 2018). Data reorganization and manipulations were done using the following R packages: PLYR (Wickham 2011), Dplyr (Xie 2018), Knitr (Xie 2018), STRINGI (Gagolewski 2015), RESHAPE (Wickham 2007) and doBy (Hojsgaard and Halekoh 2014).

Quantifying bear activity in urban areas

I classified bears as “urban” if they spent the majority of their time (> 50% of their GPS locations) in urban areas, and the analysis was repeated for all four urban spatial extents. All urban extents were buffered by 250m to account for bears that were likely to enter an urban area shortly after a location was recorded just outside the urban limit. GPS locations within the limits of the area identified as urban were considered urban, while those outside the urban area were considered wild. The number of locations in the specific urban patch (urban definition) divided by the total number individual animal locations defined the percentage of urban use.

Temporal differences between urban and wild areas

Temporal analyses were completed to understand hourly, monthly, and seasonal urban space use patterns. This analysis focused on urban use percentages based on the Combined urban extent in comparison to wild use percentages. Proportions were calculated by taking the total number of urban locations divided by the total locations for each temporal scale of interest. Pearson's Chi-square analyses were performed to understand whether space use varied in urban and wild locations and how sex may influence temporal patterns. The null hypothesis for the monthly analyses was defined as urban and wild percentage deviations from 50%. This percentage was selected because use was in one of two categories (urban and wild).

Habitat use comparison in urban and wild areas

Differences in habitat use between urban and wild areas were assessed by associating each bear's GPS locations with the National Land Cover Database (NLCD) habitat type at each GPS location (Homer et al. 2015), based on the Combined spatial extent analysis because it was the most inclusive spatial extent. Areas within the Combined urban extent were considered urban and ones outside the Combined extent were considered wild. While this may seem circular, the "wild" GPS locations outside of the urban definition may have urban land habitat types associated with them. The original NLCD classification consisted of 16 categories, of which 11 were present within the study area (Table 1). I assessed which NLCD categories were used by associating the NLCD value for each bear to the individual GPS location. The ones used the most, based on percentage of data points within each habitat type, were Evergreen Forest (72%), Shrubs / Scrub (13%), and Develop Open Space (8%). All utilized categories were retained, except for Barren, because habitats may be used seasonally or sporadically and fill an important function. The other habitat types taken into consideration were Developed Low Intensity (representing 4% of the observations), Developed Medium Intensity (1%), Developed High Intensity (0.22%), Deciduous Forest (0.07%), Mixed Forest (0.06), Grasslands/Herbaceous (0.20%), and Emerging Herbaceous Wetlands (0.29%).

Locations and associated land cover categories were analyzed in three ways. First, the analysis combined all sexes and contrasted proportional monthly habitat use in urban and wild patches. Second, the data were partitioned by season and year to illuminate inter-annual variation between proportional urban and wild usage. Third, the data were compared by season and sex. All comparisons were completed by comparing proportions with Pearson's Chi Square analyses.

Habitat preference analysis

Habitat preference, or the disproportionate use of habitats (Krausman 1999), was calculated by comparing usage to availability. Preferences were reviewed at three orders: first, the total study area (Figure 1); second, the 95% Kernel Density Estimation (KDE) home range for each bear; third, the urban and wild patch within the aforementioned home range. In particular, the wild patch was defined as the area outside the urban extent but within the home range, and the urban patch was defined as the urban area within the bear's home range.

Relative availability was calculated from the NLCD habitat types, as described earlier. Proportional availability was calculated by dividing the total number of raster cells for each habitat type by the total number of raster cells for all habitat types combined. Availability was calculated for the entire study area (first order), for the home range (second order) and for the

wild and the urban patch within the home range (third order). Relative use was defined by associating the appropriate NLCD habitat type to each bear GPS location. The total number of locations for each habitat type was divided by the total number of GPS locations for each bear and repeated for all three orders.

Preferences were assessed based on a comparison of the means of availability and use (i.e., two sample t-tests) and at the individual level by comparing individual use percentages directly with available habitat availability percentages. Preferred habitats were those used more than the relative availability of that habitat. Finally, I compared the three orders to each other to illuminate different habitat preferences at different scales.

Results

Urban definitions – defining urban spatially

Applying different definitions to the term “urban” resulted in varying estimates and configurations of urban portions of the study area. The area identified using the Combined criterion (161 km²) was, as expected, larger than the area identified using one of the other three criteria. The second largest was eVeg and represented 66% (107 km², Figure 3) of the Combined area size. City Limits represented 56% (90 km², Figure 3) and Census 43% (70 km², Figure 3) of the Combined extent (Figure 4). The size of the areas represented by the three definitions were marginally statistically different from each other ($\chi^2 = 10.29$ df= 2 p=0.058). While the Combined spatial extent is an aggregation, the three spatial extents were not cumulative because the extents overlap with each other. When looking at each spatial extent, City Limits overlapped 43% with Census, and 54% with Remote Sensing. On the other hand, Census overlapped 55% with City Limits and 70% with Remote Sensing. Finally, the Remote Sensing overlap with the other two spatial extents was the same, 45% overlap with both City Limits and Census.

Configuration of the three urban extents varied considerably (Figure 3). If urban is defined using City Limits, the polygons are centered around the main towns and cities in the Basin. For example, in the city of South Lake Tahoe, City Limits included portions of the lake but did not include developed areas away from towns such as around the Squaw Valley Ski Resort. Additionally, the town of Tahoma on the West shore has grown significantly beyond its city limits. In contrast, if urban areas are defined using remote sensing, urban encompassed all roads and buildings that could be identified through remote sensing (Figure 4). This included areas that fell outside of the City Limits definition. The Census definition included all homes in the study area (Figure 3), resulting in many small polygons categorized as urban. However, roads were not included in this definition.

City Limits, Census, and Remote Sensing varied greatly in terms of the identified urban areas, but all three have elements that make intuitive sense. Thus, the Combined definition might be most appropriate as it aggregates results from the three definitions.

Measurements of bear activity in urban areas differs based on urban classification approach

Twenty-four bears were included in this analysis. As expected, the Combined definition resulted in the highest mean urban use percentage (43% \pm SD 25%); this percent use was significantly greater than those for the other spatial extents (t-test: $t_{(72)} = 3.40$, $p < 0.01$; Figure 5). Under the Combined definition, nine bears (37.5%) had an urban percentage greater than 50%, indicating that nine bears would be considered “urban” if urban is defined as spending at least 50% of their time in urban areas. Of the nine bears, six were females, one was a female with cubs, and two were males. Mean percent urban usage for the four spatial extents differed significantly from each other (linear mixed-model, $F_{3,96} = 2.79$, $p < 0.05$). The City Limits definition returned a mean urban use percentage of 30.5% (\pm SD 25.4%); including eight bears (33.3%) with urban usage above 50%, including five females, one female with cubs, and two males. Urban usage based on the Remote Sensing definition was 31.8% (\pm SD 24.6%), including six bears (25%) with usage above 50% (four females and two males). The urban usage for the Census definition was 24% (\pm SD 18.3%) and showed just two (8.33%) females with a usage above 50%.

Temporal differences between urban and wild areas

Next, I examined temporal differences of space use based on hourly, monthly, and seasonal urban space use patterns, using data from the Combined spatial extent. Bears utilized the landscape differently over the course of a day. Bears were found predominantly in urban areas before 06:00 h and after 18:00 h. Occurrences in urban areas typically decreased between 04:00 and 06:00 and increased after 18:00. This pattern was similar for all sexes classes (Figure 6) and appeared to be most pronounced for male bears. An hourly comparison of urban to wild use with the use of Pearson’s Chi Square tests for the three sex classes revealed that relative proportions were significantly different among sex classes, except for one hour (8:00) ($\chi^2 = 6.48$ df= 2 $p = 0.084$). Sample estimates at 8:00 were 43% for females, 40% for females with cubs, and 40% for males. At all other hours at least one proportion of one of the sex classes was significantly different from each other (Table 2).

Urban use differed among the sex classes for all months except for July (50%, $\chi^2 = 0.009$ df= 1, $p = 0.924$) and October (51%, $\chi^2 = 2.68$ df= 1 $p = 0.10$). On a monthly basis, female urban use proportions differed significantly from 50% except for January (49%, $\chi^2 = 0.383$ df= 1 $p = 0.54$) and June (51%, $\chi^2 = 0.38$ df= 1 $p = 0.539$). Females generally used the urban envelope more than 50% in April, September and October. Among females with cubs, proportion of urban use differed significantly from 50% for all months, and females with cubs generally used the urban envelope more than 50% from June through September. Among males, proportions of urban use differed significantly from 50% for all months except October (50%, $\chi^2 = 0.136$ df= 1 $p = 0.713$, Table 3). Males used the area more than 50% in February, August and December. It appeared that females used wild lands more than urban lands from January until the middle of March (Figure 7), with use of urban areas decreasing again from October to November. Females with cubs did not use urban lands from January to April and then used wild areas more in the fall months compared to females without cubs. Peak use of urban areas by females with cubs was in June. Males used urban areas more than wild areas in July and August; however, use after July decreased and increased again in September with peak use in October.

Seasonal variation in use of urban areas (Table 4) was significantly different from 50% for all seasons (51%, $\chi^2 = 3.54$ df= 1 $p > 0.05$). During the spring, sample estimates of urban use were 39% for females, 43% for females with cubs, and 31% for males; ($\chi^2 = 215$ df= 2 $p < 0.0001$). In the summer, these values were 51% for females, 63% for females with cubs, and 54% for males; again, these values were significant ($\chi^2 = 171$ df= 2 $p < 0.0001$). In the fall, all sexes displayed greater use of urban areas, with values of 59% for females, 44% for females with cubs, and 44% for males, and values also differed significantly from each other ($\chi^2 = 603$ df= 2 $p < 0.0001$). Finally, values in the winter were 33% for females, 21% for females with cubs, and 61% for males; these values were also significantly different from each other ($\chi^2 = 1343$ df= 2 $p < 0.0001$).

Habitat use

Annual habitat use based on NLCD showed that the importance of different habitat types to bears varied across years (Figure 8). In 2012, Evergreen Forest was used more in urban patches ($\chi^2 = 1533$ df= 11, $p < 0.001$) compared to wild areas. In contrast, Evergreen Forest was used more within wild areas in all other years (2011, 2013, 2014, and 2015). Similar use of Emergent Herbaceous Wetlands in urban and wild areas was reported in 2013 ($\chi^2 = 0.99$ df= 1, $p > 0.05$) and 2014 ($\chi^2 = 0.57$, df= 1, $p > 0.05$). Grasslands also appeared important within City Limits; in 2011, Grasslands were used more in urban than in wild areas ($\chi^2 = 15.51$ df= 1, $p < 0.001$), while in the remaining years this trend was reversed (Table 5). During the fall of 2011 and 2013, Shrubs / Scrub was used more in relation to other land cover types in wild areas (Figure 9).

Seasonal habitat analysis suggested that during the summer use of Evergreen Forest was significantly greater ($\chi^2 = 109$ df= 1, $p < 0.001$) within the urban envelope in comparison to wild areas; the converse was found for the other three seasons. A similar pattern, although less pronounced, was found for Shrubs / Scrub in the summer, during which over 35% of the total for this habitat type was within the urban envelope. During the fall, use of Grasslands in urban and wild areas did not differ ($\chi^2 = 0.80$ df= 1, $p > 0.05$, Table 6).

When examined at the level of months (Table 7), I found that monthly use of Evergreen Forest differed between urban and wild areas, with 40% of all Evergreen Forest use recorded within the urban area. During June, use of Emergent Herbaceous Wetlands did not differ between urban and wild areas ($\chi^2 = 1$, df= 1, $p > 0.05$). The highest use of Developed Open Space by bears occurred during September, October, and November. Shrub / Scrub use was highest in wild areas during January, March, April, May, September, and October (Figure 10), with use of Developed Open Space being highest during the remaining months. February was the only month in which use of Shrubs / Scrub was greater in urban compared to wild areas ($\chi^2 = 37.54$, df= 1, $p > 0.001$).

I examined use of Shrubs / Scrub in greater detail because of its importance as a berry-producing habitat. I also explored use of Developed Open Space in greater detail because this habitat type includes golf courses, which anecdotally appear to attract bears. I found seasonal differences based on sex (Figure 11) for the Shrubs / Scrubs habitat type. Females with cubs appeared to use this habitat predominantly during times that males were not using the habitat as heavily. This was most pronounced during the summer when I found percent use to be 22% for females, 7% for females with cubs, and 35% for males; these differences among sex classes were significant ($\chi^2 = 764$ df= 2, $p < 0.001$, Table 8). A similar observation was made for summer use of Developed Open Space areas, in which I estimated use of 37% for females, 19% for females with cubs, and

41% for males, and again sex classes significantly differed from each other ($\chi^2=235$ df= 2, $p<0.001$).

Habitat preference analysis

Twenty-six bears were used for this analysis. Analyses of the percentage use and availability (two sample t-test) of first order habitat preferences (Table 9) found that all habitat types were selected ($P<0.05$) except Grasslands, Evergreen Forest, and Wetlands. Direct comparison of availability to percent use found that Developed Open Space, Developed Low Intensity, and Developed Medium Intensity were preferred by 17, 16, and 14 bears respectively. Evergreen Forest was preferred by nine and Shrubs / Scrubs was preferred by five bears (Table 10).

Analyses of mean use and availability at second order habitat preference found that Grasslands (two-sample t: $t(1) = -3.08$, $p < 0.05$) was the only habitat type preferred within individual home ranges (Table 11). When assessing use relative to availability at the level of individual bears, I found that developed areas were preferred by 12, 13 and 11 out of 26 bears for Developed Open Space, Developed Low Intensity, and Developed Medium Intensity areas, respectively (Table 12). Eighteen bears preferred Evergreen Forest, five bears preferred Emerging Herbaceous Wetlands, three bears preferred Grasslands / Herbaceous, and nine bears preferred Shrubs / Scrubs habitat.

Finally, I found that within wild areas, none of the habitat types were selected based on comparison (t-tests) of means for third order habitat preferences (use mean > available mean and $p<0.05$, Table 13). When comparing use and availability for each bear, I found four bears preferred Developed Open Space and one bear preferred Developed Low Intensity. Evergreen Forest was preferred by eighteen bears, Shrub / Scrubs was preferred by nine bears, while one bear preferred Grasslands (Table 14). When assessing the availability and use for the urban patch, I found a marginal preference for Evergreen Forest (two-sample t: $t(1) = 2.02$, $p=0.054$); no other habitat types were preferred (Table 15). I found that within urban areas, seven bears preferred Developed Open Space, and six bears preferred Developed Low Intensity and Developed Medium Intensity. Evergreen Forest was preferred by seventeen bears, while Shrubs / Scrubs was preferred by eight bears, and only two bears preferred Emerging Herbaceous Wetlands (Table 16).

Discussion

I examined how different definitions of the urban extent generated different results and whether urban bears use mixed space strategies. Mixed strategies would entail use of both urban and wild habitats and suggest that bears should not be labeled as either “urban” or “wild”. Furthermore, I looked into temporal variation of bear use within urban areas. Finally, I assessed habitat use and preference at three scales.

The comparison of urban definitions sends a cautionary signal regarding imprecise definitions for urban areas, as different definitions can generate vastly divergent results regarding patterns of bear activity. Additionally, considering bears in a binary fashion, defining them either as urban or wild, oversimplifies the complex ecology of bears utilizing urban areas. For example, when

assessing habitat use in urban areas, bears select for natural habitat vestiges. Patterns of habitat selection suggest resource partitioning between the sexes, especially between males and females with cubs. Finally, habitat selection varied between the three spatial scales assessed and demonstrated how preference for certain habitats was scale dependent. I will now address the implications of these results in light of the three main hypotheses considered in this study.

Urban extents and mixed space use

Regardless of spatial extent used (City Limits, U.S. Census, Remote Sensing and Combined), all analyses of habitat selection indicated that bears employed a mixed space use strategy that included urban as well as wild areas. For the majority of bears, less than 50% of GPS fixes were located in urban areas regardless of spatial extent used. If bears were not exclusively spending time in urban areas, then perhaps the term "urban" bear does not accurately describe patterns of space use. Consequently, bears should not be labeled on a binary scale as either wild or urban but, rather, on a sliding scale describing the amount of urban use.

Moreover, the dependence on urban areas will likely vary within species, even at relatively small spatial scales. For example, a study on the Nevada side of Lake Tahoe reported that urban bears had at least 90% of their locations within the urban area (Beckmann and Lackey 2008).

Understanding the factors that lead to a consistent high dependence on urban areas and why results vary among locations are important avenues of future research. One reason might be changes in technology over the last ten years. GPS technology utilized in this study may provide a more reliable means of understanding animal locations, while field triangulation and fixed-winged plane aircraft might have limited the number of data points in the Nevada study by Beckmann and Lackey (2008a). In particular, a limited number of points might artificially increase the amount of urban locations detected. In addition to changes in technology, and specific to the Lake Tahoe Basin, it is possible that habitat differences between the Eastern and Western Basin contributed to this variation in results (Johnson et al. 2015).

Beyond the waypoint data collected here, anecdotal observations from bear scats encountered in urban areas suggested that bears were using a mixed space strategy. Thus, my findings indicate a more complex pattern of habitat use than was assumed previously; most bears were not just eating garbage. Foraging theory suggests that a bear would maximize its caloric intake while at the same time reducing risk and travel costs associated with locating food resources (Stephens and Krebs 1986). Anthropogenic food sources are often high in calories, and if a bear ranked food resources on the basis of profitability then it is puzzling why certain bears did not stay in urban areas to capitalize fully on easily accessible, high calorie food but instead foraged in wild areas at least part of the time. There may be a connection between perceived risk and selected foraging location, or natural food sources may be preferred when plentiful.

Temporal Variation in space use

My results suggest that bears are using a mixed space strategy, using wild areas extensively in addition to urban areas. Consequently, I explored whether there were patterns in space use across the day and in different months and seasons and whether the results differed by sex. Hourly activity patterns showed that bears were less active in urban areas during day light hours, a result that was consistent across sex classes. This pattern of nocturnality is consistent with responses of a wide variety of species and also has been reported for black bears in Aspen, Colorado and

elsewhere in California (Ditchkoff et al. 2006, Matthews et al. 2006, Baruch-Mordo et al. 2014). Nocturnal behavior in urban areas may be a behavioral response that serves to reduce the amount of bear-human conflict, since people are less active in the Basin during these hours.

Differences among the sex classes emerged when considering monthly and seasonal patterns. Females with cubs did not use urban areas as extensively during the periods when males were particularly active in those areas. This suggests that males might exclude females with cubs from urban and from wild areas in the fall, forcing females with cubs to use less optimal habitats during these periods. Females with cubs did not demonstrate urban use during the early spring, whereas males did use urban areas. During spring, cubs are still small and potentially more vulnerable to predation by males. Consequently, females with cubs may avoid areas with males to reduce the chances of infanticide (Merkle et al. 2013). Similar observations were made in Canada, where males excluded females with cubs and sub-adults from visiting a landfill (Pacas and Paquet 1994). In this study, females utilized urban areas more than males during the fall, which might be related to a smaller female home range size. A smaller home range adjacent to urban areas likely increases the dependency on urban areas. Males, have much larger home ranges and might control access to wild areas of high food abundance (Beckmann and Berger 2003a)

Habitat Use and Preference

Habitat Usage. Habitat usage suggested that bears selected for vestiges of original habitat when in urban areas. For example, Evergreen Forest was used more in 2012 in the urban area; and other years saw heavy use of Shrubs / Scrubs in urban areas.

Resource partitioning might be happening between sexes in the Shrubs / Scrubs habitat type. During mating season males might be pursuing females in developed areas and females with cubs may be using Shrub / Scrubs habitat as an alternative habitat to avoid males, since males bears represent an infanticide risk (Ben-David et al. 2004). Temporal variability across the various sexes and years may also reflect reduced natural food production.

The aggregated developed habitat categories were used much more in 2013 and 2014 in comparison to other years. This may have been a result of reduced natural food availability. Reduced natural food, including reduced berry production, might be in response to a multi-year drought affecting the Tahoe region during this time (Jones 2015). The scarcity of natural food sources might impact the distribution of bears, and more anthropogenic resources were likely sought by bears within the developed habitats. This is consistent with observations in other study systems (Baruch-Mordo et al. 2014, Johnson et al. 2015).

Pronounced use of the Developed Open Space in fall may have occurred because bears were entering hyperphagia (late summer and fall) and additional calories may have been important (Massé et al. 2014). During the hyperphagia periods of 2011 and 2013, females with cubs used this habitat up to three times more than females without cubs. This might be related to manzanita (*Arctostaphylos sp.*) and huckleberry oak (*Quercus vacciniifolia*) becoming available as important fall food resources. A study in the Tahoe National Forest supports this idea based on the bear use of manzanita berries in summer and fall (Grenfell and Brody 1986).

With regard to the use of the NLCD dataset, these data were gathered through remote sensing and thus may not provide sufficient detail for fine scale analyses. The fine scale is needed to address remote sensing scale issues and spatial heterogeneity of the urban environment (Cadenasso et al. 2007). A finer scale would provide a more detailed view of how bears use urban areas and address potential problems arising from the incorrect assignment of locations to different habitat types. Additionally, greater spatial resolution would provide a more in-depth understanding of which microhabitats within developed areas were preferred by bears.

Preference. Analyses identified differences among the three orders of habitat preference. The three orders identify preferences at three different scales: at first order the scale included the entire study area, at second order it referred to the home range of the individual animal and third order refers to the urban and wild patch within the home range. This means that there is both an urban and wild third order preference. These differences were also reported in other species such as raccoons (*Procyon lotor*) and mountain lions (Dickson and Beier 2002, Beasley et al. 2007). At first glance and congruent with expectations, bears appeared to select for urban areas, specifically at first order habitat analysis. However, the relative availability of urban habitat at this scale was expected to be much smaller than at second order or third order because urban areas are relatively small in relation to the overall study area. Relative availability of urban habitat at the second order scale was not uniformly greater than at the first order, and indeed, eight bears (of 26) had less relative availability of urban area in their home range. If bears select urban areas as part of their home ranges, then it would be expected that the number of bears that preferred urban areas would be greater at a second order scale and that the relative percentage urban habitat available would be greater at this level too. Bears also appear to reduce preference for urban areas at finer scales; this is further collaborated by the finding that within the urban patch (third order), approximately 50% fewer bears selected for developed habitat types than at second order.

In urban areas, Evergreen Forest was preferred to a greater degree at finer scales, which suggested that bears preferred vestiges of their original habitat within urban landscapes. Similarly, Shrubs / Scrubs was also more preferred at finer scales, suggesting that this habitat type is also important within the urban interface.

I expected that wetlands would be more preferred than the findings suggested. Only three bears referred this habitat at first order and two bears preferred wetlands within the urban envelope. Other studies suggested that bear sign was disproportionately found in wetlands in California (Kelleyhouse 1980) or that bears preferred wetlands over other habitats in Florida and New Jersey (Stratman et al. 2001, Tri et al. 2016). Divergent results may be a result of the fact that Herbaceous Wetlands are not a homogeneous habitat type across different locales.

Future research should examine individual bears' habitat preference with the aid of a fine scale habitat classification. Determining which bears preferred urban habitat within the urban patch might provide an understanding of the level of habituation and potential for increased nuisance activities. Additionally, preference indicated that the bears were using urban areas, but future research should examine whether bears were primarily foraging in urban areas or using the area for other activities as well.

Management Implications

I found that bears detected in urban areas did not spend the majority of their time in urban areas, and thus it seems logical that they did not exclusively sustain themselves with anthropogenic food sources. Research suggests that drought and other stochastic events (Johnson et al. 2015) affecting natural forage may force bears into the Wildlife Urban Interface in pursuit of resources. Spending time in urban areas is often equated to causing conflict, regardless of how much time individual bears spend in urban relative to wild areas. Wildlife designated as urban wildlife may be considered to have a lesser ecological value than its wild counterparts. This is particularly the case when animals are thought to be reliant on garbage and other human provided food sources. However, as wild habitats shrink, wildlife cannot be exclusively preserved in remote wilderness settings. Additionally, stochastic events such as drought may increase in frequency and intensity, potentially forcing wildlife to make a living in closer proximity to people. This will likely cause additional bear-human conflict. There may be a need to have different management options between bears that are a nuisance when natural foods are abundant and when natural foods are unavailable.

Anecdotal evidence and personal observations indicated that sows with cubs might be more aggressive in their pursuit of anthropogenic food sources, suggesting that conflict might differ among sex classes. In fact, based on qualitative law enforcement reports, some of the most notorious break-in bears were sows with cubs (Placer and El Dorado Sheriff). The energetic expenditure required to care for cubs might create an additional caloric requirement that favors pursuing alternative food sources, including anthropogenic sources. Human conflict with sows with cubs is particularly challenging because the public responds strongly to lethal removal of cubs. However, these cubs may grow up to be a problem for the community and may create personal safety concerns (law enforcement reports and personal observations). Bears can turn into destructive animals by the time they are two years old. A comprehensive community-backed approach needs to be developed to address this bear-human conflict more proactively.

One key component of this approach needs to be a reduction in the availability of garbage to bears. Garbage has long been recognized as a bear attractant and various Tahoe communities have created ordinances to address the issue. Due to multiple jurisdictions, the result has been a patchwork of laws. The only governmental body that supersedes municipal jurisdictions and even state boundaries is the Tahoe Regional Planning Agency. In the spring of 2015, this entity was requested to manage bear issues Basin-wide, with follow up meetings in the spring of 2018. Removal of attractants has shown to reduce conflict behavior and will likely translate into less use of the urban area. Bear management is complex and challenging, but generating a single point of accountability and enforcement of garbage availability to bears will likely benefit conflict resolution.

Another component of this new approach needs to focus on education and enforcement. Education has been a priority for CDFW for over a decade, as evidenced by a “Keep Me Wild” campaign (<https://www.wildlife.ca.gov/Keep-Me-Wild/Bear>). Additionally, a local bear advocacy group known as the Bear League has created various educational materials, including a ‘Grim Reaper/Don’t Feed Our Bears’ educational campaign (<http://www.savebears.org/events/grimreaper.htm>). This campaign featured the Grim Reaper

feeding bears and showed the unfortunate outcome for those bears. After more than ten years of educational campaigns, it might be concluded that education did not alleviate the problem and that a more prominent enforcement process is warranted. Enforcement has been required to achieve a reduction in available garbage in other areas. For example, in Aspen, Colorado enforcement generated more compliance in comparison to educational efforts; when garbage became less available, the interest of bears in urban areas appeared to wane (Gore et al. 2006, Baruch-Mordo et al. 2011). In the Basin, garbage and even deliberate feeding was discouraged by State Parks personnel (personal observation) but these efforts were of marginal interest to other agencies tasked with enforcement. The Basin's interpretation of bear policies is lenient on people and bears: black bears would be removed in most parts of their range if they engaged in activities that are routine in the Basin, such as entering buildings and cars. These bears were often not removed in the Basin because of concern about retaliation by people (Mazaika 2013). Additionally, people both feed bears and leave garbage unsecured without consequence, providing limited motivation to comply with regulations designed to reduce bear-human conflict.

Keeping garbage inaccessible is pivotal to achieving success. Bear boxes, which are metal bear-proof garbage receptacles, are used in several Basin communities. The boxes are costly (~\$1,000) and may be unattainable for lower income families, affecting the ability to keep bears out of trash. A centralized bear management jurisdiction would assure that programs are in place to allow for better compliance, including assistance for low-income communities. It has been suggested that bear boxes are the cause of increased break-ins into homes, since bears that previously were able to obtain food from unsecured garbage receptacles are, now that bear boxes are in use, forced to go into homes in pursuit of food. If this were the case then break-ins or depredation permits should be less common in areas with fewer bear boxes, since bears do not need to break into homes to obtain food. South Lake Tahoe is an area with fewer bear boxes, and at first glance appears to have similar levels of conflict as areas with bear boxes (Klip, unpublished data). Further study of this relationship is warranted, especially since CDFW advocates for the use of bear boxes to reduce conflict.

The bear management approach eventually identified and agreed upon by community stakeholders needs to gain a further understanding of social carrying capacity. Social carrying capacity in this context is how much bear interaction and nuisance behavior the local community is willing to accept. It is unclear how many people would support various levels of lethal control when people are concerned about human-human conflict. Local bear advocates may provide negative implications to individuals who consider lethal control. It remains ambiguous whether the silent majority would consider more control options if the concern of human-human conflict is abated.

Tables and Figures

NLCD Habitat Usage

NLCD Habitat	Description	Relative Usage	Included in Analysis
11	Open water		No
12	Perennial ice/snow		No
21	Developed, open space	8.0%	Yes
22	Developed, low intensity	4.0%	Yes
23	Developed, medium intensity	1.0%	Yes
24	Developed, high intensity	0.2%	Yes
31	Barren land (rock/sand/clay)		No
41	Deciduous forest	0.1%	Yes
42	Evergreen forest	72.0%	Yes
43	Mixed forest	0.1%	Yes
51	Dwarf scrub		No
52	Shrub/scrub	13.0%	Yes
71	Grassland/herbaceous	0.2%	Yes
72	Sedge/herbaceous		No
73	Lichens		No
74	Moss		No
81	Pasture/hay		No
82	Cultivated crops		No
90	Woody wetlands		No
95	Emergent herbaceous wetlands	0.3%	Yes

Table 1. This table shows NLCD (National Land Cover Database) habitat categories and the relative usage by bears within study area and which habitat categories were included in the analyses.

Urban Proportions by Hour

Hour	Female	Female with Cubs	Male
2	0.601	0.522	0.633
4	0.583	0.530	0.612
6	0.520	0.535	0.497
8	0.429 (NS)	0.403 (NS)	0.400 (NS)
10	0.428	0.365	0.393
12	0.417	0.353	0.363
14	0.433	0.343	0.366
16	0.417	0.344	0.347
18	0.448	0.356	0.371
20	0.500	0.432	0.456
22	0.551	0.487	0.548
24	0.566	0.503	0.586

Table 2. This table shows hourly urban usage by sex. Chi Square tests on three proportions were completed and proportions were significantly different from each other for all hours except at 8:00.

Urban Proportion by Sex per Month

Month	Female	Female with Cubs	Male
January	0.490	0.000	0.708
February	0.242	0.000	0.718
March	0.379	0.000	0.408
April	0.633	0.000	0.287
May	0.240	0.436	0.299
June	0.508	0.606	0.408
July	0.554	0.646	0.551
August	0.473	0.573	0.654
September	0.522	0.673	0.344
October	0.709	0.353	0.497
November	0.518	0.440	0.459
December	0.301	0.370	0.561

Table 3. This table shows urban usage by sex by month expressed as a proportion.

Urban Proportion by Sex per Season			
Season	Female	Female with Cubs	Male
Winter	0.334	0.214	0.615
Spring	0.389	0.435	0.307
Summer	0.510	0.628	0.539
Fall	0.595	0.439	0.440

Table 4. This table shows urban usage by sex and season.

Habitat Urban and Wild Percentages by Year

Habitat	2011		2012		2013		2014		2015	
	Urban	Wild	Urban	Wild	Urban	Wild	Urban	Wild	Urban	Wild
21	0.9845***	0.0155	0.9937***	0.0063	0.9900***	0.01	0.9964***	0.0036	1	0
22	0.9873***	0.0127	1	0	0.9903***	0.0097	0.9995***	0.0005	1	0
23	1	0	1	0	0.9947	0.0053	1	0	1	0
24	1	0	1	0	1	0	1	0	0	0
31	0	1	0	1	0.0909**	0.9091	1	0	1	0
41	0	0	0	0	0.0185	0.9815	0	1	0	0
42	0.1551***	0.8449	0.5203*	0.4797	0.3398***	0.6602	0.4793***	0.5207	0.3241***	0.6759
52	0.1375***	0.8625	0.2448***	0.7552	0.2258***	0.7742	0.4459***	0.5541	0.2971***	0.7029
71	0.2128***	0.7872	0.2222	0.7778	0.4490	0.5510	0.8364***	0.1636	0	1
95	0	1	1	0	0.4646	0.5354	0.5714	0.4286	0	0

Table 5. This table shows annual habitat usage based on NLCD habitat categories. Urban is defined as locations within the Combined spatial extent for urban, which is an aggregate of City Limits, U.S. Census and eVeg urban spatial data sets. Comparison of proportions performed with Pearson’s Chi Square analysis. *** indicating significance greater than 0.001, ** greater than 0.01 and * greater than 0.05. Landcover types include 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed. Medium Intensity, 24: Developed High Intensity, 41: Deciduous Forest, 42; Evergreen Forest, 43: Mixed Forest, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands.

Habitat Urban and Wild Percentages by Season

Habitat	Spring		Summer		Fall		Winter	
	Urban	Wild	Urban	Wild	Urban	Wild	Urban	Wild
21	0.9691***	0.0309	0.9965***	0.0035	0.9958***	0.0042	0.9946***	0.0054
22	0.9917***	0.0083	0.9986***	0.0014	0.9955***	0.0045	0.9922***	0.0078
23	1	0	0.9976	0.0024	1	0	1	0
24	1	0	1	0	1	0	1	0
31	0.3	0.7	0.5789	0.4211	0.4211	0.5789	0	0
41	0	1	0	1	0.0185	0.9815	0	0
42	0.3335***	0.6665	0.4612***	0.5388	0.4223***	0.5777	0.2912***	0.7088
52	0.2421***	0.7579	0.3519***	0.6481	0.2441***	0.7559	0.2871***	0.7129
71	0.3	0.7	0.2581***	0.7519	0.5574	0.4426	0.9643***	0.0357
95	0.4	0.6	0.8941***	0.1059	0.2158***	0.7842	1	0

Table 6. This table shows seasonal habitat usage based on NLCD habitat categories. Urban is defined as locations within the Combined spatial extent for urban, which is an aggregate of City Limits, U.S. Census and eVeg urban spatial data sets. Comparison of proportions performed with Pearson’s Chi Square analysis. *** indicating significance greater than 0.001, ** greater than 0.01 and * greater than 0.05. Landcover types include 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed. Medium Intensity, 24: Developed High Intensity, 41: Deciduous Forest, 42; Evergreen Forest, 43: Mixed Forest, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands.

Habitat Urban and Wild Percentages by Month

	January		February		March		April	
Habitat	Urban	Wild	Urban	Wild	Urban	Wild	Urban	Wild
21	0.9640***	0.0360	1	0	1	0	0.9008***	0.0992
22	1	0	1	0	1	0	0.9855***	0.0145
23	1	0	1	0	1	0	1	0
24	1	0	0	0	0	0	1	0
31	0	0	0	0	1	0	0	1
41	0	0	0	0	0	0	0	0
42	0.3967***	0.6033	0.2872***	0.7128	0.2917***	0.7083	0.2491***	0.7509
52	0.0510***	0.9490	0.5917***	0.4083	0.3110***	0.6890	0.3474***	0.6526
71	1	0	1	0	0.5	0.5	0.4	0.6
95	0	0	0	0	0	0	1	0
	May		June		July		August	
Habitat	Urban	Wild	Urban	Wild	Urban	Wild	Urban	Wild
21	0.9730***	0.027	0.9956***	0.0044	0.9949***	0.0051	0.9977***	0.0023
22	0.9821***	0.0179	1	0	1	0	0.9981***	0.0019
23	1	0	1	0	1	0	0.9921	0.0079
24	1	0	1	0	1	0	1	0
31	0	1	0	1	1	0	0.4286	0.5714
41	0	1	0	1	0	0	0	0
42	0.3345***	0.6655	0.4389***	0.5611	0.4761***	0.5239	0.4615***	0.5385
52	0.1626***	0.8374	0.3859***	0.6141	0.3602***	0.6398	0.3426***	0.6574
71	0	1	0.7	0.3	0.5714	0.4286	0.0690***	0.931
95	0.3333	0.6667	0.3333	0.66676	0.9231	0.0769	0.9516***	0.0484
	September		October		November		December	
Habitat	Urban	Wild	Urban	Wild	Urban	Wild	Urban	Wild
21	0.9938***	0.0062	0.9945***	0.0055	1	0	0.9984***	0.0016
22	0.9885***	0.0115	0.9983***	0.0017	0.9979***	0.0021	0.9900***	0.001
23	1	0	1	0	1	0	1	0
24	1	0	1	0	1	0	1	0
31	0.3824	0.6176	0.35	0.65	1	0	0	0
41	0	1	0.027	0.973	0	0	0	0
42	0.3786***	0.6214	0.4893	0.5107	0.3666***	0.6334	0.2296***	0.7704
52	0.2061***	0.7939	0.1701***	0.8299	0.4273***	0.5727	0.2295***	0.7705
71	0.1579**	0.8421	0.3571	0.6429	0.8889***	0.1111	1	0
95	0.1875*	0.8125	0.2***	0.8	0.2727***	0.7273	1	0

Table 7. This table shows monthly habitat usage based on NLCD habitat categories. Urban is defined as locations within the Combined spatial extent for urban, which is an aggregate of City Limits, U.S. Census and eVeg urban spatial data sets. Comparison of proportions performed with Pearson's Chi Square analysis. *** indicating significance greater than 0.001, ** greater than 0.01 and * greater than 0.05. Landcover types include 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed, Medium Intensity, 24: Developed High Intensity, 41: Deciduous Forest, 42: Evergreen Forest, 43: Mixed Forest, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands.

Habitat Urban and Wild Percentages by Year and Season

2011	Spring		Summer		Fall		Winter	
Habitat	Urban	Wild	Urban	Wild	Urban	Wild	Urban	Wild
21	NA	NA	0.9730	0.027	0.9825	0.0175	1	0
22	NA	NA	0.9615	0.0385	0.9886	0.0114	1	0
23	NA	NA	1	0	1	0	1	0
24	NA	NA	0	0	1	0	1	0
31	NA	NA	0	1	0	1	0	0
41	NA	NA	0	0	0	0	0	0
42	NA	NA	0.3161***	0.6839	0.1410***	0.8590	0.1305***	0.8695
52	NA	NA	0.1516***	0.8484	0.1113***	0.8887	0.2272***	0.7728
71	NA	NA	0	1	0.5455	0.4545	1	0
95	NA	NA	0	1	0	1	0	0
2012	Spring		Summer		Fall		Winter	
Habitat	Urban	Wild	Urban	Wild	Urban	Wild	Urban	Wild
21	0.92	0.08	1	0	1	0	1	0
22	1	0	1	0	1	0	1	0
23	1	0	1	0	1	0	1	0
24	0	0	1	0	1	0	1	0
31	0	1	0	1	0	0	0	0
41	0	0	0	0	0	0	0	0
42	0.3138***	0.6862	0.2146***	0.7854	0.6713***	0.3287	0.3168***	0.6832
52	0.1337***	0.8663	0.2473***	0.7527	0.85***	0.15	0.0964***	0.9036
71	0	1	0.2	0.8	0	0	1	0
95	1	0	0	0	0	0	0	0
2013	Spring		Summer		Fall		Winter	
Habitat	Urban	Wild	Urban	Wild	Urban	Wild	Urban	Wild
21	0.9184***	0.0816	0.9958	0.0042	0.9911***	0.0089	1	0
22	0.9756	0.0244	0.9961	0.0039	0.9901	0.0099	0.9895	0.0105
23	1	0	0.9821	0.0179	1	0	1	0
24	1	0	1	0	1	0	0	0
31	0	0	0	1	0.1111	0.8889	0	0
41	0	0	0	0	0.0185	0.9815	0	0
42	0.2859***	0.7141	0.3502***	0.6498	0.4123***	0.5877	0.2047***	0.7953
52	0.3996***	0.6004	0.2982***	0.7018	0.1909***	0.8091	0.0611***	0.9389
71	0.6667	0.3333	0.1429	0.8571	0.4737	0.5263	1	0
95	0.3333	0.6667	0.9545	0.0455	0.2109***	0.7891	1	0

2014		Spring		Summer		Fall		Winter	
Habitat	Urban	Wild	Urban	Wild	Urban	Wild	Urban	Wild	
21	0.9908	0.0092	0.9972***	0.0028	1	0	0.9667***	0.0333	
22	1	0	1	0	0.9984	0.0016	1	0	
23	1	0	1	0	1	0	1	0	
24	1	0	1	0	1	0	0	0	
31	0	0	1	0	1	0	0	0	
41	0	1	0	1	0	0	0	0	
42	0.3660***	0.6340	0.5438***	0.4562	0.5728***	0.4272	0.3907***	0.6093	
52	0.1817***	0.8183	0.5070	0.4930	0.6151***	0.3849	0.4096***	0.5904	
71	0.25	0.75	0.7778	0.2222	0.8333	0.1667	1	0	
95	0	1	0.7222	0.2778	0.3333	0.6667	0	0	
2015		Spring		Summer		Fall		Winter	
Habitat	Urban	Wild	Urban	Wild	Urban	Wild	Urban	Wild	
21	1	0	NA	NA	NA	NA	1	0	
22	1	0	NA	NA	NA	NA	1	0	
23	1	0	NA	NA	NA	NA	1	0	
24	0	0	NA	NA	NA	NA	0	0	
31	1	0	NA	NA	NA	NA	0	0	
41	0	0	NA	NA	NA	NA	0	0	
42	0.1911***	0.8089	NA	NA	NA	NA	0.3511***	0.6489	
52	0.1923***	0.8077	NA	NA	NA	NA	0.6176	0.3824	
71	0	0	NA	NA	NA	NA	0	1	
95	0	0	NA	NA	NA	NA	0	0	

Table 8. This table shows seasonal habitat analysis by year. Urban is defined as locations within the Combined spatial extent for urban, which is an aggregate of City Limits, U.S. Census and eVeg urban spatial data sets. Comparison of proportions performed with Pearson’s Chi Square analysis. *** indicating significance greater than 0.001, ** greater than 0.01 and * greater than 0.05. Landcover types include 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed. Medium Intensity, 24: Developed High Intensity, 41: Deciduous Forest, 42: Evergreen Forest, 43: Mixed Forest, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands.

Comparison of Total Use to Availability

Habitat	Availability %	Mean of Use %	SD of Use %	Sig. Diff.	p-value	t-test statistic	Selected
21	2.69	6.3762	6.7053	Yes	0.0096	-2.8031	X
22	1.97	3.5985	3.4467	Yes	0.0237	-2.4091	X
23	0.37	0.9469	1.0508	Yes	0.0097	-2.7994	X
24	0.07	0.1996	0.2686	Yes	0.0211	-2.4603	X
31	1.14	0.1958	0.5164	Yes	0.0000	9.3229	
41	0.06	0.1742	0.8762	No	0.5123	-0.6647	X
42	67.49	70.9158	15.2934	No	0.2642	-1.1422	
52	24.79	16.7869	17.1680	Yes	0.0254	2.3770	X
71	1.09	0.3846	0.8365	Yes	0.0002	4.2999	
90	0.01	0.0015	0.0078	Yes	0.0000	5.5000	X
95	0.32	0.2700	0.8237	No	0.7595	0.3095	

Table 9. This table shows first order habitat preferences based on comparison by means through two-sided t-tests. Selection defined by significant p value and mean use greater than mean available habitat. Landcover types include

21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed. Medium Intensity, 24: Developed High Intensity, 41: Deciduous Forest, 42: Evergreen Forest, 43: Mixed Forest, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands.

Percent Total Preference by Bear ID

NLCD	Total Available	10611	12643	12644	12645	12647	12648	13295	13206	13207
21	2.69	4.73	15.28	25.76	1.06	2.87	10.42	3.45	4.31	7.57
22	1.97	3.71	6.74	6.74	4.07	2.11	5.82	1.79	2.20	1.04
23	0.37	0.62	2.07	3.21	0.34	1.26	0.8	0.76	1.61	0.02
24	0.07	0.03	0.52	0.72	NA	0.08	0.23	0.21	0.9	NA
31	1.14	NA	NA	NA	0.21	0.17	NA	NA	0.99	NA
41	0.06	NA	NA	0.05	NA	4.47	0.01	NA	NA	NA
42	67.49	82.89	73.83	56.45	61.24	59.02	76.33	90.42	79.7	86.37
52	24.79	7.92	1.55	6.97	29.22	24.79	6.35	3.37	9.96	4.93
71	1.09	0.06	NA	0.02	0.21	1.26	0.03	NA	0.31	0.02
90	0.01	NA	NA	NA	0.04	NA	NA	NA	NA	NA
95	0.32	0.04	NA	0.08	3.6	0.08	0.01	NA	0.02	0.05

NLCD	Total Available	13208	13209	13210	13211	13212	15441	15442	15444	15448
21	2.69	0.1	7.1	13.46	11.31	0.57	19.55	3.27	14.02	7.7
22	1.97	0.76	2.94	4.72	5.65	0.13	7.38	15.5	5.16	7.13
23	0.37	0.19	0.48	0.34	0.53	NA	2.17	3.92	1.22	1.71
24	0.07	NA	0.06	0.1	0.18	NA	0.32	0.07	0.05	0.71
31	1.14	NA	NA	NA	NA	0.09	NA	NA	NA	NA
41	0.06	NA	NA	NA	NA	NA	NA	NA	NA	NA
42	67.49	47.18	85.71	77.61	72.79	48.66	59.27	70.48	74.45	77.32
52	24.79	48.04	3.71	3.73	9.54	48.04	11.19	6.19	5.11	4.71
71	1.09	3.72	NA	0.03	NA	0.13	0.1	0.14	NA	0.57
90	0.01	NA	NA	NA	NA	NA	NA	NA	NA	NA
95	0.32	NA	NA	NA	NA	2.38	0.02	0.43	NA	0.14

NLCD	Total Available	30579	30581	30582	30583	30584	30585	30586	30587
21	2.69	1.5	0.05	5.53	NA	3.11	1.79	NA	1.27
22	1.97	1.2	NA	4.64	NA	2.03	1.3	NA	0.8
23	0.37	NA	NA	2.15	NA	0.68	0.43	NA	0.11
24	0.07	NA	NA	0.65	NA	0.2	0.11	NA	0.05
31	1.14	NA	NA	NA	NA	NA	1.73	1.9	NA
41	0.06	NA	NA	NA	NA	NA	NA	NA	NA
42	67.49	85.89	77.62	74.96	82.86	90.88	30.32	47.94	73.62
52	24.79	11.41	22.2	11.74	16.57	2.9	62.05	50.17	24.1
71	1.09	NA	0.05	0.31	0.57	0.2	2.22	NA	0.05
90	0.01	NA	NA	NA	NA	NA	NA	NA	NA
95	0.32	NA	0.09	0.03	NA	NA	0.05	NA	NA

Table 10. This table shows first order (study area scale) preference for individual bears. Comparison was done by individual bear; if usage was smaller than availability, then the habitat type was considered preferred. NLCD refers to National Land Cover Database and included the following landcover types: 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed. Medium Intensity, 24: Developed High Intensity, 41: Deciduous Forest, 42: Evergreen Forest, 43: Mixed Forest, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands

Comparison of Home Range Use to Availability

Habitat	Mean of Use %	SD of Use %	Mean of Available %	SD of Available %	Sig. Diff.	p-value	t-test statistic	Selected
21	6.3762	6.7053	5.3023	4.5466	No	0.3569	0.9387	
22	3.5985	3.4467	3.9923	3.9079	No	0.4924	-0.6968	
23	0.9469	1.0508	0.8435	0.8709	No	0.5593	0.5918	
24	0.1996	0.2686	0.1627	0.2353	No	0.6114	0.5146	
31	0.1958	0.5164	0.9792	2.0141	Yes	0.0330	-2.2576	
41	0.1742	0.8762	0.0473	0.1425	No	0.3901	0.8746	
42	70.9158	15.2934	68.7258	13.1603	No	0.3797	0.8942	
43	0.1492	0.7609	0.1000	0.4778	No	0.3860	0.8824	
52	16.7869	17.1680	18.3392	12.5507	No	0.3575	-0.9375	
71	0.3846	0.8365	0.9004	0.8451	Yes	0.0049	-3.0846	X
90	0.0015	0.0078	0.0119	0.0485	No	0.2726	-1.1218	
95	0.2700	0.8237	0.5942	1.0047	No	0.1654	-1.4288	

Table 11. This table shows second order (home range scale) habitat comparisons based on means with two-sided t-tests. Selection defined by significant p value and mean use greater than mean available habitat. Landcover types include 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed, Medium Intensity, 24: Developed High Intensity, 41: Deciduous Forest, 42: Evergreen Forest, 43: Mixed Forest, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands.

Percent Home Range Preference by Bear ID

10611		12643		12644		12645		
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	4.99	4.73	13.84	15.28	5.52	25.76	2.62	1.06
22	3.29	3.71	16.42	6.74	3.52	6.74	6.28	4.07
23	0.62	0.62	3.12	2.07	0.63	3.21	1.49	0.34
24	0.1	0.03	0.15	0.52	0.12	0.72	0.51	NA
31	0.17	NA	NA	NA	0.42	NA	7.22	0.21
41	0.01	NA	NA	NA	0.05	0.05	0.01	NA
42	75.44	82.89	54.36	73.83	77.01	56.45	38.25	61.24
43	NA	NA	NA	NA	NA	NA	NA	NA
52	14.5	7.92	9.7	1.55	12.47	6.97	39.75	29.22
71	0.57	0.06	1.89	NA	0.15	0.02	2.27	0.21
90	NA	NA	NA	NA	NA	NA	0.07	0.04
95	0.3	0.04	0.51	NA	0.11	0.08	1.53	3.6

12647		12648		13205		13206		
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	1.24	2.87	4	10.42	12.41	3.45	2.47	4.31
22	0.65	2.11	2.85	5.82	6.57	1.79	2.07	2.20
23	0.19	1.26	0.56	0.8	1.10	0.76	0.51	1.61
24	0.05	0.08	0.1	0.23	0.27	0.21	0.06	0.9
31	1.69	0.17	0.19	NA	NA	NA	0.02	0.99
41	0.72	4.47	0.03	0.01	NA	NA	0	NA
42	67.33	59.02	80.31	76.33	72.02	90.42	82	79.7
43	2.44	3.88	NA	NA	NA	NA	NA	NA
52	23.82	24.79	11.72	6.35	6.77	3.37	12.06	9.96
71	1.55	1.26	0.14	0.03	0.57	NA	0.44	0.31
90	0	NA	NA	NA	NA	NA	NA	NA
95	0.33	0.08	0.09	0.01	0.29	NA	0.37	0.02

13207		13208		13209		13210		
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	5.75	7.57	1.51	0.1	13.12	7.1	6.22	13.46
22	2.42	1.04	1.37	0.76	7.2	2.94	3.83	4.72
23	0.19	0.02	1.07	0.19	1.8	0.48	1	0.34
24	0.03	NA	0.04	NA	0.32	0.06	0.18	0.1
31	0.29	NA	NA	NA	NA	NA	0.05	NA
41	0.11	NA	NA	NA	NA	NA	NA	NA
42	74.16	86.37	43.83	47.18	73.37	85.71	83.48	77.61
43	NA	NA	NA	NA	NA	NA	NA	NA
52	16.36	4.93	44.15	48.04	4.11	3.71	5.14	3.73
71	0.28	0.02	3.02	3.72	0.02	NA	0.06	0.03
90	NA	NA	NA	NA	NA	NA	NA	NA
95	0.42	0.05	5.02	NA	0.07	NA	0.03	NA

13211			13212		15441		15442	
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	5.4	11.31	1.77	0.57	7.06	19.55	4.58	3.27
22	3.16	5.65	0.69	0.13	4.88	7.38	12.58	15.5
23	0.45	0.53	0.06	NA	0.93	2.17	3.23	3.92
24	0.06	0.18	NA	NA	0.2	0.32	1.14	0.07
31	0.01	NA	3.86	0.09	0	NA	0.93	NA
41	NA	NA	NA	NA	NA	NA	NA	NA
42	72.41	72.79	48.27	48.66	77.73	59.27	52.83	70.48
43	NA	NA	NA	NA	NA	NA	NA	NA
52	16.69	9.54	42.84	48.04	9.04	11.19	20.55	6.19
71	1.74	NA	1.62	0.13	0.1	0.1	2.19	0.14
90	NA	NA	NA	NA	NA	NA	0.24	NA
95	0.09	NA	0.88	2.38	0.06	0.02	1.72	0.43
15444			15448		30579		30581	
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	17.66	14.02	7.99	7.7	7.1	1.5	0.77	0.05
22	9.04	5.16	5.29	7.13	3.42	1.2	0.3	NA
23	2.02	1.22	0.9	1.71	0.23	NA	NA	NA
24	0.35	0.05	0.2	0.71	0.02	NA	NA	NA
31	NA	NA	NA	NA	0.03	NA	0.05	NA
41	NA	NA	NA	NA	NA	NA	NA	NA
42	66.91	74.45	78.23	77.32	75.41	85.89	69.53	77.62
43	NA	NA	NA	NA	NA	NA	NA	NA
52	3.94	5.11	7.07	4.71	13.03	11.41	27.48	22.2
71	NA	NA	0.23	0.57	0.36	NA	0.92	0.05
90	NA	NA	NA	NA	NA	NA	NA	NA
95	0.08	NA	0.1	0.14	0.41	NA	0.95	0.09
30582			30583		30584		30585	
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	4.43	5.53	NA	NA	2.93	3.11	1.17	1.79
22	3.48	4.64	NA	NA	1.9	2.03	0.72	1.3
23	0.76	2.15	NA	NA	0.48	0.68	0.13	0.43
24	0.13	0.65	NA	NA	0.09	0.2	0.02	0.11
31	0	NA	NA	NA	0.19	NA	6.67	1.73
41	NA	NA	NA	NA	0.15	NA	0.02	NA
42	78.99	74.96	90.02	82.86	74.05	90.88	53.51	30.32
43	NA	NA	NA	NA	0.05	NA	NA	NA
52	11.58	11.74	8.54	16.57	18.28	2.9	36.66	62.05
71	0.25	0.31	0.64	0.57	1.81	0.2	0.98	2.22
90	NA	NA	NA	NA	NA	NA	NA	NA
95	0.36	0.03	0.8	NA	0.05	NA	0.12	0.05

NLCD	30586		30587	
	Availability	Usage	Availability	Usage
21	0.03	NA	3.28	1.27
22	0.02	NA	1.85	0.8
23	0	NA	0.46	0.11
24	NA	NA	0.09	0.05
31	3.25	1.9	0.42	NA
41	0.06	NA	0.07	NA
42	56.8	47.94	70.62	73.62
43	0.01	NA	0.1	NA
52	39.19	50.17	21.38	24.1
71	0.47	NA	1.14	0.05
90	NA	NA	NA	NA
95	0.17	NA	0.59	NA

Table 12. This table shows second order defined as the preference for individual bears or preference within the 95% Kernel Density Estimate home range. Comparison was done by individual bear; if usage was smaller than availability, then the habitat type was considered preferred. NLCD refers to National Land Cover Database and included the following landcover types: 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed, Medium Intensity, 24: Developed High Intensity, 41: Deciduous Forest, 42: Evergreen Forest, 43: Mixed Forest, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands

Comparison of Wild Use to Availability

Habitat	Mean of Use %	SD of Use %	Mean of Available %	SD of Available %	Sig. Diff.	p-value	t-test statistic	Selected
21	0.1323	0.2797	0.2731	0.3141	Yes	0.0265	-2.3575	
22	0.0642	0.1994	0.1935	0.2836	Yes	0.0342	-2.2410	
23	0.0019	0.0098	0.0462	0.0704	Yes	0.0028	-3.3105	
24	0.0000	0.0000	0.0031	0.0138	No	0.2660	-1.1378	
41	0.2165	1.0521	0.0538	0.1462	No	0.3733	0.9066	
42	79.6792	22.0958	77.0412	17.6145	No	0.2568	1.1604	X
43	0.1788	0.9119	0.1062	0.4974	No	0.3822	0.8895	
52	19.1800	21.0751	20.0412	15.1058	No	0.6788	-0.4190	
71	0.2146	0.5583	0.7819	0.7601	Yes	0.0020	-3.4460	
90	0.0000	0.0000	0.0000	0.0000	No	1.0000	1.0000	
95	0.1619	0.5206	0.3012	0.3480	No	0.1856	-1.3611	

Table 13. Third order habitat defined as the wild patch within the 95% Kernel Density Estimate home range, comparisons based on means. Selection defined by significant p value and mean use greater than mean available habitat. Landcover types include 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed, Medium Intensity, 24: Developed High Intensity, 41: Deciduous Forest, 42: Evergreen Forest, 43: Mixed Forest, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands.

Percent Wild Preference by Bear ID

10611		12643		12644		12645		
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	0.12	0.28	NA	NA	0.29	0.23	1.13	0.17
22	0.05	0.05	NA	NA	0.13	NA	1.24	NA
23	0.01	NA	NA	NA	0.03	NA	0.07	NA
24	NA	NA	NA	NA	NA	NA	0	NA
31	0.26	NA	NA	NA	0.61	NA	9.09	0.28
41	0.02	NA	NA	NA	0.08	0.23	0.01	NA
42	82.92	91.51	99.17	100	83.8	85.55	38.73	67.99
43	NA	NA	NA	NA	NA	NA	NA	NA
52	15.97	8.08	0.83	NA	14.84	13.61	47.11	30.91
71	0.57	0.05	NA	NA	0.11	NA	1.94	0.28
90	NA	NA	NA	NA	NA	NA	NA	NA
95	0.08	0.05	NA	NA	0.11	0.38	0.68	0.39

12647		12648		13205		13206		
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	0.62	0.72	0.21	0.03	NA	NA	0.18	0.03
22	0.17	0.41	0.21	NA	NA	NA	0.25	NA
23	0.08	NA	0.05	NA	NA	NA	0.09	NA
24	0.01	NA	NA	NA	NA	NA	0	NA
31	1.77	0.21	0.26	NA	NA	NA	0.02	NA
41	0.73	5.37	0.04	0.03	NA	NA	0.01	NA
42	67.92	59.4	86.62	90.39	92.08	97.03	87.48	93.04
43	2.54	4.65	NA	NA	NA	NA	NA	NA
52	24.3	27.69	12.51	9.47	6.15	2.97	11.62	6.86
71	1.54	1.45	0.08	0.05	0.89	NA	0.25	0.07
90	0	NA	NA	NA	NA	NA	NA	NA
95	0.32	0.1	0.03	0.03	0.87	NA	0.1	NA

13207		13208		13209		13210		
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	0.41	0.08	0.15	NA	0.12	NA	0.16	NA
22	0.01	NA	0.04	NA	0.42	0.05	0.43	NA
23	NA	NA	NA	NA	0.15	0.05	0.1	NA
24	NA	NA	NA	NA	NA	NA	NA	NA
31	0.41	NA	NA	NA	NA	NA	0.07	NA
41	0.16	NA	NA	NA	NA	NA	NA	NA
42	77.49	87.54	41.78	22.22	94.79	95.81	93.6	94.33
43	NA	NA	NA	NA	NA	NA	NA	NA
52	20.66	12.21	56.33	77.78	4.48	4.09	5.54	5.63
71	0.35	NA	1.32	NA	0.04	NA	0.09	0.04
90	NA	NA	NA	NA	NA	NA	NA	NA
95	0.5	0.17	0.38	NA	NA	NA	NA	NA

13211			13212		15441		15442	
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	0.84	1.27	0.41	0.03	0.14	0.26	1.07	NA
22	0.59	0.95	0.03	NA	0	NA	0.24	0.06
23	0.12	NA	0.01	NA	0	NA	0.07	NA
24	0	NA	NA	NA	NA	NA	NA	NA
31	0.01	NA	4.49	0.08	0.01	NA	1.63	NA
41	NA	NA	NA	NA	NA	NA	NA	NA
42	79	88.89	45.6	40.56	90.01	86.86	64.3	87.91
43	NA	NA	NA	NA	NA	NA	NA	NA
52	17.38	8.89	46.92	56.5	9.77	12.81	29.05	11.56
71	1.94	NA	1.81	0.17	0.04	0.07	2.44	0.17
90	NA	NA	NA	NA	NA	NA	NA	NA
95	0.12	NA	0.72	2.65	0.03	NA	1.19	0.29
15444			15448		30579		30581	
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	0.14	NA	0.24	NA	0.01	NA	0.09	NA
22	0.49	NA	NA	NA	NA	NA	0.02	NA
23	0.09	NA	NA	NA	NA	NA	NA	NA
24	NA	NA	NA	NA	NA	NA	NA	NA
31	NA	NA	NA	NA	0.04	NA	0.05	NA
41	NA	NA	NA	NA	NA	NA	NA	NA
42	96.11	95.7	93.18	99.61	81.67	87.14	69.08	77.43
43	NA	NA	NA	NA	NA	NA	NA	NA
52	3.17	4.3	6.46	0.39	17.37	12.86	28.91	22.43
71	NA	NA	0.08	NA	0.45	NA	0.97	0.05
90	NA	NA	NA	NA	NA	NA	NA	NA
95	NA	NA	0.03	NA	0.46	NA	0.88	0.09
30582			30583		30584		30585	
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	0.26	0.13	NA	NA	0.37	0.15	0.06	0.06
22	0.13	NA	NA	NA	0.51	0.15	0.01	NA
23	0.02	NA	NA	NA	0.31	NA	0	NA
24	NA	NA	NA	NA	0.07	NA	NA	NA
31	0	NA	NA	NA	0.23	NA	7.23	1.97
41	NA	NA	NA	NA	0.17	NA	0.02	NA
42	88.7	92.38	90.02	82.86	76.97	96.97	52.47	27.88
43	NA	NA	NA	NA	0.06	NA	NA	NA
52	10.72	7.49	8.54	16.57	19.31	2.73	39.06	67.49
71	0.1	NA	0.64	0.57	1.94	NA	1.03	2.53
90	NA	NA	NA	NA	NA	NA	NA	NA
95	0.07	NA	0.8	NA	0.06	NA	0.12	0.06

NLCD	30586		30587	
	Availability	Usage	Availability	Usage
21	NA	NA	0.08	NA
22	NA	NA	0.06	NA
23	NA	NA	0	NA
24	NA	NA	NA	NA
31	3.29	1.9	0.62	NA
41	0.06	NA	0.1	NA
42	56.54	47.88	73.04	74.78
43	0.01	NA	0.15	NA
52	39.47	50.22	24.6	25.14
71	0.48	NA	1.23	0.08
90	NA	NA	NA	NA
95	0.16	NA	0.12	NA

Table 14. This table shows third order preference for individual bears in the wild patch within the 95% Kernel Density Estimate home range. Comparison was done by individual bear; if usage was smaller than availability, then the habitat type was considered preferred. NLCD refers to National Land Cover Database and included the following landcover types: 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed. Medium Intensity, 24: Developed High Intensity, 41: Deciduous Forest, 42; Evergreen Forest, 43: Mixed Forest, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands.

Comparison of Urban Use to Availability

Habitat	Mean of Use %	SD of Use %	Mean of Available %	SD of Available %	Sig. Diff.	p-value	t-test statistic	Selected
21	13.8000	10.2211	14.7108	6.4130	No	0.5452	-0.6136	
22	8.4836	6.1999	10.8940	6.3517	Yes	0.0023	-3.4126	
23	2.2652	2.1835	2.2200	1.7488	No	0.9175	0.1047	
24	0.5016	0.6726	0.4828	0.6529	No	0.9262	0.0936	
31	0.1228	0.5935	0.0592	0.2111	No	0.6201	0.5022	
41	0.0184	0.0920	0.0168	0.0840	No	0.3273	1.0000	
42	63.4132	16.0693	58.2324	10.4255	No	0.0544	2.0228	X almost
43	0.0184	0.0920	0.0176	0.0880	No	0.3273	1.0000	
52	10.3488	10.4966	11.4360	7.1443	No	0.4166	-0.8266	
71	0.3544	0.8436	0.8660	1.0351	Yes	0.0086	-2.8628	
90	0.0072	0.0360	0.0344	0.1240	No	0.2363	-1.2146	
95	0.6640	2.8530	1.0304	1.6824	No	0.4787	-0.7197	

Table 15. This table shows third order defined as the habitat preference for the urban patch within the 95% Kernel Density Estimate home range, comparisons based on means. Selection defined by significant p value and mean use greater than mean available habitat. Landcover types include 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed. Medium Intensity, 24: Developed High Intensity, 41: Deciduous Forest, 42; Evergreen Forest, 43: Mixed Forest, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands.

Percent Urban Preference by Bear ID

10611		12643		12644		12645		
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	14.18	10.37	15.94	19.28	17	32.76	8.19	4.03
22	9.39	8.35	18.91	8.5	10.95	8.59	25.12	17.58
23	1.78	1.4	3.6	2.61	1.95	4.08	6.76	1.47
24	0.3	0.06	0.17	0.65	0.38	0.92	2.39	NA
31	NA	NA	NA	NA	NA	NA	0.26	NA
41	NA	NA	NA	NA	NA	NA	NA	NA
42	61.32	71.99	47.57	66.99	62.11	48.47	36.44	38.83
43	NA	NA	NA	NA	NA	NA	NA	NA
52	11.73	7.71	11.05	1.96	7.27	5.15	12.29	23.63
71	0.58	0.09	2.18	NA	0.25	0.02	3.52	NA
90	NA	NA	NA	NA	NA	NA	0.31	0.18
95	0.72	0.03	0.59	NA	0.09	NA	4.71	14.29
12647		12648		13205		13206		
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	12.94	12.39	15.05	20.41	17.84	7.06	10.04	12.88
22	9.88	9.63	10.56	11.41	9.45	3.66	8.1	6.61
23	2.44	6.88	2.07	1.56	1.59	1.55	1.88	4.82
24	0.7	0.46	0.4	0.44	0.39	0.43	0.24	2.71
31	0.17	NA	NA	NA	NA	NA	0.01	2.97
41	0.42	0.46	NA	NA	NA	NA	NA	NA
42	56.1	57.34	61.93	62.82	63.22	83.51	63.88	52.97
43	0.44	0.46	NA	NA	NA	NA	NA	NA
52	14.67	11.93	9.4	3.35	7.05	3.79	13.52	16.18
71	1.71	0.46	0.32	NA	0.42	NA	1.06	0.79
90	NA	NA	NA	NA	NA	NA	NA	NA
95	0.53	NA	0.27	NA	0.04	NA	1.28	0.07
13207		13208		13209		13210		
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	17.75	10.46	2.23	0.1	24.92	17.56	21.32	37.18
22	7.82	1.44	2.04	0.78	13.35	7.2	12.3	13.05
23	0.61	0.03	1.6	0.2	3.29	1.10	3.21	0.95
24	0.09	NA	0.06	NA	0.61	0.15	0.63	0.28
31	0.01	NA	NA	NA	NA	NA	NA	NA
41	NA	NA	NA	NA	NA	NA	NA	NA
42	66.67	85.91	44.85	47.84	53.94	70.83	58.27	48.16
43	NA	NA	NA	NA	NA	NA	NA	NA
52	6.66	2.12	37.98	47.25	3.77	3.16	4.16	0.39
71	0.12	0.03	3.87	3.82	NA	NA	NA	NA
90	NA	NA	NA	NA	NA	NA	NA	NA
95	0.26	NA	7.37	NA	0.13	NA	0.1	NA

13211			13212		15441		15442	
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	25.22	23.9	7.88	2.6	17.64	27.83	9.31	5.56
22	14.33	11.55	3.68	0.62	12.34	10.56	29.19	26.28
23	1.89	1.2	0.31	NA	2.34	3.1	7.49	6.65
24	0.3	0.4	NA	NA	0.5	0.45	2.69	0.12
31	NA	NA	1.03	0.1	NA	NA	NA	NA
41	NA	NA	NA	NA	NA	NA	NA	NA
42	43.72	52.59	60.22	78.79	58.97	47.42	37.4	58.31
43	NA	NA	NA	NA	NA	NA	NA	NA
52	13.68	10.36	24.55	16.53	7.91	10.5	9.11	2.43
71	0.87	NA	0.73	NA	0.19	0.11	1.84	0.12
90	NA	NA	NA	NA	NA	NA	0.55	NA
95	NA	NA	1.61	1.35	0.1	0.03	2.42	0.53
15444			15448		30579		30581	
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	25.78	19.58	19.29	12.22	20.29	9.43	7.61	2.5
22	13.01	7.2	13.02	11.31	9.78	7.55	3.1	NA
23	2.91	1.71	2.20	2.71	0.65	NA	NA	NA
24	0.52	0.06	0.5	1.13	0.06	NA	NA	NA
31	NA	NA	NA	NA	NA	NA	NA	NA
41	NA	NA	NA	NA	NA	NA	NA	NA
42	53.37	66.01	56.38	64.25	63.76	79.25	74.01	87.5
43	NA	NA	NA	NA	NA	NA	NA	NA
52	4.3	5.43	7.95	7.24	4.95	3.77	13.31	10
71	NA	NA	0.46	0.9	0.18	NA	0.35	NA
90	NA	NA	NA	NA	NA	NA	NA	NA
95	0.12	NA	0.19	0.23	0.33	NA	1.62	NA
30582			30584		30585		30586	
NLCD	Availability	Usage	Availability	Usage	Availability	Usage	Availability	Usage
21	12.44	11.46	17.32	27.5	14.42	14.16	3	NA
22	9.92	9.74	9.75	17.5	9.18	10.62	1.48	NA
23	2.19	4.51	1.46	6.25	1.61	3.54	0.23	NA
24	0.38	1.36	0.2	1.88	0.27	0.88	NA	NA
31	NA	NA	NA	NA	0	NA	NA	NA
41	NA	NA	NA	NA	NA	NA	NA	NA
42	60.38	55.8	57.63	40.62	65.92	47.79	82.32	100
43	NA	NA	NA	NA	NA	NA	NA	NA
52	13.22	16.4	12.53	4.38	8.03	23.01	12.37	NA
71	0.55	0.64	1.07	1.88	0.44	NA	NA	NA
90	NA	NA	NA	NA	NA	NA	NA	NA
95	0.93	0.07	0.03	NA	0.13	NA	0.6	NA

NLCD	Availability	Usage
21	10.17	3.78
22	5.7	2.36
23	1.44	0.31
24	0.29	0.16
31	NA	NA
41	NA	NA
42	65.43	71.34
43	NA	NA
52	14.44	22.05
71	0.94	NA
90	NA	NA
95	1.59	NA

Table 16. This table shows third order, defined as the preference for individual bears in the urban patch within the 95% Kernel Density Estimate home range. Comparison was done by individual bear; if usage was smaller than availability, then the habitat type was considered preferred. NLCD refers to National Land Cover Database and included the following landcover types: 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed, Medium Intensity, 24: Developed High Intensity, 41: Deciduous Forest, 42: Evergreen Forest, 43: Mixed Forest, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands.

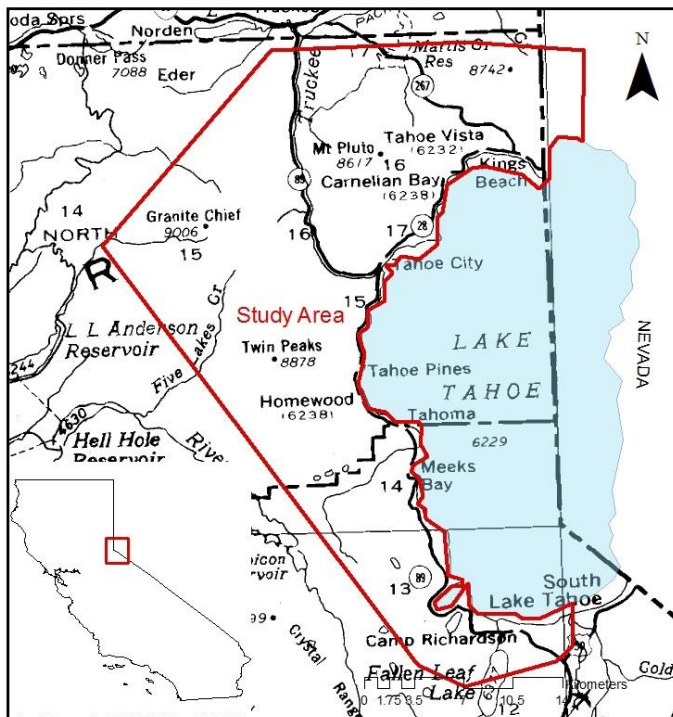


Figure 1. Study area consisting of the western portion of Lake Tahoe (CA) including El Dorado, Placer and Nevada counties, and part of the city of Truckee and the area east of Truckee to the Nevada state border.



Figure 2. A box shaped trailer mounted bear trap, allowing for movement of bears to nearest possible habitat for release (Photo credit: Mario Klip).

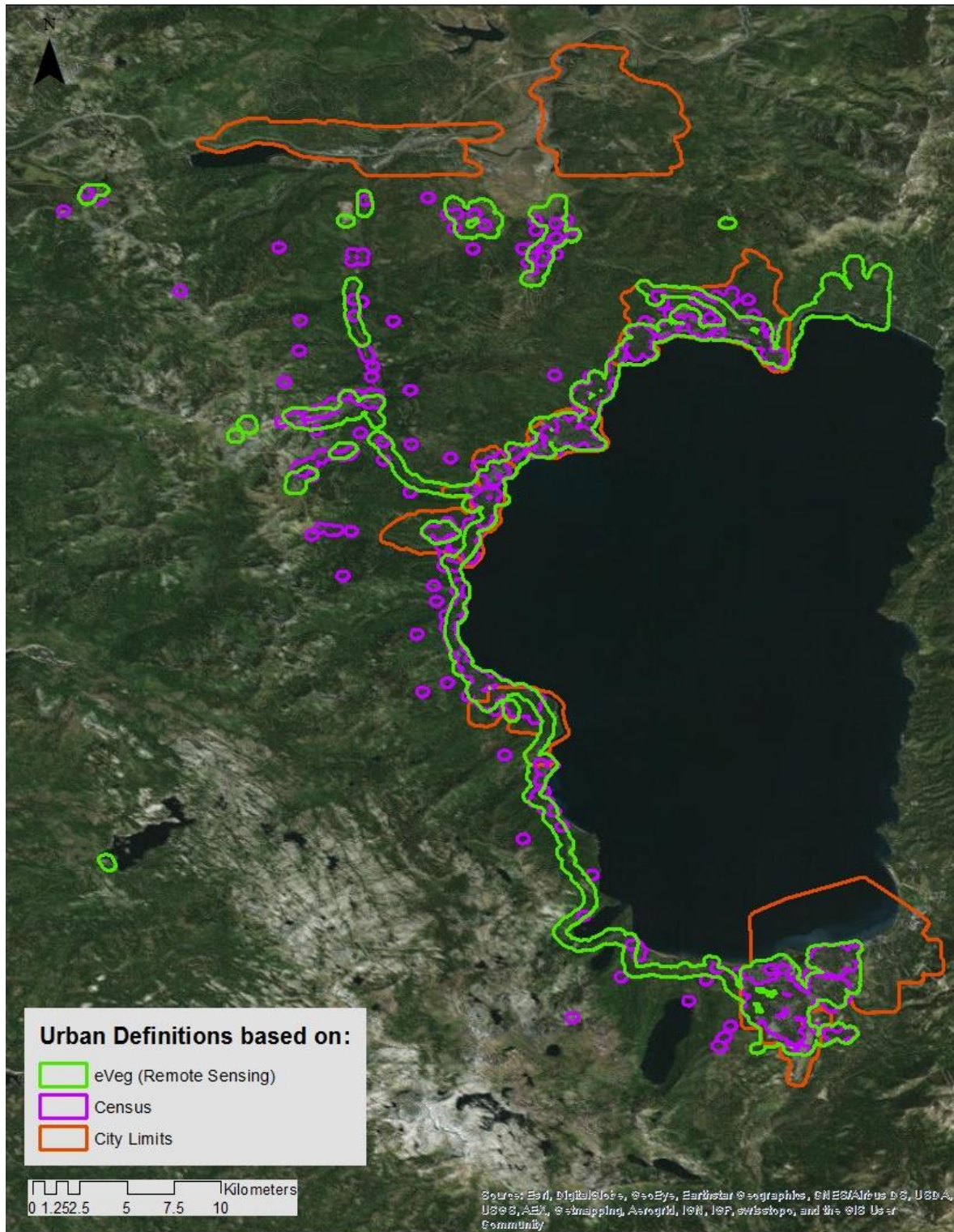


Figure 3. This map illustrates the three urban extents utilized. The extents are City Limits, Census and eVeg (Remote Sensing). All bounding polygons were buffered by 250m to include bears close to the urban extents.

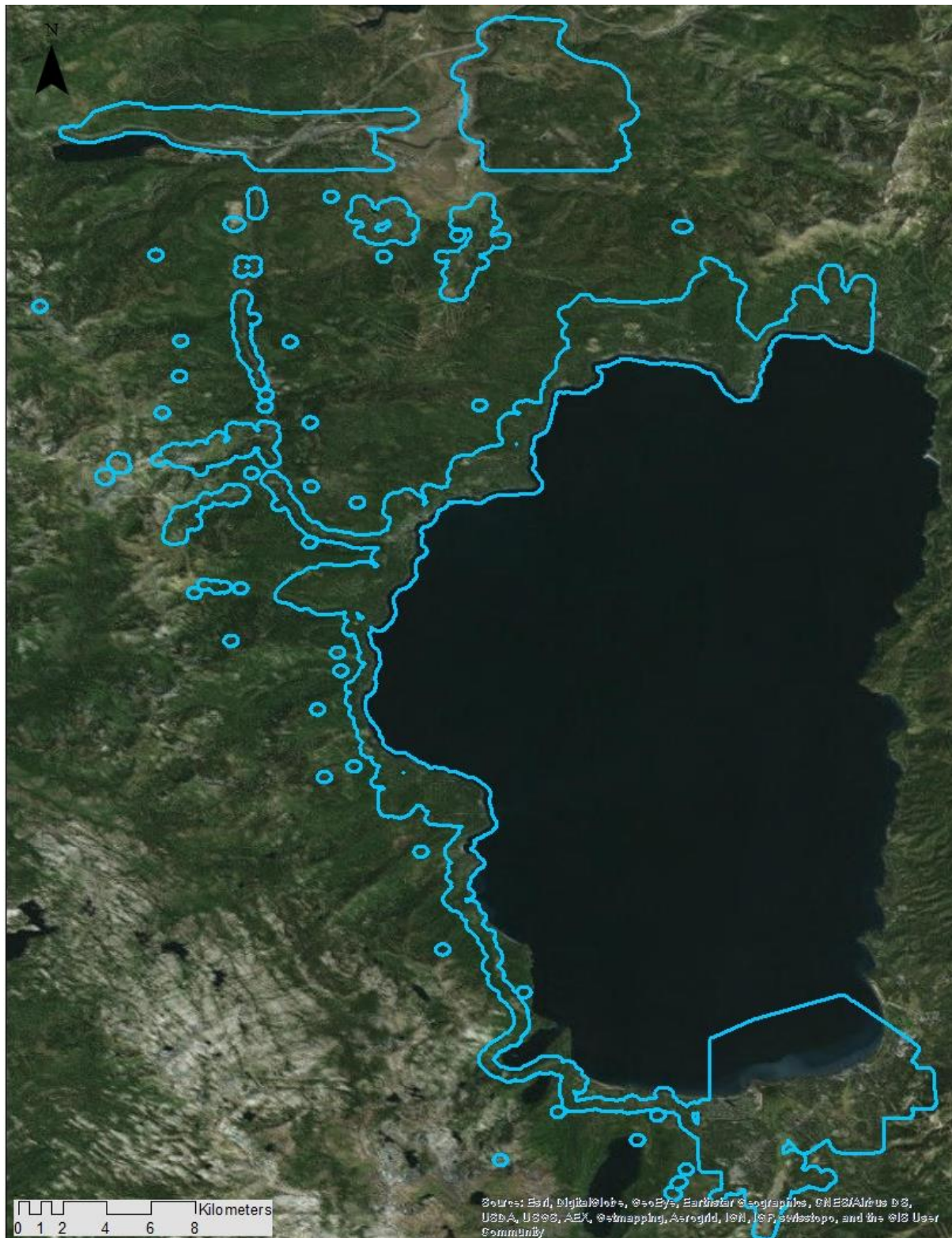


Figure 4. This map illustrates the aggregation of three urban extents; City Limits, U.S. Census and eVeg (Remote Sensing) into one combined extent. Bear fixes found within the blue polygons were considered urban.

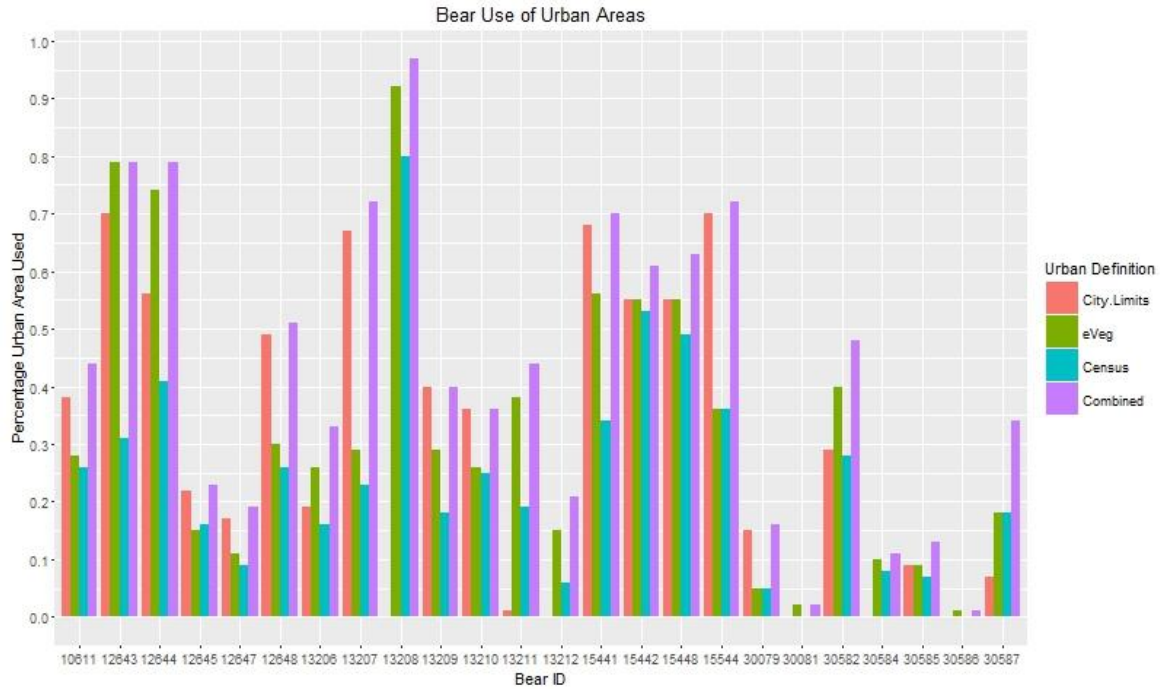


Figure 5. This figure shows black bear usage of urban areas based on four different definitions of urban: City Limits, U.S. Census, eVeg (Remote Sensing) and Combined.

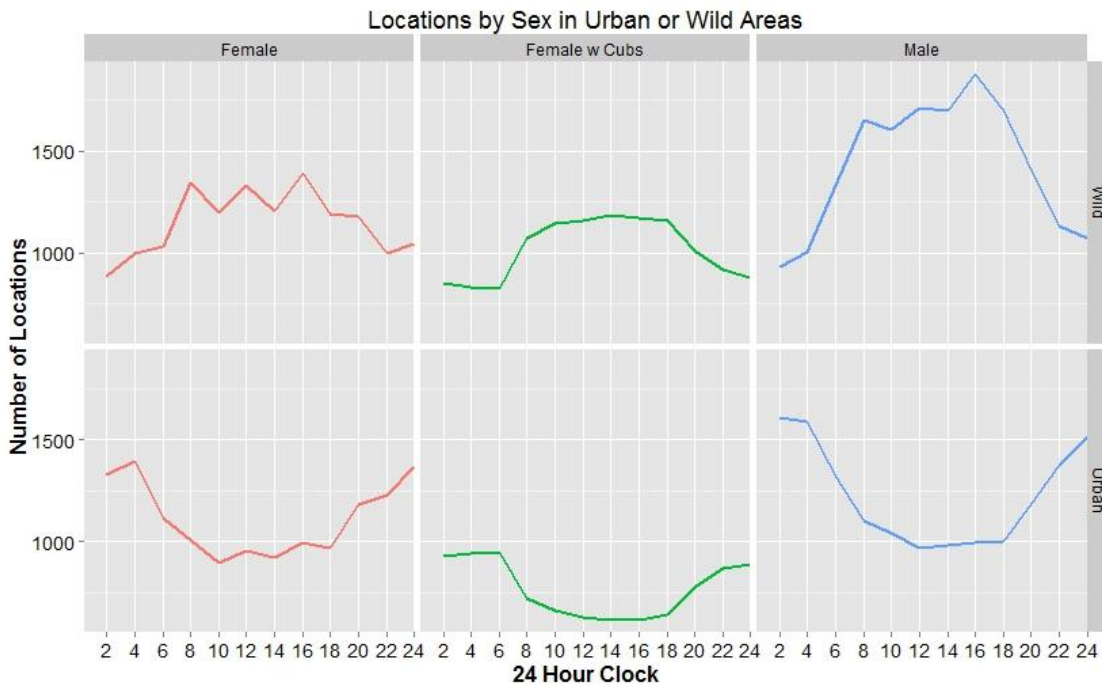


Figure 6. This figure shows twenty-four hour activity patterns by sex in urban and wild areas. Bears utilized resources differently during the day; all sexes see pronounced use patterns, where bears are utilizing urban areas more intensively during the evening hours and early morning hours.

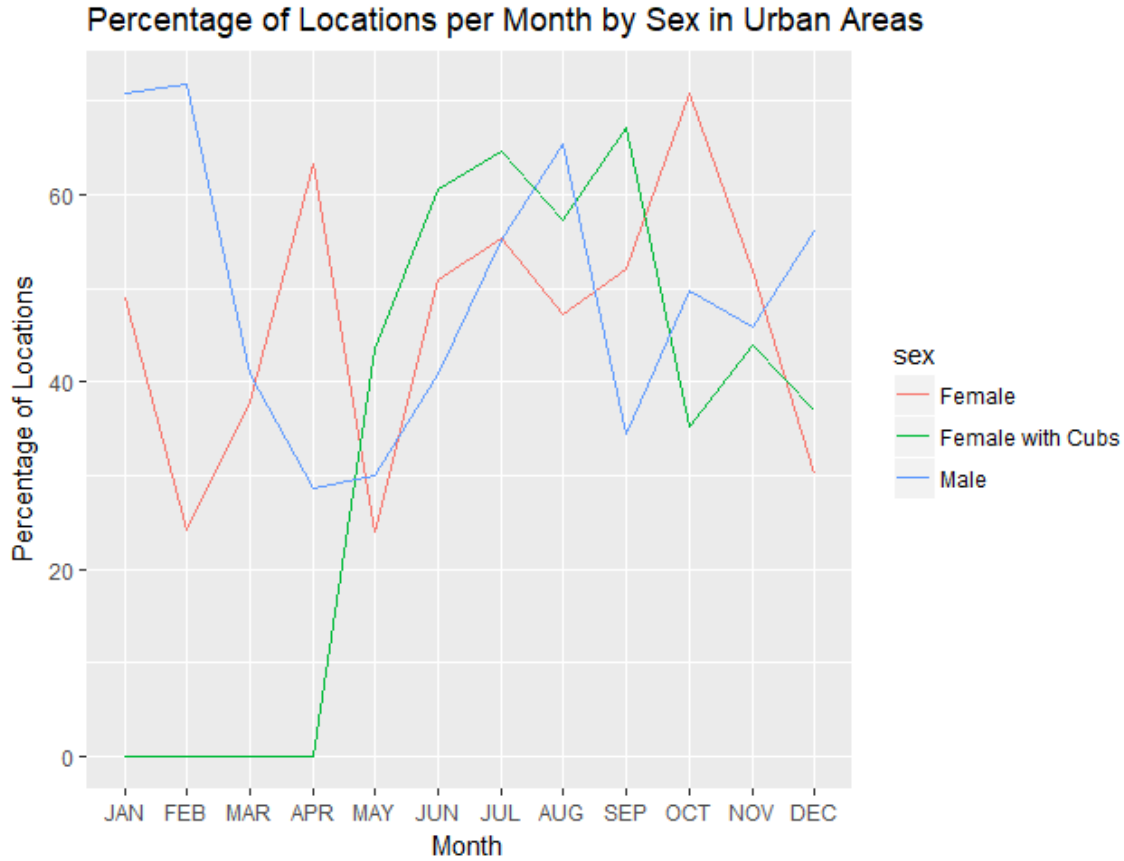


Figure 7. This figure illustrates the monthly use of the urban areas during the year. Females with cubs do not use the urban area until April. Females have a peak usage in April and in November and male use of the urban area is high during the summer.

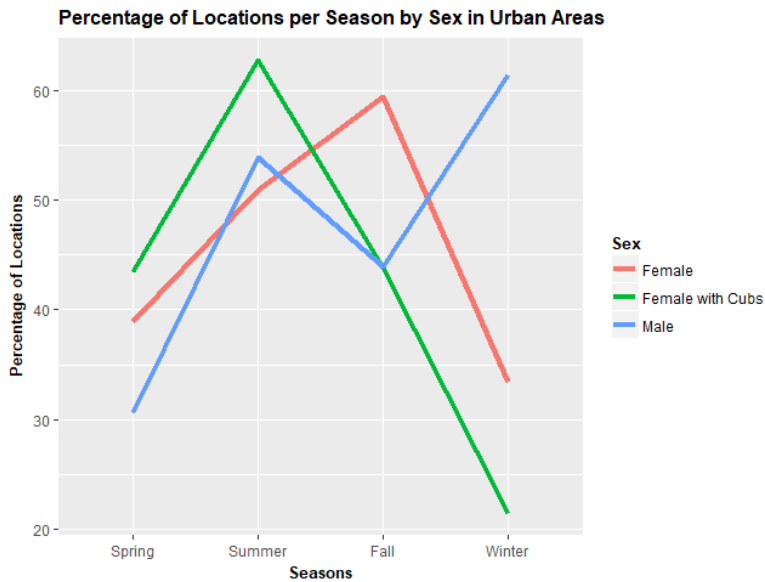


Figure 8. This figure shows seasonal use by sex of the urban area, indicating that seasonal use was highest in proportional urban use by sex.

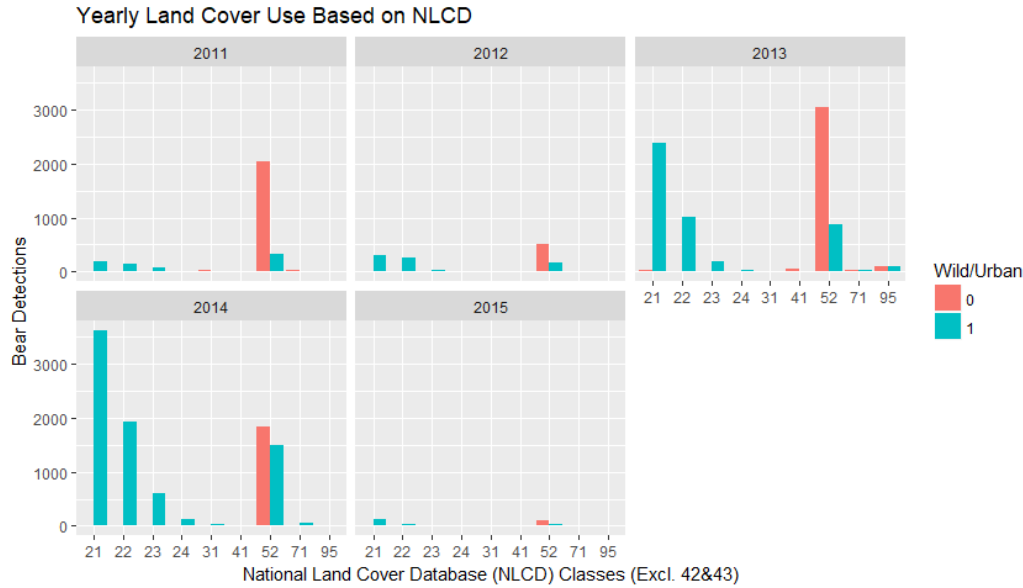


Figure 9. Annual habitat use based on NLCD habitat classes based on GPS fixes, omitting (41) Evergreen Forest to provide additional contrast. Urban is defined as 1 (blue) and wild as 0 (red). The most important categories included 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed, Medium Intensity, 24: Developed; High Intensity, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands. 2015 is not a full year and includes spring season only.

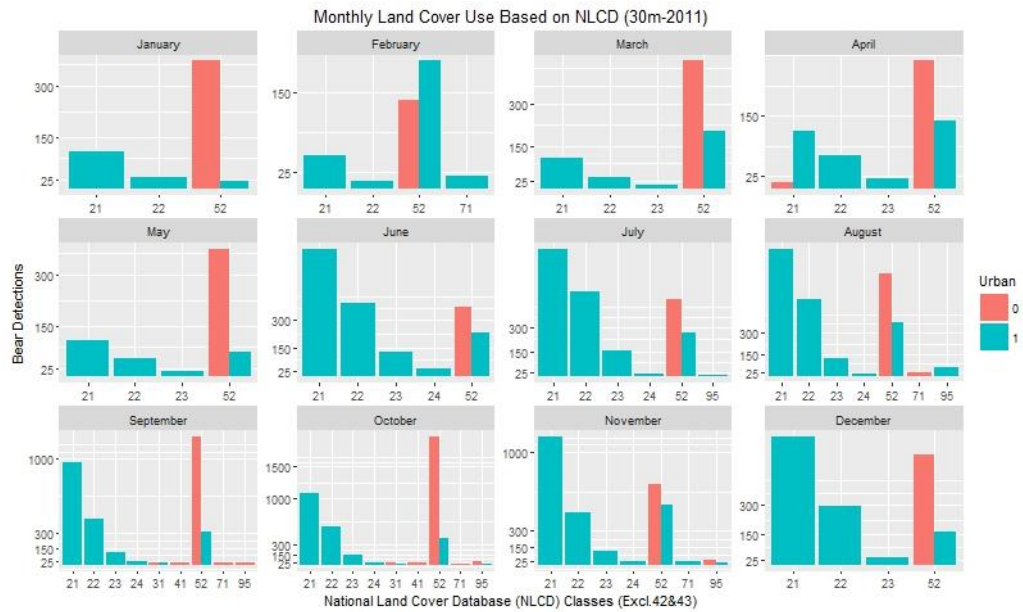


Figure 10. Monthly land cover use contrasted between urban and wild areas. Urban is defined as 1 (blue) and wild as 0 (red). Note that the y-axis is flexible in order to allow for monthly comparisons. Most important categories included 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed, Medium Intensity, 24: Developed; High Intensity, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands.

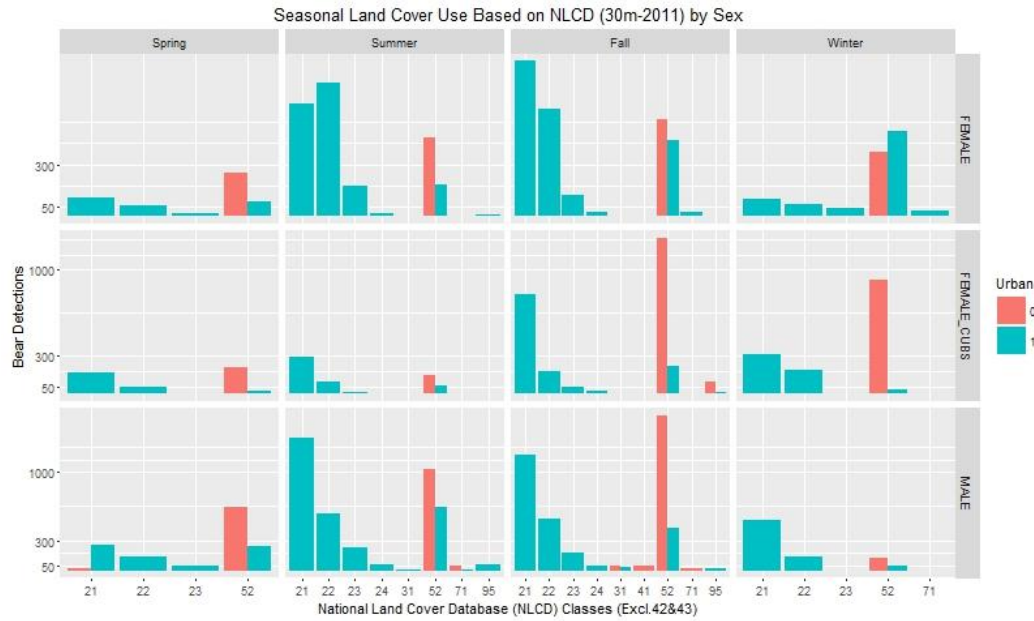


Figure 11. Landcover use by NLCD categories by season and sex based on GPS fixes. Urban is defined as 1 (blue) and wild as 0 (red). The most important categories included 21: Developed Open Space, 22: Developed, Low Intensity, 23: Developed, Medium Intensity, 24: Developed High Intensity, 52: Shrubs, 71: Grasslands/Herbaceous, 95: Emerging Herbaceous Wetlands.

3. Home range and resource selection of an urban carnivore; The American black bear

Introduction

How wildlife uses space can generate important insights into multiple aspects of a species' biology and behavior including resource selection, distribution across the landscape, and reproduction (Boyce et al. 2002, Mitchell and Powell 2007, Nathan et al. 2008, Powell and Mitchell 2012). This information can also be used to guide management decisions. For example, studies of mammalian migratory pathways can be used to modify the design of proposed roadways to reduce the risk of collisions between vehicles and wildlife (Lewis et al. 2011). Many aspects of the ecology of mobile animals captured by spatial data may be particularly affected when those animals live in the Wildlife Urban Interface (WUI, McKinney 2008). Increased WUI in the U.S. forces animals to live in closer proximity to humans and may cause shifts in animal behavior (Thompson and Henderson 1998, Ditchkoff et al. 2006, George and Crooks 2006, Cahill et al. 2012). Additionally, species occurring at the WUI may experience increased conflict with humans due to livestock predation or attacks on pets (Lukasik and Alexander 2012). Spatial analyses of activity can be used to mitigate predation on livestock or other domestic species (Graham et al. 2005) by for example, illuminating hotspots and represent a critical component of efforts to manage negative human-wildlife interactions (Baruch-Mordo et al. 2008, Atwood and Breck 2012).

Spatial analyses were conducted using multiple methods, including home range analysis and Resource Selection Functions (RSF). An organism's home range is defined as "the area traversed by the individual in its normal activities of food gathering, mating and caring for its young" (Burt 1943). Insight into animal home ranges has helped to illuminate several aspects of wildlife ecology, including intraspecific interactions, mating behavior, and foraging strategies (Powell 2000, Beckmann and Berger 2003b). The term "home range" was established over 70 years ago, but the methods used to calculate home ranges have changed over time such that the field now lacks a standard method (Laver and Kelly 2008). An alternative is to calculate the RSF, which is defined as the "probability that a resource unit is used" (Manly et al. 1993, Boyce et al. 2002). RSFs are often modeled by exploring the influence of various covariates on the probability of using a particular habitat unit. Common covariates include landscape-level features such as roads, wetlands, agriculture, and urban gradients (Ciarniello et al. 2009, Costello et al. 2013, Dellinger et al. 2013, Mowat et al. 2013, Montgomery et al. 2014).

Both the home range and resource selection function methods have been applied at the WUI recently (e.g., Benson et al. 2016, Duquette et al. 2016). Both methods have potential to illuminate the effects of human disturbance, including impacts on wildlife activity, reproduction, etc. For example, mammals move into developed areas seeking anthropogenic food sources (Ditchkoff et al. 2006) or are following and seeking prey. Mammalian species that are particularly active at the WUI include raccoons (*Procyon lotor*; Riley et al. 1998), red foxes (*Vulpes vulpes*; Harris 1981), and coyotes (*Canis latrans*; Grindler and Krausman 2001). However, there are indications that home range and RSF analyses may yield different results for wildlife living at the WUI in comparison to more "wild" locales (Baruch-Mordo et al. 2013). Specifically, reported home ranges for wildlife may be smaller in the WUI (Karelus et al. 2016).

A quintessential example of a mammal utilizing WUI areas is the American black bear (*Ursus americanus*). As a common, widespread, and charismatic large mammal in North America, the black bear has been a frequent subject of home range analyses. For example, Moyer et al. (2007) described various factors affecting bear home range size, including habitat carrying capacity and population density. Beckmann (2003a; 2008) quantified the role of resource availability, including the use of garbage. Multiple studies have shown that black bears move into the WUI in pursuit of anthropogenic food sources (Rogers et al. 1974, Herrero 1980, Mccullough 1982). However, surprisingly little is known about how increased use of anthropogenic food sources affects home range sizes. If the size of the home range indicates needs other than food, bears with territories overlapping urban areas may appear similar to those that use natural areas. Yet previous work (e.g. Beckmann and Berger 2003, Baruch-Mordo et al. 2014, Karelus et al. 2016) reported much smaller home ranges for urban bears in comparison to their wild counterparts. For example, Beckmann (2003) reported 70-90% smaller home ranges for urban bears compared to bears that relied on natural areas. Additionally, he reported that bears may occur at higher densities where they have access to human-derived foods. Beyond home range analyses, RSF analyses for bears have produced mixed results as well, with Tri et al (2016) reporting that bears utilizing the WUI did not differ in their selection from their wild cousins but Hiller et al. (2015) indicating that wild bears avoided developed areas.

Patterns of space use may also vary temporally. Developed areas are often used as an alternative or supplement to wild foods, and such alternatives likely hold additional appeal during bad food years, including drought years (Baruch-Mordo et al. 2008, Lackey and Beausoleil 2010, Garshelis et al. 2017). During 2012-2016 California experienced a severe multi-year drought (Jones 2015). Such extreme conditions might lead to bears moving into town in search for food at a higher rate than during “normal” conditions. Thus, analyses of space use during extreme events like the recent multi-year drought may also reveal important insights about the conditions that lead to greater use of the WUI.

Here, I test for a link between urban habitat and ranging behavior using three commonly-used methods to measure home range, described below. I compare KDE urban home range sizes from this study to those from about 80 previously reported home range results to determine whether “urban” home ranges vary consistently from “wild” home ranges. Additionally, I investigate how season and sex affect home range sizes (hereafter; home range analysis). Second, I examine the dependency of bears on the urban envelope by calculating the seasonal home range overlap with urban areas and whether this changed due to drought (hereafter; home range overlap). Finally, I investigate temporal patterns of habitat selection within the home range by means of an applied resource selection model (hereafter; RSF analysis) I predicted that different home range methods would yield different results and that urban bears would have smaller home ranges than bears in wilderness areas. I also predicted that core home ranges would suggest disproportionate importance of the urban area and that overlap with urban areas was elevated during drought. Finally, I predicted that the RSF would reveal that bears select for areas of known past bear-human conflict. My results provide important insights into space use by bears in a WUI environment and the impacts of different space use methods on assessment of home ranges for these animals.

Quantifying home ranges

The first of the three home range estimation methods that I used was the Minimum Convex Polygon (MCP) – a classic method applied by drawing the smallest convex polygon that encompasses a given percentage of known locations, typically 95%, for a focal animal (Hayne 1949). This approach is simple to apply and intuitive in its interpretation (Powell 2000). However, because the MCP assumes all areas within its borders receive equal use, it ignores finer-scale selection of resources within the MCP. Additionally, the borders of an MCP home range are interpreted as hard barriers, whereas home range boundaries for most species, including black bears, are generally diffuse (Powell and Mitchell 2012). Additionally, the MCP method is highly sensitive to outliers (Powell 2000). Despite these shortcomings, MCP is still widely used (Belant 2002) because of its simplicity and ease of interpretation and because it allows for comparison across studies, particularly older ones.

The second method of home range estimation that I employed was the Kernel Density Estimator (KDE), which was first described by Worton (1989). KDE is considered a major advance over MCP because it produces contours (kernels) that indicate different frequencies of use by the study animal within the home range (Seaman et al. 1998, Powell 2000, Laver and Kelly 2008). Additionally, KDE allows more than one center of activity for a focal animal and is not unduly sensitive to outlying points (Hemson et al. 2005). However, KDE does not take the temporal sequence of observed locations into consideration and thus clumps of location points may be highly auto-correlated and thereby violate statistical assumptions of independence (Aebischer et al. 1993, Powell 2000).

The final method that I used to calculate home ranges was the Brownian Bridges Movement Model (BBMM). This approach was selected because, unlike KDE methods, it statistically controls for spatial auto-correlation among GPS locational data (Kernohan et al. 2001). BBMM is based on the properties of a conditional random walk between successive pairs of locations, dependent on the time interval between locations (Horne et al. 2007). The BBMM estimates the probability that an animal selected a particular area of the home range over the analysis period. While both KDE and BBMM attempt to understand the utilization distribution of a focal animal, KDE violates temporal independence (Worton 1989) while BBMM does not (Horne et al. 2007).

Methods

I collected bear movement data through GPS collars from Spring 2011 to Spring 2015. During these periods, 27 bears were captured, including 12 females, 10 males, and five females with cubs.

Study area

This study was conducted in the western portion of the Tahoe Basin (hereafter; Basin), in El Dorado, Placer and Nevada counties, California. The outer extent for analysis was defined by enclosing all bear GPS locations with a 500m buffer. The full study area encompassed approximately 850 km², consisting of both private and public property. Elevation within the study area ranged from 1897m at lake level to 3317m. Vegetation in this area was dominated by a mixed conifer forest of white fir (*Abies concolor*), Jeffrey pine (*Pinus jeffreyi*), lodgepole pine

(*Pinus contorta*), and red fir (*Abies magnifica*; Roth et al. 2004). California Wildlife Habitat Relationships (CWHR) plant communities present in the study area included montane hardwood, montane hardwood-conifer, riparian, chaparral, wet meadow, and barren (Mayer and Laudenslayer 1988).

Capture methods

Bears were captured between May and November of 2011 to 2014 using a heavy-duty box trap mounted on a trailer. Trapped bears were chemically immobilized using Telazol (Fort Dodge Laboratories Inc., Fort Dodge, IA) following the California Department of Fish and Wildlife (CDFW) Capture and Restraint Manual (Jessup et al. 2001). UC Berkeley's Institutional Animal Care and Use Committee (IACUC) approved all animal handling procedures (IACUC: R358-0315, Sikes 2016). Adult bears were outfitted with ATS Iridium collars (model G2110E, Advanced Telemetry Systems, Isanti, MN) in 2011 and 2012. During later years, Vectronic Iridium collars (Model GPS PLUS Vectronic Aerospace GmbH Carl-Scheele-Str. 12D-12489 Berlin Germany) were used. During the first six weeks of deployment, collars were programmed to gather locations every 20 minutes to monitor for post-capture mortality. After six weeks, positions were gathered every two hours to conserve battery life. All collars were also equipped with VHF transmitters to facilitate location on the ground in real time.

Three sex classes were defined: (1) females, (2) females with cubs, and (3) males. I assigned all individuals to one of the following age classes: cubs less than one year of age and accompanied by a sow, sub-adults over one year old and not accompanied by a sow (40 and 100kg), and adults (> 100kg). Captured bears also participated in an Aversive Conditioning (AC) study with three treatment groups (control, AC with dogs, and dogs and less-lethal ammo). The effects of AC are reported in chapter 4.

Data preparation

Initial investigation revealed that some GPS locations for individual bears were too extreme to represent biologically feasible rates of bear movement. Velocities above 4 km/h speed appeared to be spurious and were removed. All remaining GPS locations (2D and 3D) were used in spatial analyses unless otherwise stated. No subsampling was performed because spatial estimates based on a subset of data point may differ from those based on the entire GPS dataset (Fieberg 2007, Kie et al. 2010). Error rates for GPS locations were not calculated in the field; however, error estimates for a similar collar based on 38,756 GPS localities revealed mean errors of 1.77 m for latitude, 1.59 m for longitude, and 2.25 m for elevation (Chris Kochanny, Senior Project Consultant/Wildlife Biologist Vectronic Aerospace, personal communication). While these values provide an indication of the accuracy of the GPS data, actual error rates in the field may differ substantially (D'Eon and Delparte 2005).

Animals 15544 and 13209 were the same bear; similarly, animals 30585 and 12647 were the same bear. These were the only bears that were outfitted with two collars due to a chance recapture when the original collar was nearing battery depletion. In the case of 30585, the original unit was an ATS collar (model G2110E, Advanced Telemetry Systems, Isanti, MN) that was no longer on the bear when recaptured. Further analyses treated the two collars independently. Analyses were conducted with and without these two bears with no detectable impact on overall outcomes.

All spatial analyses were completed in ArcGIS 10.2 (ESRI 2015, ArcGIS Desktop, Redlands, CA, Environmental Systems Research Institute) and R (version 3.1.3 R Core Team 2014, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>). Graphs were made in GGPLOT2 (Wickham 2009) or base R. Data reorganization and manipulations were done using the following R packages: PLYR (Wickham 2011), STRINGI (Gagolewski 2015), RESHAPE (Wickham 2007) and doBy (Hojsgaard and Halekoh 2014).

Home range size analysis by method and sex

All home ranges were calculated using ArcGIS plugin ArcMET (Wall 2014). The KDE utilized a fixed bandwidth smoothing parameter (h) because adaptive bandwidth smoothing tends to overestimate the sizes of the areas used (Seaman et al. 1998). A 30 meter raster and 1.5 meter raster expansion ratio were selected. All other values remained at default. Within ArcMet, BBMM parameters were set up with a maximum tolerated gap of 72 hours, a telemetry error standard deviation of 10 meters, and an integration time-step of 10 minutes. Raster resolution was set at 30 meters and the raster expansion ratio set at 1.5 meter. Home ranges were calculated by considering a different percentage of GPS locations. MCP home ranges were calculated at 50, 95, 99 and 100% of locations, while KDE and BBMM calculations were at 50, 95, and 99% of locations. Differences in home range sizes were assessed in relation to method, sex, and year through linear mixed effect models (Kuznetsova et al. 2016).

Comparison to published home range sizes

Urban home ranges (km^2) were expected to be considerably smaller than wild home ranges. I compared home ranges from my study to home ranges published from previous studies because wild home range sizes for wild bears within the study area were unavailable. The vast majority of the previously published home ranges were in wild settings. Home ranges were grouped into three geographical areas: California, West Coast (defined as California, Oregon, and Washington state), and North America. I compared mean home range sizes from my study to wild home range sizes for the three groups using Welch's two sample t-test. I did not differentiate among methods used for estimating previously published home range sizes, although differences in the methods used may have affected the resulting size estimates. Females and females with cubs were combined because most papers did not differentiate between these two classes.

Seasonal home range sizes

Seasonal differences in home range sizes were also calculated within ArcMET and utilized the KDE method including 50 and 95% of bear GPS locations. Seasonal variation in home range sizes was analyzed using linear mixed effect models in LmerTest (Kuznetsova et al. 2016). Year and season were part of these models and seasons were defined as follows: spring as March 16th - June 15th, summer as June 16-August 31, fall as September 1– November 30, winter as December 1-March 15.

Home range overlap with the urban envelope

Overlap with the urban envelope was defined as the portion of the seasonal home range that coincided with the urban extent. Seasonal home ranges were used to understand whether overlap varied during the year. The urban extent was defined as the combination of urban limits demarcated by U.S. Census, City Limits, and Remote Sensing, that is, the ‘Combined’ urban extent from Chapter 1 (see full details in in Chapter 1). I utilized KDE home ranges at 50 and 95% to calculate the proportion (%) of the home range that fell within the urban extent. Core areas were defined as 50% of the locations (Powell 2000, Hemson et al. 2005, Spencer 2012). A core area can be defined as the area that is used most intensively (Seaman et al. 1998, Powell 2000). A longstanding convention typically looks at 95% of the locations since exploratory behavior (5%) might be excluded from the home range assessment (Powell 2000). The area of the portion of the home range that overlapped the urban extent was divided by the total home range size for both 50% and 95% of locations and expressed as a percentage. The area overlaying the urban extent was identified as “urban” and the area outside of this was identified as “wild”, adding up to a 100% of the home range for each bear. Sex, season, year and their interactions were maintained as covariates in linear mixed model analyses (Kuznetsova et al. 2016); the year 2011 was marked as a wet year and all subsequent years were marked as dry (Jones 2015).

Temporal selection of resources within the home range

To gain a deeper understanding of temporal variation in the use of various anthropogenic and other habitat features within the home range, I calculated Resource Selection Functions (RSF) focused on seasonal variation by sex. This approach quantifies attraction to or avoidance of landscape features. GPS locations for individual bears were used to calculate distances to specific landscape features or extract values such as elevation. The RSF model considered distances to fire roads, all surface roads, roads with speed limits greater than 35 mph, trails, wetlands, sites of known bear-human conflict, and elevation. The locations of all road types, trails, wetlands, and elevation were downloaded from Tahoe Regional Planning Agency (TRPA 2017). The layers were clipped to include only the study area. Data regarding the locations of known bear conflicts were obtained from Placer Sheriff’s Department and El Dorado Sheriff’s Department. 2413 conflicts were recorded by the Placer Sheriff’s Department, and 386 conflicts were recorded by the El Dorado Sheriff’s Department for the 2011-2014 time period. Locations of features and bear-human conflicts were geocoded in ArcGIS and were only included if the location could be determined with over 90% accuracy. Accuracy was defined within the geocoding process; if the location to be geocoded could not be matched to a physical street address, then the incident was discarded. Only “true” conflict data were retained and calls for service other than conflict – for example bear sightings, garbage disturbances, and nuisance activities – were removed from the conflict data set.

The data pool for the RSF model spanned from 2011 to 2015, whereas the home range analysis focused on the more restricted timeframe from 2014-2016. This was due primarily to data availability. Specifically, a total of 13 bears were added to the RSF analysis by including the additional years. Eight bears that had been outfitted with an ATS Collar were added for 2011 and five bears that had been outfitted with Vectronic collars (Model GPS PLUS Vectronic Aerospace GmbH Carl-Scheele-Str. 12D-12489 Berlin Germany) were added for 2013. Thus, the total

number of bears included in the RSF model was 26. The RSF was built by creating 95% KDE seasonal home ranges in adehabitat (Calenge 2006) to illuminate seasonal variation. KDE at 95% of locations was used because of its universal use and ability to perform comparisons (Powell 2000, Laver and Kelly 2008). Spatial information such as shape files and polygon data were accessed through maptools and rgeos packages in R (Bivand and Nicholas 2016, Bivand and Rundel 2017), raster files were managed with the raster package in R (Hijmans 2015). All data layers downloaded were re-projected from their native projection to WGS-84 UTM Zone 10 with the sp package in R (Bivand and Pebesma 2018). The presence locations for bears was multiplied by five to account for random locations (Cooper and Millspaugh 1999, Sawyer and Brashares 2013) and functions as the null hypothesis. Random placement was constrained by a seasonal home range polygon so that the random locations would be within the general area the animal was using during that season.

The analysis of the RSF model followed a Bayesian approach which estimated partial regression parameters based on a sub-sample of the data, i.e. 500 random locations, unless 500 locations could not be achieved because there were not enough locations (e.g. females with cubs in winter). For each sub-sample, I performed a multiple logistic regression with presence/absence as the response variable and each environmental factor as an independent variable. I then used every sub-sample (N = 1000) to determine the distribution of the regression resource use parameters, which were considered significantly different from zero when more than 95% of the sub-samples were either larger or smaller than zero (Figure 1).

Results

Home range analysis by method and sex

For the home range analyses based on 50, 95, and 99% of the locations, data from 12 bears were utilized: three males, six females, and three females with cubs. During the fall time period, fewer adult males were captured compared to the spring.

The total number of GPS locations for this analysis was 43,359, or a mean of 3613 ± 2147 locations per bear (range: 567 to 7,875 locations per bear). The mean number of days for which these positions were gathered was 224 ± 113 (range: 61 to 499 days, Table 1). Although the fix schedule for all animals was similar, the total number of GPS locations gathered differed among animals, even over a relatively similar number of days of collar deployment. Reasons for these differences included variation in terrain, slipped collars, collar variability and other logistical reasons. During the study period, more adult females were trapped than adult male bears and, accordingly, the sex ratio for adult bears was skewed towards females. Most of the trapped males were sub-adults. Other studies previously reported that sex ratios of urban bears were skewed toward males (Hellgren and Vaughan 1987, Beckmann and Berger 2003b). Here, the sex ratio is only skewed towards males when sub-adult males are considered.

50% of locations

Analyses based on 50% of the fixes recorded per individual revealed that home range sizes differed significantly in relation to home range method (linear mixed-model, $F_{2,20.4} = 16.11$, $p < 0.001$) and sex (linear mixed-model, $F_{2,13.8} = 4.65$, $p < 0.05$), but not the interaction between the two (linear mixed-model, $F_{4,20.3} = 0.15$, $p > 0.05$). With regard to analytical method, estimates of

home range sized based on MCPs were largest ($t_{(25)} = 6.18$, $p < 0.001$), followed by estimates based on KDE ($t_{(25)} = 5.71$, $p < 0.001$), with estimates based on BBMM being smallest.

95 and 99% of locations

Analyses based on 95 and 99% the GPS localities generated results similar to those based on 50% of locations. Sex and analytical method remained significant while their interaction remained non-significant. MCP home ranges remained largest at 95% of locations, while BBMM ranges were smallest at 95 and at 99% of locations (Table 2). However, the difference between methods decreased as the percentage of locations included in the analysis increased (Table 2). In fact, at 50 and 95% of locations, MCP calculated the largest estimates, however at 99% of locations KDE home ranges were larger than MCPs. Differences between home ranges sizes, however, were small (Table 2). MCP/BBMM ratios were at 2.23 for males, 1.72 for females and 1.85 for females with cubs. KDE/BBMM ratios were at 2.22 for males, 1.65 for females and 1.49 for females with cubs. KDE and MCP home ranges were very similar in size, with MCP/KDE ratios of 1.007 for males, 1.04 for females and 1.15 for females with cubs. For males, the average MCP home range size at 95% of locations (Table 3) was 77.96 km² (\pm SD 46.80 km²), 77.37 km² (\pm SD 32.77 km²) for KDE and 34.82 km² (\pm SD 4.57 km²) for BBMM. For females, the average MCP home range at 95% of locations was 17.57 km² (\pm SD 11.21 km²), for KDE 16.85 km² (\pm SD 10.59 km²) and 10.17 (\pm SD 8.92 km²) for BBMM. For females with cubs, the average MCP size at 95%, was 25.70 km² (\pm SD 9.37 km²), 22.36 km² (\pm SD 7.93 km²) for MCP, and 14.95 km² (\pm SD 4.70 km²) for BBMM (Table 3).

Effects of sex

With regard to analyses that included sex class, I found that sex affected home range sizes at all percentages of points taken into consideration. Females with cubs did not differ statistically from females for any of the three methods used or for any of the data sets (50, 95 and 99% of points) considered (Table 3). At 50% of locations, home ranges for males were significantly larger than those for females for analyses based on MCPs and KDE ($t_{(12.32)} = 8.45$, $p < 0.00001$; ($t_{(25)} = 3.68$, $p < 0.05$); no significant home range size difference between the sexes was detected when using BBMM ($P > 0.05$). Males displayed larger home ranges for all methods and percentages (Table 3). The home range of males and females differed significantly for all three methods when based on 95 and 99% of locations, while females did not differ from females with cubs for any of these comparisons (Table 3). Summary home range statistics for individual bears as a function of analytical method can be found in Figure 2A-F.

MCP at 100%

All MCP home ranges were mapped at 100% of locations (Figure 3). Home range overlap was observed among animals and was not further analyzed. Individual MCP, KDE and BBMM home ranges are represented by Figures 4A-L. The BBMM method defined visibly smaller use areas in comparison to MCP and KDE. Additionally, BBMM reported more distinct areas in comparison to the MCP and KDE method.

Comparison to other published home ranges

Mean home range sizes generated from this black bear data set were compared to published home range sizes for bears from California, the West Coast, and all of North America. For California, I found seven studies describing male and nine studies female home ranges, including

one from the Nevada side of Lake Tahoe. For the West Coast, I found seven studies reporting male home ranges and 11 reporting female home ranges. For all of North America, I was able to locate 64 home ranges for males and 91 for females.

Comparisons of published data with the results of my analyses revealed that home range sizes for males ($n=3$) in this study ($77.37 \text{ km}^2 \pm \text{SD}32.77 \text{ km}^2$) were not significantly different from those for males in other CA studies ($28.3 \text{ km}^2 \pm \text{SD}13.7 \text{ km}^2$, (Welch t-test; $t_{(2.04)} = 2.58$, $p=0.12$). Similarly, I found that female home ranges ($n=9$) in Tahoe ($16.85 \text{ km}^2 \pm 47.9 \text{ km}^2$) were not significantly smaller than those for other CA female bears ($21.5 \text{ km}^2 \pm \text{SD}15.3 \text{ km}^2$, (Welch t-test; $t_{(17.67)} = -1.06$, $p=0.30$). Mean home range sizes for male West Coast bears ($n=14$; $95.7 \text{ km}^2 \pm \text{SD}106.9 \text{ km}^2$) did not differ significantly from the results of this study (Welch t-test; $t_{(2.82)} = -0.89$, $p=0.44$); in contrast, for females, West Coast home range sizes ($n=17$; $25.4 \text{ km}^2 \pm \text{SD}15.8 \text{ km}^2$) were significantly larger than those in this study (Welch t-test; $t_{(10.27)} = -2.28$, $p=0.045$). For all of North America, average home range sizes for males ($n= 85$; $288.6 \text{ km}^2 \pm \text{SD}153.5 \text{ km}^2$) and for females ($n=104$; $28.4 \text{ km}^2 \pm \text{SD}35.8 \text{ km}^2$) were significantly larger from results reported here (Welch t-test; males: $t_{(3.04)} = -3.62$, $p=0.035$; females: $t_{(8.94)} = -3.18$, $p=0.01$).

Seasonal home ranges

All individual seasonal home ranges were mapped for KDE 50 and 95% of locations to allow for visual inspection and comparison to full home ranges, and can be found in Figure 4A-L. I found that home range sizes did not differ statistically with season when using 50% of locations (linear mixed model, $F_{3,16.3} = 2.28$, $p = 0.12$). In contrast, significant seasonal variation in home range size was detected when using 95% of locations (linear mixed model $F_{3,18.42} = 4.59$, $p = 0.014$). While home range sizes at 50% were not statistically different, the configuration did appear to shift across the landscape with season (Figure 4A-L). At 95% of locations, home ranges were smaller in spring ($t_{24.39}=-2.103$, $p<0.05$) and winter ($t_{23.89}=-3.259$, $p<0.01$) than the fall; home-ranges in summer appeared slightly larger than those for the fall although this difference was not significant ($t_{24.2}=0.096$, $p>0.05$).

Effects of sex on seasonal home ranges

Sex affected the size of seasonal home ranges when using 50% of locations (linear mixed model, $F_{3,57.2} = 4.43$, $p = 0.025$) and at 95% of locations (linear mixed model; $F_{2,23.09} = 5.40$, $p = 0.012$). No interaction was found between season and sex at 50% of locations (linear mixed model, $F_{6,50.9} = .25$, $p = .91$) or at 95% of locations (linear mixed model, $F_{3,63.51} = 9.16$, $p < 0.0001$). At 50% of locations, home range sizes did not differ between females and females with cubs during any season (Table 4). Males occupied larger home ranges than females during the summer ($t_{13.63}=4.01$, $p<0.01$) and possibly the fall ($t_{18.34}=2.08$, $p=0.0519$), but home range sizes for these sex classes did not differ during spring and winter. At 95% of locations, home ranges for females with cubs also did not differ significantly from females without cubs for all seasons (t-test; $p>0.05$). At 95% of locations male home ranges were significantly larger than female home ranges in the summer ($t_{15.54}=4.22$, $p<0.001$) and fall ($t_{20.5}=3.15$, $p<0.05$), but did not differ in size during the spring and winter (t-test; $p>0.05$).

When associating year with season, differences in home range sizes between males, females, and females with cubs were most pronounced in the fall of 2014 (Figure 5), with home ranges for males being 3.72 and 4.33 times larger than those for females and females with cubs,

respectively (Table 5). The smallest ratios were reported during the fall of 2013, during which male home ranges were 1.59 and 1.75 times greater than females and females with cubs, respectively. Male/female ratios ranged from 6.3 (summer 2014) to 22.98 (spring of 2015); those for males/females with cubs ranged from 2.65 (spring 2014) and 54.48 (spring 2015).

Home range overlap with urban envelope

Data for 24 bears (13 females, four females with cubs, and 9 males) were used in calculating overlap with the urban envelope for data collected from 2011 to 2015.

Overlap at 50% of locations

Overlap with the urban area, expressed in percentages, was analyzed for home ranges based on 50 and at 95% of locations utilizing the KDE method (Figure 6). Home range overlap with the urban area was smaller at 95% of locations ($44.86\% \pm \text{SD}25.03\%$, $t_{127.52} = -3.58$, $p < 0.001$) than at 50% of locations ($58.98\% \pm \text{SD}29.41\%$). Only season emerged as a significant predictor when assessing overlap size (linear mixed model, $F_{3,53.99} = 3.38$, $p < 0.05$); in contrast, the effects of sex and the interaction between sex and season were not statistically significant. Additionally, year, drought status, and the interaction of these variables with sex were not significant. However overlap in the summer of 2014 ($65.33 \pm \text{SE}13.54\%$) was significantly larger than the overlap in the summer of 2011 ($t_{19.99} = 2.21$, $p < 0.05$), and overlap in summer 2014 was larger than overlap during the summer in the other years considered.

Overlap with urban areas differed across seasons. Fall had the greatest overlap ($71\% \pm \text{SE}8\%$), followed by summer ($61\% \pm \text{SE}10\%$, $t_{22,23} = -0.96$, $p > 0.05$), spring ($51\% \pm \text{SE}22\%$, $t_{-22.53} = -2.10$, $p < 0.05$), and winter ($50\% \pm \text{SE}10\%$, $t_{-22.53} = -2.21$, $p < 0.05$). Males displayed the greatest overlap with urban areas independent of season or year ($40.13\% \pm \text{SE}9.7\%$, $t_{20.87} = -2.59$, $p < 0.05$). While the results based on sex were not significantly different, differences based on sex were greatest during the fall for all sexes, with mean overlap consisting of 54% ($\pm \text{SE}18\%$) for males, 85% ($\pm \text{SE}10\%$) for females, and 61% ($\pm \text{SE}30\%$) for females with cubs. Overlap with urban areas was smallest during the spring, with mean overlap of 29% ($\pm 23\%$) for males, 26% ($\pm 3\%$) for females with cubs, and 64% ($\pm 37\%$) for females.

Annual variation in overlap with urban areas was calculated for home ranges based on 50% of locations; this analysis revealed that mean overlap was greatest in 2014 ($60\% \pm \text{SE}13\%$), followed by 2013 ($50\% \pm \text{SE}3\%$), 2012 ($48\% \pm \text{SE}13\%$), 2011 ($47\% \pm \text{SE}11\%$), and 2015 ($39\% \pm \text{SE}18\%$).

Overlap at 95% of locations

When only year and drought status were considered, no significant differences in home range sizes were found across years for analyses based on 95% of locations, although the result was marginally significant in 2014 in comparison to 2011 (t-test; $t_{39.42} = 1.72$, $p = 0.09$), hinting at greater use of urban areas in this year in comparison to a much wetter 2011. When exploring seasonal differences across years, I found that home ranges in the falls of 2012 ($44\% \pm \text{SE}22\%$, $t_{21.29} = 10.45$, $p < 0.01$) and 2014 ($53.56\% \pm \text{SE}11.89\%$, $t_{21.38} = 2.72$, $p < 0.05$) were significantly larger than for the fall of 2011. Differences in overlap size based on a model containing season, sex, and their interactions were not significant. Direct comparison of means suggested that seasonal overlap did not vary markedly, ranging from 39% to 47% (Figure 6). While differences between sexes were not significant, direct comparison of mean home range overlap values provided the

following results: females (65% \pm SE30%) and males (36% \pm SE27%) had the highest overlap in spring, while females with cubs (53% \pm SE28%) had the greatest overlap during the summer. In contrast, females displayed the smallest overlap in the summer (53% \pm SE14%); for males in the summer, overlap was considerably smaller (26% \pm SE15%). Females with cubs displayed the smallest overlap in winter (18% \pm SE18%).

Selection of resources within the home range

Data for 26 bears (13 females, four females with cubs, and nine males) were used in the Resource Selection Function analyses. Data from these animals were collected from July 2011 through April 2015. Two bears (13211 and 13212) were removed during the analysis due to analytical problems with the dataset and calculating appropriate home ranges in R.

Females selected for trails throughout the year, with this selection being strongest in winter ($p < 0.001$). In contrast, males avoided trails in winter ($p < 0.01$) but used them in spring and summer ($p < 0.001$). Females with cubs also selected for trails in spring and summer but avoided them in the fall ($p < 0.001$). Males selected for trails most strongly during spring ($P < 0.001$), continued to use them through the fall ($p < 0.001$), but then showed avoidance of trails during the winter ($p < 0.01$) (Figure 7). Male bears also selected for roads throughout the year; this pattern appeared most pronounced in the spring ($p < 0.001$) and least pronounced in winter ($P < 0.01$). Females with cubs appeared to select against roads most strongly during the fall ($p < 0.001$) but selected for roads during the spring and summer ($p < 0.001$). In contrast, females avoided roads in the winter ($p < 0.001$); results for females during the remaining seasons revealed no significant patterns in terms of use of roads. Wetlands were selected most strongly by females with cubs during spring and fall ($p < 0.001$). Other sex classes did not show an obvious selection for wetlands, and there was no pattern in terms of the seasonal variation in use of wetlands.

With the exception of females in winter and females with cubs in summer, all bears selected areas of known bear-human conflict during all seasons ($p < 0.05$). The preference for areas of known conflict appeared to be strongest for females with cubs in spring and fall. More generally, females selected for fire roads during spring and summer ($p < 0.05$) although no significant selection of this feature was detected for the fall and winter. Females with cubs avoided fire roads in the spring ($p < 0.05$) but selected for them in the fall ($p < 0.001$). Males avoided fire roads during all seasons, with the strongest avoidance occurring during the fall ($p < 0.001$). Females tended to select lower elevational areas more than males; this pattern remained unchanged throughout the year and appeared similar to females with cubs.

Discussion

I examined the relationship between urban habitat and space use in black bears from the Lake Tahoe Basin using three commonly used methods to measure home range. Additionally, I compared urban home range sizes from this study to over 80 previously reported home range results from California, the Western United States and all of North America to understand how urban home ranges vary from reported “wild” home ranges. Moreover, I investigated how season and sex affected home range sizes, and I examined dependency of bears on the urban envelope by calculating the seasonal home range overlap with urban areas, including how this overlap may

change due to drought. Finally, I investigated temporal patterns of habitat selection within the home range by means of an applied resource selection.

My results indicate that different home range tools and methods yielded different home range sizes and configurations. Home range sizes were not consistently statistically different from other published, mostly wild, bear home ranges. Furthermore, home range sizes for all methods and percentages of locations for females and females with cubs did not statistically differ in size. Home range overlap suggested that the urban area is of disproportionate importance to these bears, as supported by the finding that at 50% the overlap with urban was greater than at 95%. Additionally, the increase in overlap with the urban area in the fall of 2014 is likely attributable to the impacts of drought. Finally, the RSF indicated that males selected for roads and that females with cubs selected areas of conflict. Collectively, these efforts revealed several patterns of space use that have direct relevance for understanding the ecology and management of black bears that live in and around urban areas. Below, I discuss and interpret these findings in light of previous work.

Home range analysis

The differences in home range sizes relative to analytical method reported here are consistent with the results of other studies that compared multiple methods (Mitchell 2007, Walter et al. 2011, Fieberg and Börger 2012). BBMM home ranges were likely smaller due to their relatively high resolution, which may have reduced the width of the smoothing parameter employed and, thus, home range size (Wall et al. 2014). BBMM home ranges were hard to interpret visually due to the great number of distinct polygons per animal. Generally, sex affected home range sizes, although home range sizes for females with cubs did not differ significantly from those for females without cubs, similar to the results from a study in Idaho (Reynolds et al. 1980). However, other studies have found differences between females with and without cubs. For example, a study on bears in Florida documented an interaction between year and breeding status that influenced home range size (Moyer et al. 2007); while in North Carolina, decreases in resource availability had a greater effect on home ranges of lactating females in comparison to breeding females (Mitchell and Powell 2007). Together, these results suggest that other factors may be important in explaining home range size, some of which may vary geographically. Home range sizes for females both with and without cubs were smaller than male home ranges at 95% percent of locations for all three methods. This finding is common across other published studies (Koehler and Pierce 2003) and for other bear species in general; sloth bears (*Melursus ursinus*) (Joshi et al. 1995) and grizzly bear (*Ursus Arctos*) (Mace and Waller 1997).

Future research should focus on whether the age of cubs affects the home range size of females with cubs. For example, small cubs may impede female mobility, thereby reducing home range size when the cubs are young. As cubs grow, they require more resources and become more mobile, which may favor larger home ranges for females with older cubs.

My findings suggest that for females, urban home ranges might be smaller than reported by Beckmann and Berger (2003a), even when bears were not strictly urban. Efforts to examine this pattern for populations outside of the Tahoe Basin did not yield additional insights. The differences in home range sizes between California and Nevada might be explained by the smaller sample size in this study and different methods for recording locality data. For example,

Beckmann and Berger (2003a) gathered locations by fixed wing aircraft with a minimum of 60 annual locations during daylight hours. In contrast, I used Iridium collars that on average generated a GPS location every two hours, yielding hundreds to thousands of locations per individual. Additionally, although Tahoe Basin bears could be considered one contiguous population, habitat differences between the California and Nevada sides of the Basin may result in differences in resource availability that impact home range sizes (Johnson et al. 2015). More research is needed to compare urban home ranges to wild home ranges within the same study system while utilizing the same methods for calculating home range. This is warranted to understand fully how urban bears vary their use of the landscape in comparison to wild bears. Additionally, while spatial shift was not quantified, visual inspection suggested that core (50% of data points) portions of home ranges shifted spatially across the landscape among seasons. Future research should address whether shifting locations for core home ranges (50% of locations) are relevant when assessing potential for bear-human conflict and habitat requirements during each season.

Home range overlap with urban areas

Overlap with the urban area was expected to explain dependence on the urban area. Contrary to expectation, drought conditions did not appear to substantially increase home range overlap with the urban area. In contrast, previous studies found that years with poor natural food production (e.g., drought years) increased bear use of urban areas (Baruch-Mordo et al. 2014). Bears in Tahoe may already have been dependent on urban food sources well before the drought and this may have precluded a dramatic increase in utilization of urban areas during drier years of this study.

For home ranges based on both 50 and 95% of locations, overlap with the urban envelope was lower for males than for females and females with cubs. Understanding overlap with the urban envelope is important because seasonal, sex-specific intra-annual variation might provide insights into resource partitioning and potential conflict with humans. Male overlap with urban areas was greater in spring compared to other seasons, while for females with cubs this overlap was lower in spring than in other seasons. Home ranges in spring would be expected to be larger for males than for females because males are in pursuit of females during the mating season and this is expected to cause them to travel more. Contrary to this expectation, however, home range overlap with urban areas did not differ between males and females for either 50 or 95% of spring locations. This outcome may reflect differences between urban versus total home range size; although the former may not have differed, overall home range sizes may have been greater for males. It is also possible that male bears actively exclude females with cubs from urban areas, where the male presence may pose a threat of infanticide (Ben-David et al. 2004, Garrison et al. 2007). Consequently, females may utilize the urban area less during the spring.

Reduced overall urban overlap for male bears might explain why mature males were captured less frequently and were underrepresented (3 out of 12) among the bears sampled. Males had larger home ranges but the urban area represented a smaller percentage of their home range, thereby likely reducing the chance of a bear encountering a trap in the urban area. Noyce et al. (2001) found that bears were more likely to be trapped when spending >50% of time in an area. My trapping efforts suggested that mature males were not using the urban envelope during certain times of the year. Personal observations suggest that habitat utilization of male bears may

change as they mature. Young bears seemed to be heavily dependent on urban areas, whereas mature males appeared to use wild lands more. Adult males may be able to monopolize highly profitable wildland resources and force immature males to use urban areas. Future research should examine a large number of sub adult male bears utilizing the WUI over multiple years to understand this pattern.

Selection of resources within the home range

Contrary to expectation, bears in this study generally appeared to select for roads. Road avoidance was detected anecdotally for members of the study population via deployment of critter cams on black bears in the Tahoe Basin (Klip, unpublished data); this pattern was not replicated in analyses of GPS collar data. Roads have long been identified as a source of habitat fragmentation (Forman et al. 1997) and negative impacts on black bears have been reported previously (Unsworth et al. 1989, Gaines et al. 2005, Benson and Chamberlain 2007). Avoidance of roads may also be influenced by the activity of other bears (Unsworth et al. 1989), coupled to human development (Lewis et al. 2011), selected when habitat is dense or during the mating season (Hiller et al. 2015), or may be dependent on traffic volume, road density, and or road speeds (Young and Beecham 1986, Brody and Pelton 1989, Gaines et al. 2005, Morgan Henderson et al. 2015). Since this study focused on bears in urban areas, there may have been greater prevalence of and therefore greater use of roads in this study compared to studies of habitat use by bears in more remote settings. In fact, all of the studies discussed above showing road avoidance took place in remote settings outside the urban interface.

Males avoided fire roads, specifically during the hunting season (fall), whereas females with cubs selected for fire roads. Avoidance of fire roads by males was consistent with the outcomes of studies conducted in North Carolina, Montana, and Shenandoah National Park in Virginia (Irwin and Hammond 1985, Grenfell and Brody 1986, Kasworm and Manley 1989). This avoidance may occur because fire roads offer hunters access to back country areas (Schwartz and Franzmann 1992). In California, females with cubs cannot be hunted and when provided with options, hunters will preferentially target larger bears, which tend to be males (Stillfried et al. 2015). Thus, while fire roads may represent a particular danger to males during hunting season, these roads may represent travel corridors for females, the use of which may increase as vegetation becomes more dense (Hellgren et al. 1991). The edges of fire roads may also be used for foraging due to additional sunlight penetration under the forest canopy (Irwin and Hammond 1985).

Beyond roads, my results suggest that bears also tended to select for trails. Female selection for trails appeared to be the strongest of any sex class, peaking in the winter. This finding may contradict results in Grand Teton National Park, where black bears tended to avoid a newly constructed trail by selecting steeper slopes and staying farther away from the trail, becoming more nocturnal and staying closer to cover when using the area (Costello et al. 2013). In northwestern Montana, bears also selected against trails, with a cutoff distance of about 300m from trails required before evidence of avoidance was no longer evident (Kasworm and Manley 1989). Anecdotal evidence suggested that hiking trails are heavily used by black bears in the Tahoe area based on observation of scat and bear sightings along trails, and Tahoe features a high density of hiking trails. Bears in this study may simply be more habituated to human presence and thus not avoid humans to the same degree as bears in other regions.

In addition to roads, areas of past bear-human conflict were selected in spring and fall. Females with cubs appeared to use these areas the most and, anecdotally, some of the worst conflict bears were females with cubs. Law enforcement report and personal observations indicated that females accompanied by cubs broke into many buildings, a behavior they did not exhibit in years without cubs. Spring and fall are both seasons when bears in general seek additional resources. Previous conflict research has tended to focus on ecological and landscape factors that contribute to the risk landscape. Each conflict location could be described by its landscape variables, although this additional complexity may not be required if conflict itself predicts future conflict. This may be particularly relevant when conflict is recorded over multiple years and a large number of conflict incidents are recorded in the study area. One challenge in recording such incidents, however, is that different people likely have different tolerances to bears. Therefore, some conflicts might go unreported because homes may be broken into without people present, with damage often not observed until later, especially in unused vacation homes that are common in the Lake Tahoe region. People whose homes sustain damage from bears may be hesitant to take action as a result of negative ramifications by neighbors and other members of the public who believe that bears should not be removed lethally (Mazaika 2013). Based on records kept by the Placer and El Dorado Sheriff's Offices, conflict locations were numerous, so I do not believe that underreported frequency of conflict impacted the results presented here.

Wetlands were selected most strongly by females with cubs, with selection by the other sex classes not being significant. This finding contradicts those of Kelleyhouse (1980), who reported that bears "overwhelmingly" selected wet habitats in California, as well as the findings of Grenfell and Broady (1986), who reported that wet meadows were selected significantly more than expected. Similar findings were reported for urban-wildland interface bears in the eastern United States (Tri et al. 2016). More research is needed to understand the differences between the outcome of my analyses and those of other studies, including consideration of differences in the methods employed and the types and availability of wetland habitats.

Management Implications

Home range methods vary widely among studies, making comparisons of data sets challenging. An initiative to share data and allow comparisons based on source data rather than already constructed home ranges would be beneficial (Börger et al. 2006). Additionally, sampling and estimation methods should be standardized to facilitate direct comparisons across studies and geographic areas (Fieberg and Börger 2012). KDE is highly dependent on the value of the smoothing parameter used and variation in this parameter can create very different home range estimates (Hemson et al. 2005); despite this, bandwidth values are often not reported. Movebank is an example platform where source data could be shared with other researchers to enable more robust comparisons (<https://www.movebank.org/>).

While not examined in this study, home range analyses may be useful to estimating how many bears occupy the Tahoe Basin. Home range sizes may be affected by bear density. Previous research reported that the eastern side of Lake Tahoe had the second highest black bear density in North America (Beckmann and Lackey 2008). My study found that female home ranges might be smaller than those reported for the eastern side of the Basin, suggesting that the density of

bears for the western side of the Basin could be even higher. Improved understanding of the relationship between home range size and population density would allow for use of spatial data to generate rough estimates of the number of bears in a given area.

In addition to providing a better understanding of the actual bear density in the Basin, future research should focus on contrasting space use and density in urban versus wild areas. Understanding the prevalence of bears in the Basin in both settings would allow for better management decisions and would provide insight into whether bears are vacating wild lands in favor of anthropogenic edges. Additionally, the relative proportion of adult to sub-adult bears should be estimated. Both may provide insights into whether urban areas are a source or a sink for bear populations.

Finally, when deploying management resources on the ground, seasonal home ranges should be a starting point for understanding which areas of the Basin are currently important to bears. Management might also utilize bear re-visitation rates to understand the effects of anthropogenic food sources. Re-visitation information would elucidate small areas, such as concentrated anthropogenic resources, that are of disproportionate importance to bears. This might allow for more proactive management in the form of abatement of bear attractants. The T-LoCoH (Time Local Convex Hull) method calculates re-visitation rates (Lyons et al. 2013); this method, combined with ground truthing of spatial data, might provide management insights into where bears are likely able to obtain anthropogenic food sources and reactively and proactively plan appropriate management responses. Thus, overall, the spatial and resource function analyses completed in this study have important implications for management of bears in the Tahoe Basin and, potentially, elsewhere in North America.

Tables and Figures

BEARID	SEX	Total positions	on	off	number of days
13205	Female	4749	5/15/2014	11/21/2014	190
13206	Male	4552	5/23/2014	4/1/2015	313
13207	Female w Cubs	4293	5/24/2014	4/2/2015	313
13208	Female	1047	11/7/2013	4/4/2014	148
13209	Female	3367	8/5/2013	3/6/2014	213
13210	Female w Cubs	7875	10/22/2013	3/5/2015	499
13211	Male	567	11/15/2013	1/15/2014	61
13212	Female w Cubs	4541	9/28/2013	3/3/2014	156
15441	Male	5078	6/14/2014	3/5/2015	264
15442	Female	4372	6/14/2014	11/27/2014	166
15544	Female	2212	9/7/2014	3/24/2015	198
15448	Female	706	9/7/2014	2/15/2015	161

Table 1. Capture details for bears utilized for home range analysis; captured bears categorized by sex, number of collar deployment days, dates between which positions were collected and total number of positions utilized for analyses.

	Female				Female with Cubs				Male			
	t	df	p	intercept	t	df	p	Δ to Female	t	df	p	Δ to Female
MCP-50	2.963	10	0.0142	1.2142	0.893	10	0.3927	0.5787	2.655	10	0.0241	1.8846
MCP-95	9.061		3.89E-06	2.6263	1.21		0.254	0.5545	3.168		0.01	1.5904
MCP-99	9.126		3.65E-06	2.7171	1.34		0.21	0.6306	3.143		0.0105	1.621
KDE-50	3.391		0.00687	0.9517	0.77		0.45895	0.3418	3.726		0.0039	1.8109
KDE-95	10.77		8.05E-07	2.6284	1.076		0.3071	0.4155	3.912		0.0029	1.6541
KDE-99	11.89		3.18E-07	3.0251	1.166		0.2707	0.4688	3.747		0.0038	1.6506
BBMM-50	-0.7	10	0.4979	-0.368	0.948	10	0.3655	0.7833	1.973	10	0.077	1.7859
BBMM-95	4.724		0.000811	1.8221	1.383		0.19673	0.8435	2.578		0.0275	1.722
BBMM-99	6.504		6.86E-05	2.3345	1.48		0.1697	0.8398	2.778		0.0195	1.7274

Table 2. Comparison by methods, percentage and sex. Females with cubs do not differ significantly from females. Males differ significantly from females. Males are significantly different except for BBMM at 50% and Δ refers to difference to the intercept (females).

SEX %	MEAN			MAX			MIN			Standard Deviation		
	MCP	KDE	BBMM	MCP	KDE	BBMM	MCP	KDE	BBMM	MCP	KDE	BBMM
F-50	4.72	3.4	1.64	11.35	7.81	4.4	0.78	0.88	0.05	3.92	2.63	1.92
F-95	17.57	16.85	10.17	33.1	31.66	22.66	3.44	5.02	0.59	11.21	10.59	8.92
F-99	19.99	25.47	15.86	42.96	45.34	32.99	3.5	7.1	1.17	14.24	16.54	12.86
F-100	21.81	N/A	N/A	46.31	N/A	N/A	3.51	N/A	N/A	15.04	N/A	N/A
FwC-50	8.68	3.87	2.05	22.4	5.68	4.4	2.34	2.16	0.48	9.23	1.47	1.71
FwC-95	25.7	22.36	14.95	33.1	29.26	19.95	12.59	10.96	9.83	9.37	7.93	4.7
FwC-99	30.81	35.24	24.81	42.96	45.34	30.61	15	16.77	14.84	12.99	12.92	7.03
FwC-100	37.19	N/A	N/A	59.48	N/A	N/A	17.07	N/A	N/A	19.25	N/A	N/A
M-50	34.82	17.8	4.17	78.95	27.08	4.96	7.78	8.02	3.56	38.54	9.54	0.72
M-95	77.96	77.37	34.82	126.64	110.09	38.71	33.3	44.55	29.78	46.8	32.77	4.57
M-99	84.05	114.94	59.03	128.67	160.89	68.35	43.78	64.07	44.94	42.61	48.6	12.41
M-100	126.33	N/A	N/A	198.28	N/A	N/A	48.18	N/A	N/A	75.24	N/A	N/A

Table 3. Full home range size statistics for all by sex (F: Female, FwC: Females with Cubs, M: Males) and percentage. The number following indicated the percentage points included in the calculation. All home range sizes were in square kilometer.

Spring					Summer				
50%									
	t	df	p	interc./Δ to F	t	df	p	interc./Δ to F	
Female	21.131	9.916	1.42E-09	15.0406	57.861	13.629	< 2e-16	15.7368	
Females with Cu	-0.176	10.565	0.863	-0.2559	-1.739	15.796	0.10155	-1.0555	
Male	0.34	9.009	0.742	0.3715	4.012	13.629	0.00135	1.5431	
95%									
Female	25.63	11.217	2.60E-11	16.22536	62.679	13.539	< 2e-16	17.139	
Females with Cu	0.024	11.885	0.982	0.03245	-0.86	14.837	0.40335	-0.5127	
Male	0.642	9.988	0.535	0.64917	4.222	13.539	0.000916	1.6325	
Fall					Winter				
50%									
	t	df	p	interc./Δ to F	t	df	p	interc./Δ to F	
Female	31.372	18.03	<2e-16	15.0713	10.934	8.962	1.75E-06	12.911	
Females with Cu	0.129	17.949	0.8985	0.1293	0.352	8.962	0.733	1.018	
Male	2.079	18.341	0.0519	1.5044	0.89	8.194	0.399	1.424	
95%									
Female	40.15	20.232	< 2e-16	16.4483	12.816	12	2.32E-08	14.24	
Females with Cu	0.347	19.996	0.73208	0.3171	0.545	12	0.596	1.285	
Male	3.146	20.501	0.00498	2.0449	0.902	12	0.385	1.475	

Table 4. Seasonal significance based on sex. Males and females with cubs compared to females. Bold numbers indicate associations that are not significant. Females with cubs did not differ significant from females. Neither did males at 50% in the spring, fall and winter and at 95% males were not significantly different from females in the spring and winter and Δ refers to the differences to intercept (females).

Sex - Season - Year	MEAN	MAX	MIN	Std. Dev.
FEMALE FALL 2013	4.74	8.36	1.12	5.12
FEMALE FALL 2014	28.75	45.21	9.87	14.51
FEMALE SPRING 2014	2.69	6.56	0.01	3.43
FEMALE SPRING 2015	5.36	8.46	2.26	4.38
FEMALE SUMMER 2013	7.61	12.41	2.80	6.79
FEMALE SUMMER 2014	15.74	19.69	11.78	5.59
FEMALE WINTER 2014	0.62	1.05	0.19	0.61
FEMALE WINTER 2015	5.66	12.95	0.01	6.63
FEMALE_CUBS FALL 2013	26.20	30.22	22.17	5.69
FEMALE_CUBS FALL 2014	24.68	45.21	11.89	17.96
FEMALE_CUBS SPRING 2014	11.12	32.68	1.18	14.54
FEMALE_CUBS SPRING 2015	2.26	2.26	2.26	NA
FEMALE_CUBS SUMMER 2013	2.80	2.80	2.80	NA
FEMALE_CUBS SUMMER 2014	16.13	25.96	10.64	8.53
FEMALE_CUBS WINTER 2014	5.58	6.31	4.84	1.04
FEMALE_CUBS WINTER 2015	6.48	12.95	0.00	9.16
MALE FALL 2013	45.84	45.84	45.84	0.00
MALE FALL 2014	106.98	111.47	102.48	6.36
MALE SPRING 2014	29.42	56.29	2.55	38.00
MALE SPRING 2015	123.13	123.13	123.13	NA
MALE SUMMER 2014	99.25	126.11	72.39	37.98
MALE WINTER 2014	26.97	26.97	26.97	NA
MALE WINTER 2015	42.04	65.60	18.49	33.31

Table 5. Seasonal home range statistics based on 95% KDE for sex, season and year.

Home Ranges

Source	Method	CI	Size(M) km ²	Size(F) km ²	HR Notes	Location	Sample Size (M)	Sample Size (F)
Piekielek (1970)	MCP		19	19		CA	7	6
Jonkel and Cowan (1971)	MR		31	5		MT	16	31
Eveland (1973)	SC		102	20		PA	11	5
Rieffenburger (1973)	DG			29		WV		3
Beeman (1975)	MCP		21	7		TN	1	7
Alt et al. (1976)	BN		196	37		PA	5	12
Amstrup and Beechman (1976)	MCP		112	49		ID	2	7
Eubanks (1976)	MCP		6	5		TN	3	3
Lindzey and Meslow (1977)	MCP		5.05	2.35		WA	8	8
Landers et al. (1979)	MCP		56	8		NC	6	4
Modafferi (1979)	MCP		88	20		AK	2	5
Alt et al. (1980)	Jennrich and Turner		173	41		PA	5	12
Garshelis and Pelton (1980)	MCP		21	8		TN	10	14
Fuller and Keith (1980)	DG			8		Canada		4
Kelleyhouse (1980)	MCP		10.6	3.6	Summer	CA	4	6
LeCount (1980)	MCP		29	18		AZ	6	5
Reynolds and Beechman (1980)	MCP		60	12		ID	4	11
Garshelis and Pelton (1981)	BN		41	15		TN	8	12
McLaughlin (1981)	MCP			25		PA		7
Hugie (1982)	MCP		17	4		ME	5	9
Kohn (1982)	MCP		71	14		WI	13	7
Novick and Stewart (1982)	MCP		22	17		CA	5	1
Quigley (1982)	MCP		30	6		TN	3	4
Villarrubia (1982)	MCP		30	12		TN	9	12
Young and Ruff (1982)	MCP		119	20		Canada	25	15
Carr (1983)	MCP		119	13	Poor mast year	TN	4	3
Carr (1983)	MCP		36	6	Good mast year	TN	4	3
Garris (1983)	MCP		192	23		TN	5	8
Manville (1983)	MCP		150	69		MI	11	5
Brody (1984)	MCP		32	9	Fall	NC	8	10
Brody (1984)	MCP		69	17	Summer	NC	10	11
Hogan (1984)	MCP			20		CA		4
Massopust (1984)	MCP		93	19		WI	4	7
Warburton (1984)	MCP		79	18		NC	2	2
Beringer (1986)	MCP			15		NC		7
Clevenger (1986)	MCP		20	4	Summer	TN	6	9
Clevenger (1986)	MCP		132	4	Fall	TN	5	12
Garner (1986)	MCP	1	195	38		VA	11	21
Garner (1986)	MCP	0.95	116	22		VA	11	21
Grenfell and Brody (1986)	HM			36.4		CA		4
Greer (1987)	MCP		163	14		MT	2	3
Hellgren and Vaughan (1987)	MCP		29.6	17.8		VA/NC	7	5
Klenner (1987)	Jennrich and Turner		2922	29		Canada	1	5
Klenner (1987)	Jennrich and Turner		149	14		Canada	1	2
Hellgren (1988)	MCP		111.7	27		VA	10	11
Mack (1988)	MCP		151	38		MT	5	9
Brody and Pelton (1989)	MCP		28.01	14.41	Summer	NC	9	7
Brody and Pelton (1989)	MCP		18.69	12.69	Fall	NC	5	8
Hellgren and Vaughan (1989)	MCP		112	27		VA	10	11
Fimbel (1990)	MCP		182	16		NJ	13	17
Smith and Pelton (1990)	MCP		116	12		AR	6	6
Braden (1991)	HM		24.2	19.5		CA	4	1
Hechtel (1991)	MCP		596	59		AK	4	7
Costello (1992)	BN			38		NY		5
Costello (1992)	MCP			31		NY		5
Stubblefield (1992)	HM	0.95	22.53	12.5	1989	CA	4	1
Stubblefield (1992)	HM	0.95	42.11	4.7	1990	CA	3	1
Fuller (1993)	HM		328	26		MA	29	35
Fuller (1993)	HM			23		MA		41
Seaman (1993)	KDE		42	18		NC	3	3
Beecham and Rohlman (1994)	MCP		145	31		ID	8	33
Beecham and Rohlman (1994)	MCP		41	13		ID	5	6
Pacas and Paquet (1994)	HM	0.95	464.7	294.8		Canada	14	21
Schrage (1994)	MCP			10		VA		10
Smith (1994)	MCP		112.8	34		AK	4	18
Manen (1994)	MCP		250	11		TN	11	12
Manen (1994)	KDE		299	17		TN	11	12
Wooding and Hardisky (1994)	MCP		170	28		FL	12	8
Marchington (1995)	KDE		52	13		LA	4	6
Storlid (1995)	MCP			21		WI		6
White (1996)	MCP		81	11		MS	3	11
White (1996)	MCP		64	10		MS	8	4
DeBruyn (1997)	Not Defined			28.32		MI		10
Gold (1997)	KDE	0.95	289.7	37.1		WA	17	9
Higgins (1997)	MCP	0.95	7.2	5.5		VA	7	16
Higgins (1997)	KDE	0.95	11.2	6.8		VA	5	27
Maehr (1997)	MCP		284	54		FL	15	14

Powell et al. (1997)	KDE		44	17		NC	43	38
Samson and Huot (1998)	MCP			12		Canada		9
Stratman (1998)	KDE	351		88		FL	6	3
Beausoleil (1999)	MCP	38		9		LA	5	12
Beausoleil (1999)	KDE	13		7		LA	5	12
Hirsch et al. (1999)	MCP	76		41		MI	3	16
Hirsch et al. (1999)	HM	65		33		MI	3	16
Heyden and Meslow (1999)	KDE			39		OR		12
Heyden and Meslow (1999)	MCP			30		OR		14
Weaver (1999)	KDE	112		7		LA	3	6
Weaver (1999)	KDE	8		5		LA	3	6
Weaver (1999)	MCP	60		4		LA	3	6
Chaulk (2001)	MCP	108*	108*			Canada	10*	10*
Fersterer et al. (2001)	MCP			7		WA	9	16
Edwards (2002)	KDE	0.95	114.8	17.6		AL	6	10
Etter (2002)	KDE		158.2	12.5	Sedentary	MI	17	36
Etter (2002)	KDE		258.2	43	Dispersers	MI	5	1
Hammond (2002)	KDE	0.95	158	36		VT	8	10
Oli et al. (2002)	MCP	1		6.57		AR		16
Oli et al. (2002)	MCP	0.95		4.9		AR		16
Oli et al. (2002)	HM			48		AR		16
Lyons et al. (2003)	KDE	0.95	289.7	37.1		WA	29	11
Beckmann and Berger (2003)	KDE	0.95	52.86	55.17	Urban	CA	20	4
Beckmann and Berger (2003)	KDE	0.95	519.57	172.78	Wild	NV	10	7
Jones and Pelton (2003)	HM	0.95		11.6		NC		5
Jones and Pelton (2003)	MCP	0.95		11		NC		8
Jones and Pelton (2003)	HM	0.95		6.6		NC		8
Jones and Pelton (2003)	MCP	0.95		5.3		NC		6
Koehler and Pierce (2003)	KDE	0.95	125.5	28.3		WA	2	4
Koehler and Pierce (2003)	KDE	0.95	90.8	18		WA	12	19
Koehler and Pierce (2003)	KDE	0.95	73.5	25.9		WA	17	8
Maehr et al. (2003)	MCP	1	283.7	54.2		FL	15	14
Maehr et al. (2003)	MCP	1	172.2	36.4	Fall	FL	15	14
Maehr et al. (2003)	MCP	1	47.2	5.4	Winter	FL	15	16
Maehr et al. (2003)	MCP	1	94.4	15.6	Summer	FL	15	14
Onorato et al. (2003)	MCP	0.95	97.7	32.1		TX	7	7
Lee and Vaughan (2004)	KDE		17.7	10		VA	2	6
McCown et al. (2004)	KDE		94	20		FL	7	23
Dobey et al. (2005)	KDE			30		FL		71
Dobey et al. (2005)	KDE		343	56		FL	16	46
Garneau et al. (2008)	MCP		218.5	65.8		AK	6	4
Benson et al. (2007)	KDE	0.95		32.5	Spring	LA		28
Benson et al. (2007)	KDE	0.95		46.4	Summer	LA		27
Benson et al. (2007)	KDE	0.95		33.1	Fall	LA		24
Benson et al. (2007)	KDE	0.95		113.5		LA		24
Czetwertynski et al. (2007)	KDE	0.9	123.5		Unhunted	Canada	7	
Czetwertynski et al. (2007)	KDE	0.9	378		Hunted	Canada	8	
Czetwertynski et al. (2007)	KDE	0.9		27.5	Female with Cubs	Canada		12
Czetwertynski et al. (2007)	KDE	0.9		58	Hunted	Canada		18
Leigh (2007)	KDE		13	1		LA	9	2
Lyda et al. (2007)	MCP	0.95		14.5		OK		13
Lyda et al. (2007)	KDE	0.95		21		OK		13
Moyer et al. (2007)	KDE	0.95		24.2		FL		48
Moyer et al. (2007)	MCP	0.95		22.6		FL		30
Unger (2007)	KDE		397	40		KY	1	3
Unger (2007)	MCP		140	19		KY	1	3
Costello (2008)	KDE		463	87		NM	17	60
Sager-Fradkin et al. (2008)	KDE		306	61		WA	10	2
Ulrey (2008)	MCP	1	162.8	69		FL	6	12
Ulrey (2008)	KDE	0.95	96	32.2		FL	6	12
Ulrey (2008)	KDE	0.5	19.7	6		FL	6	12
Early (2010)	KDE		33	27		CA	3	7
Carter et al. (2010)	KDE		606	227		MI	20	35
Rainbolt et al. (2011)	KDE			15		NY		5
Rainbolt et al. (2011)	MCP			12		NY		5
Immel et al. (2014)	KDE		199	33		OR	15	12
Masse et al. (2014)	BBMM	0.95	101.9		Control	Canada	16	
Masse et al. (2014)	BBMM	0.95	36.7		Fed	Canada	11	
Masse et al. (2014)	BBMM	0.5	9.9		Control	Canada	16	
Masse et al. (2014)	BBMM	0.5	3.2		Fed	Canada	11	
Jones et al. (2015)	KDE	0.95		8.9	Spring	MD		8
Jones et al. (2015)	KDE	0.95		15.4	Summer	MD		12
Jones et al. (2015)	KDE	0.95		20.7	Fall	MD		6
Jones et al. (2015)	MCP	0.95		6.73	Spring	MD		8
Jones et al. (2015)	MCP	0.95		10.57	Summer	MD		12
Jones et al. (2015)	MCP	0.95		14.18	Fall	MD		6
Karelus et al. (2016)	KDE	0.95	220.93	31.16		FL	10	6
Karelus et al. (2016)	MCP	0.95	226.04	34.49		FL	10	6
Karelus et al. (2016)	KDE	0.95	160.88	22.27	Summer	FL	10	6
Karelus et al. (2016)	KDE	0.95	200.22	27.78	Fall	FL	10	6

Table 6. Published home ranges. Home range method included: Brownian Bridge Movement Model (BBMM); Bivariate Normal (BN); Dot Grid (DG); Harmonic Mean (HM); Kernel Density Estimate (KDE); Minimum Convex Polygon (MCP), Mark Recapture (MR).

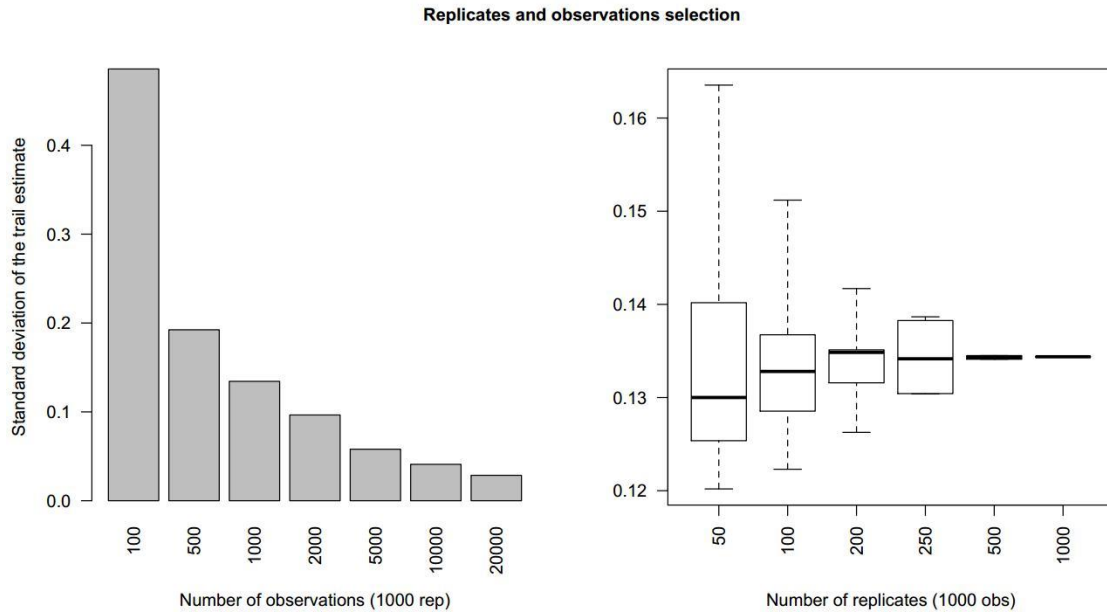


Figure 1. This figures shows the power analysis of Resource Selection Function, 500 locations were selected because standard deviation was under 0.2, 1000 repetitions were selected because the error bars are non-existent after this number of replications.

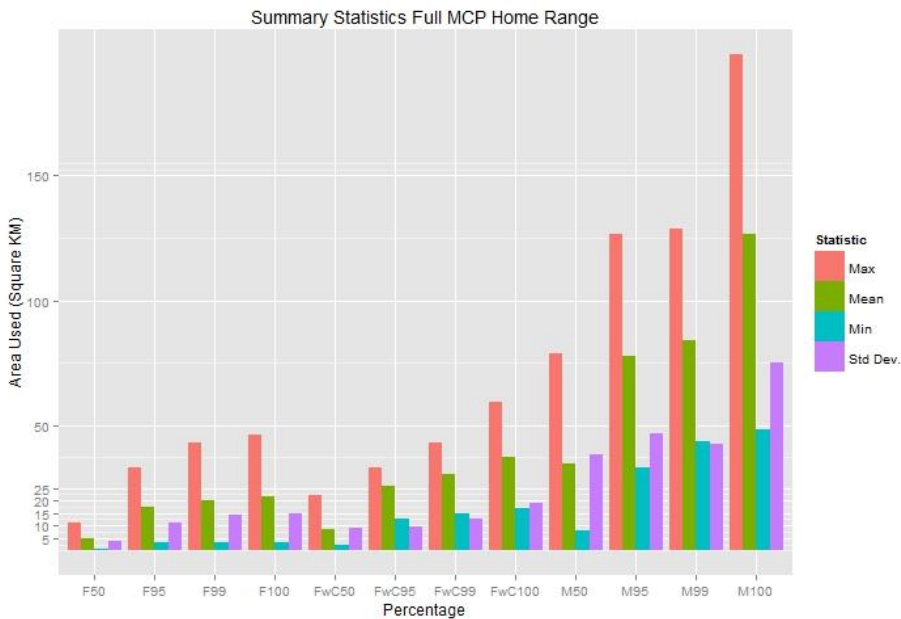


Figure 2A. Summary statistics MCP full home range by sex and percentage (50, 95, 99, 100% of locations), maximum and minimum value, mean and the standard deviation. Females (F) and females with cubs (FwC) had the smallest home range whereas males (M) had the largest home range at all percentages compared.

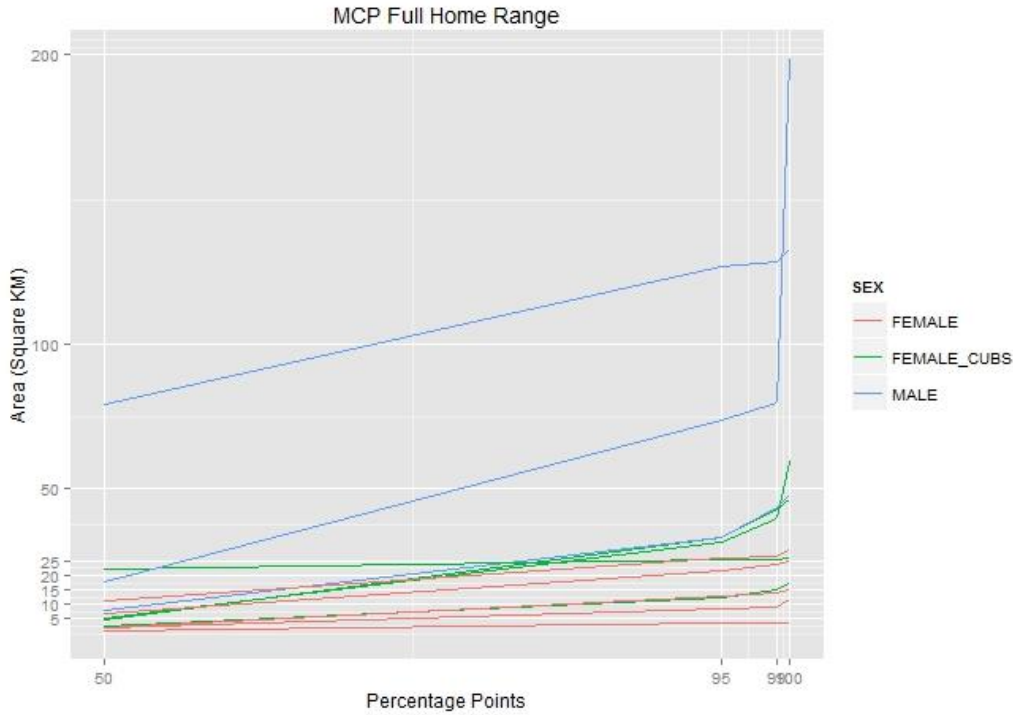


Figure 2B. Summary MCP graph full home range by sex, a steep increase in slope when increasing the number of locations might be indicative of the impact outliers have on the total home range area.

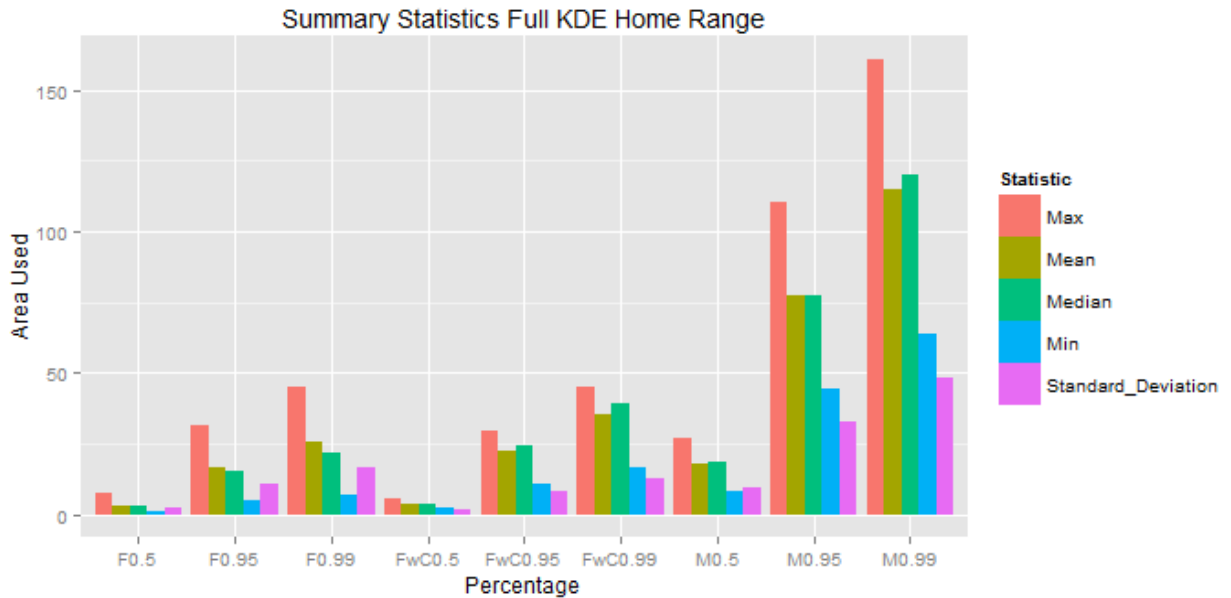


Figure 2C. Summary statistics KDE full home range by sex and percentage (50, 95, 99%), maximum and minimum value, mean and the standard deviation. Females (F) and females with cubs (FwC) appeared to have the smallest home range whereas males (M) had the largest home range at all percentages compared.

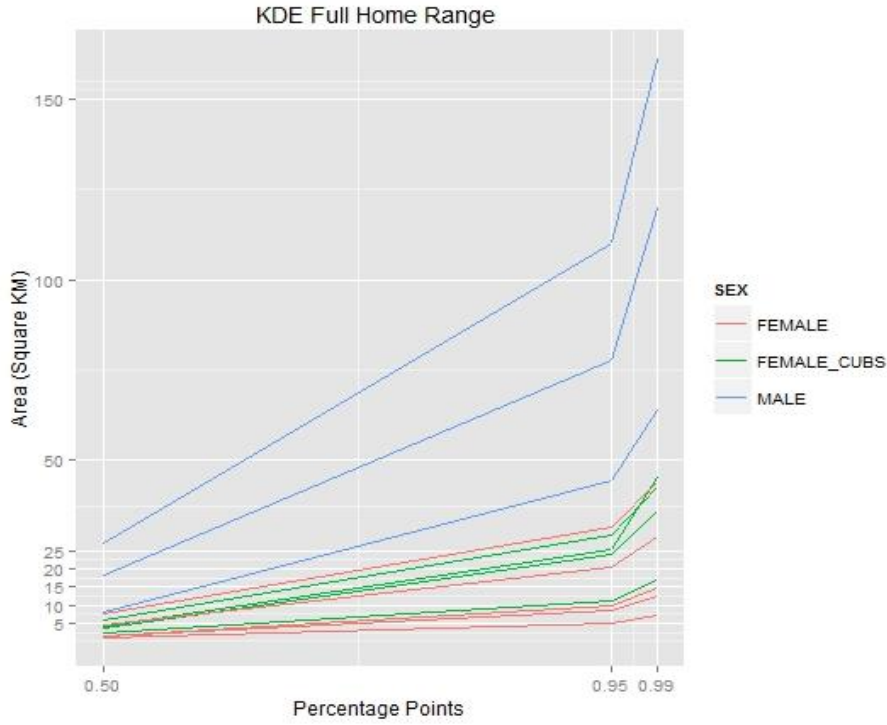


Figure 2D. Summary KDE graph full home range by sex, slope increases between 0.95 and 0.99, this might be indicative that more locations should be included in the calculation of the areas.

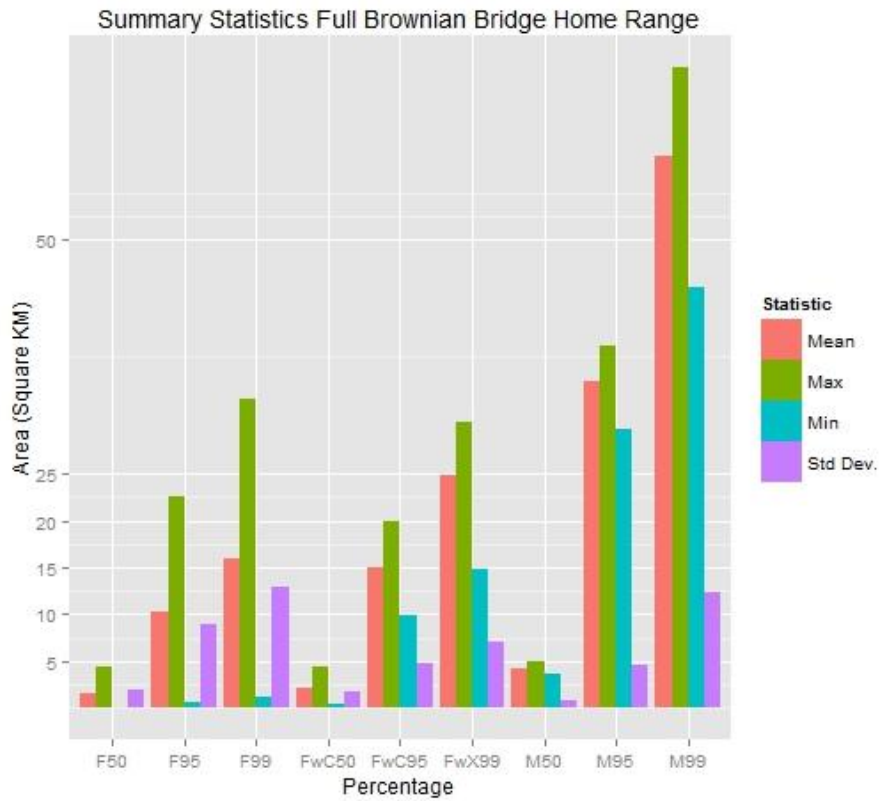


Figure 2E. Summary statistics BBMM full home range by sex and percentage (50, 95, 99%), maximum and minimum value, mean and the standard deviation. Females (F) and females with cubs (FwC) had the smallest home range whereas males (M) had the largest home range at all percentages compared.

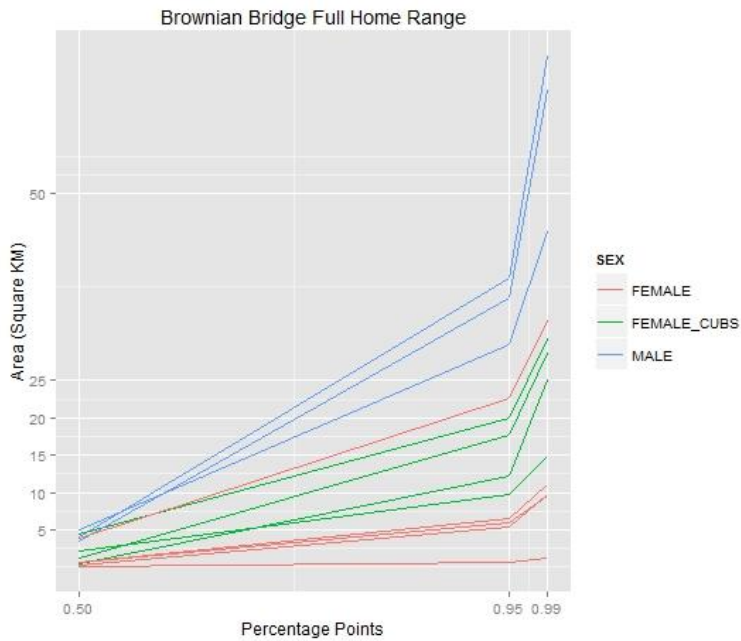


Figure 2F. Summary BBMM graph full home range by sex, a steep increase in slope when increasing the number of locations might be indicative of the impact outliers have on the total home range area. Slope change appeared to be strongest for males.

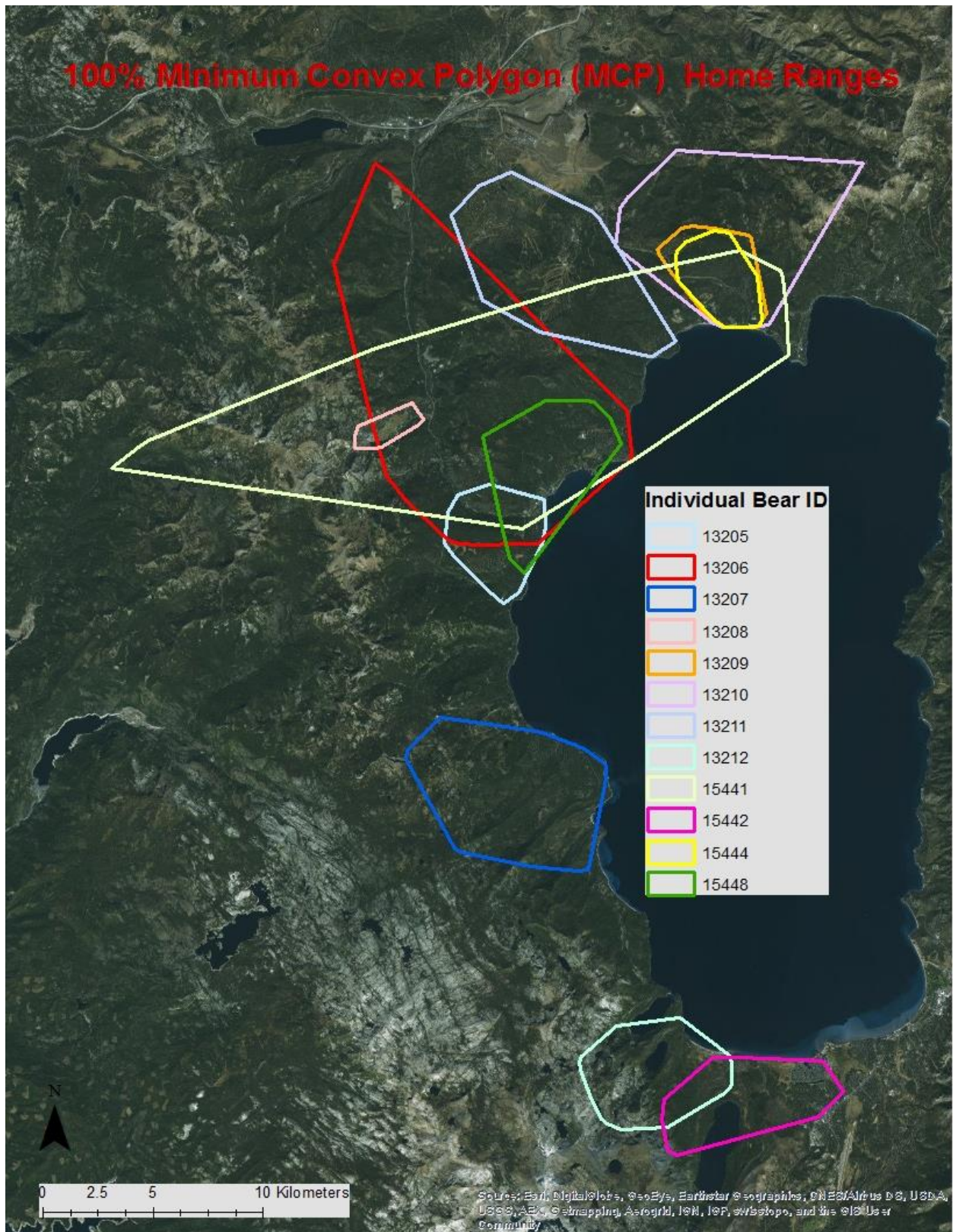


Figure 3. The total home range by bear in the study area, at 100% MCP.

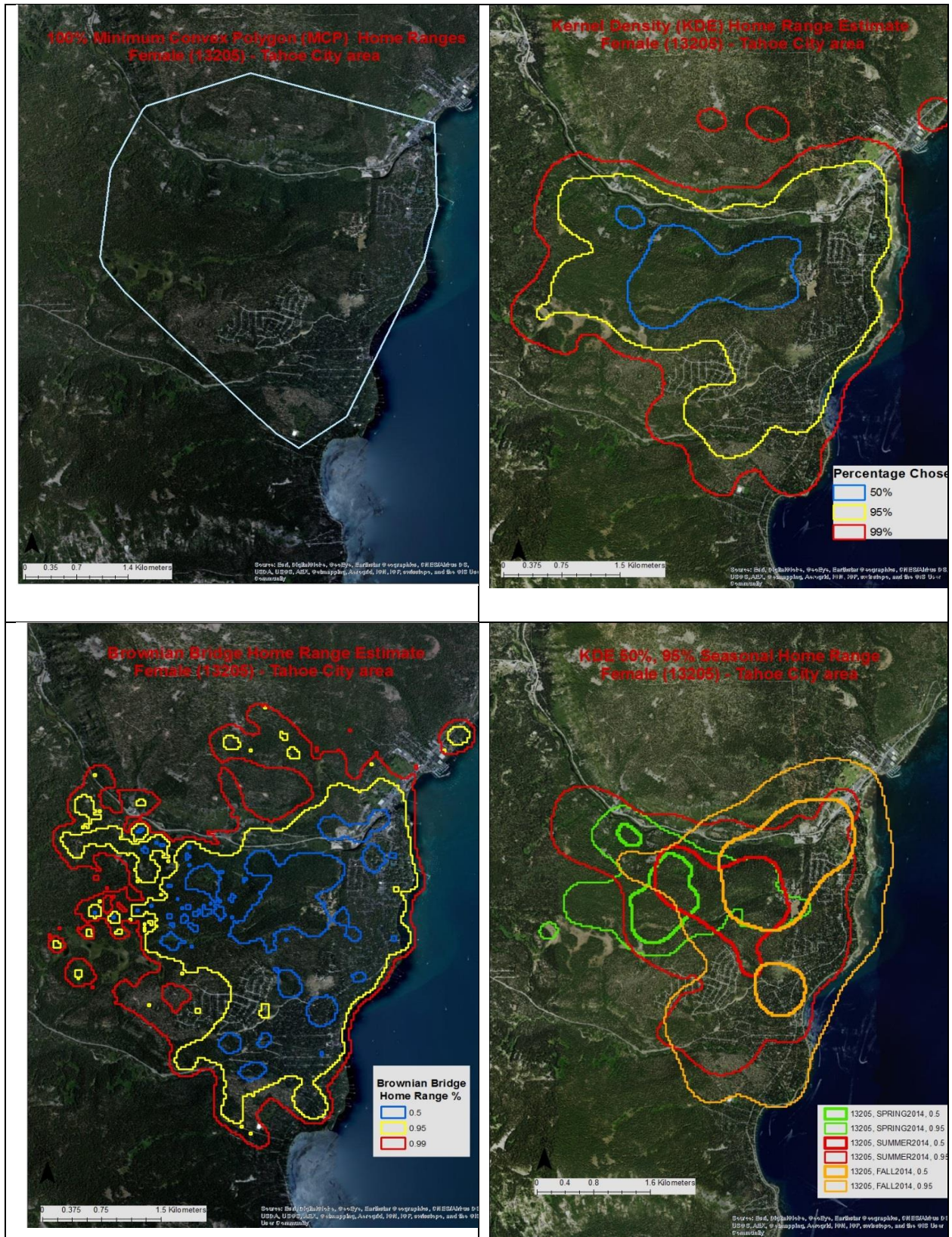


Figure 4A. Individual home ranges based on MCP, KDE, BBMM and seasonal home ranges for comparison purposes for female 13205.

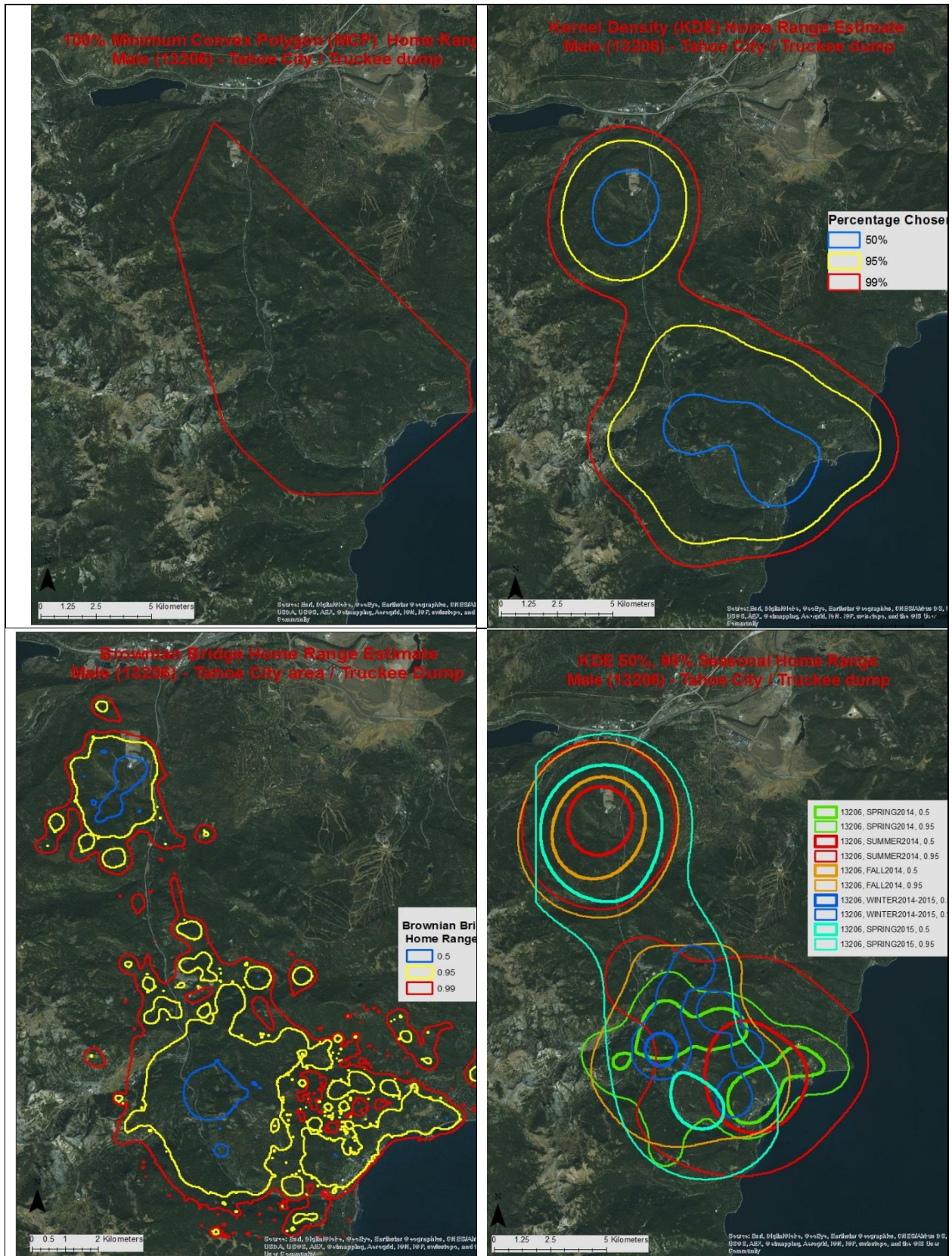


Figure 4B. Individual home ranges based on MCP, KDE, BBMM and seasonal home ranges for comparison purposes for male 13206.

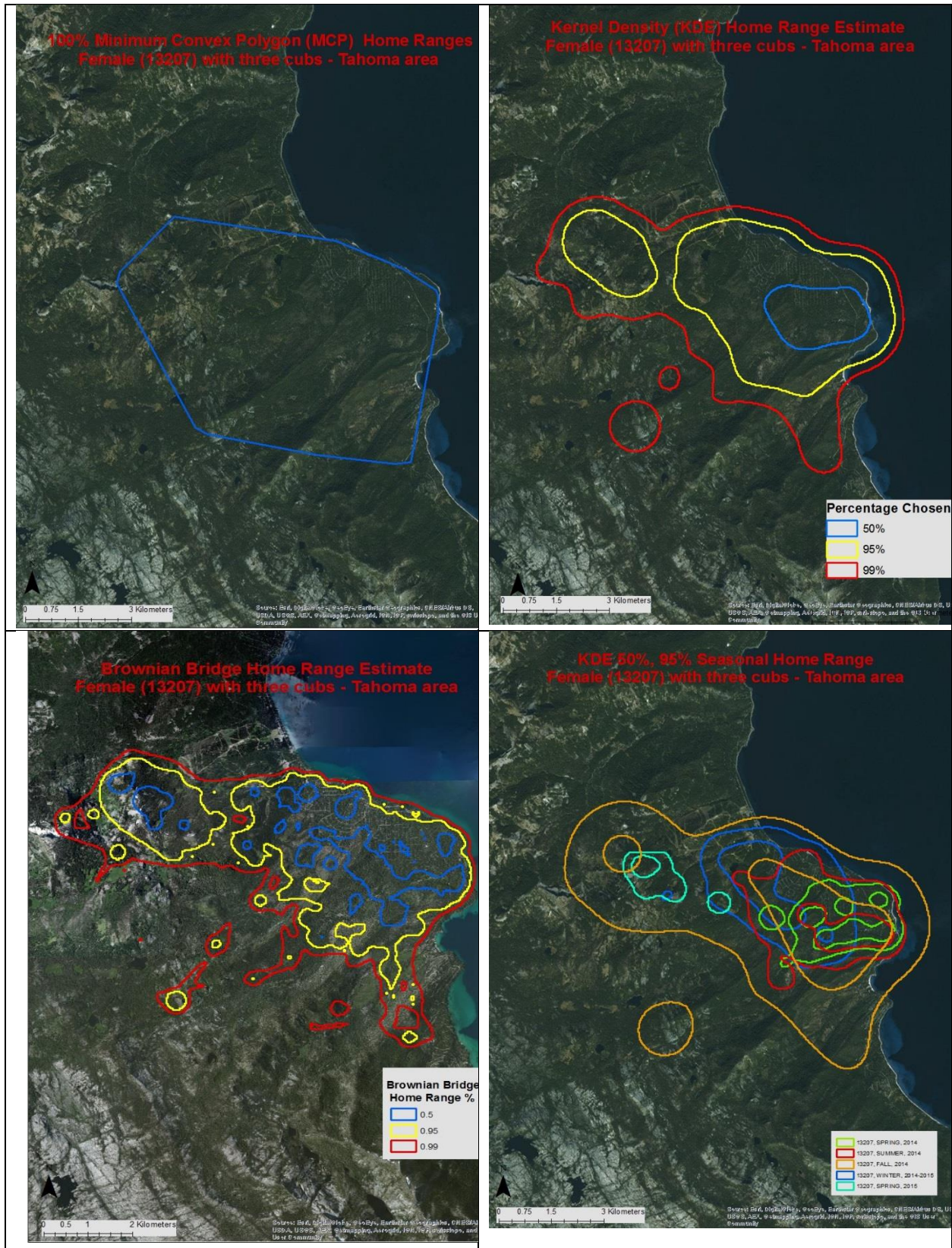


Figure 4C. Individual home ranges based on MCP, KDE, BBMM and seasonal home ranges for comparison purposes for female 13207.

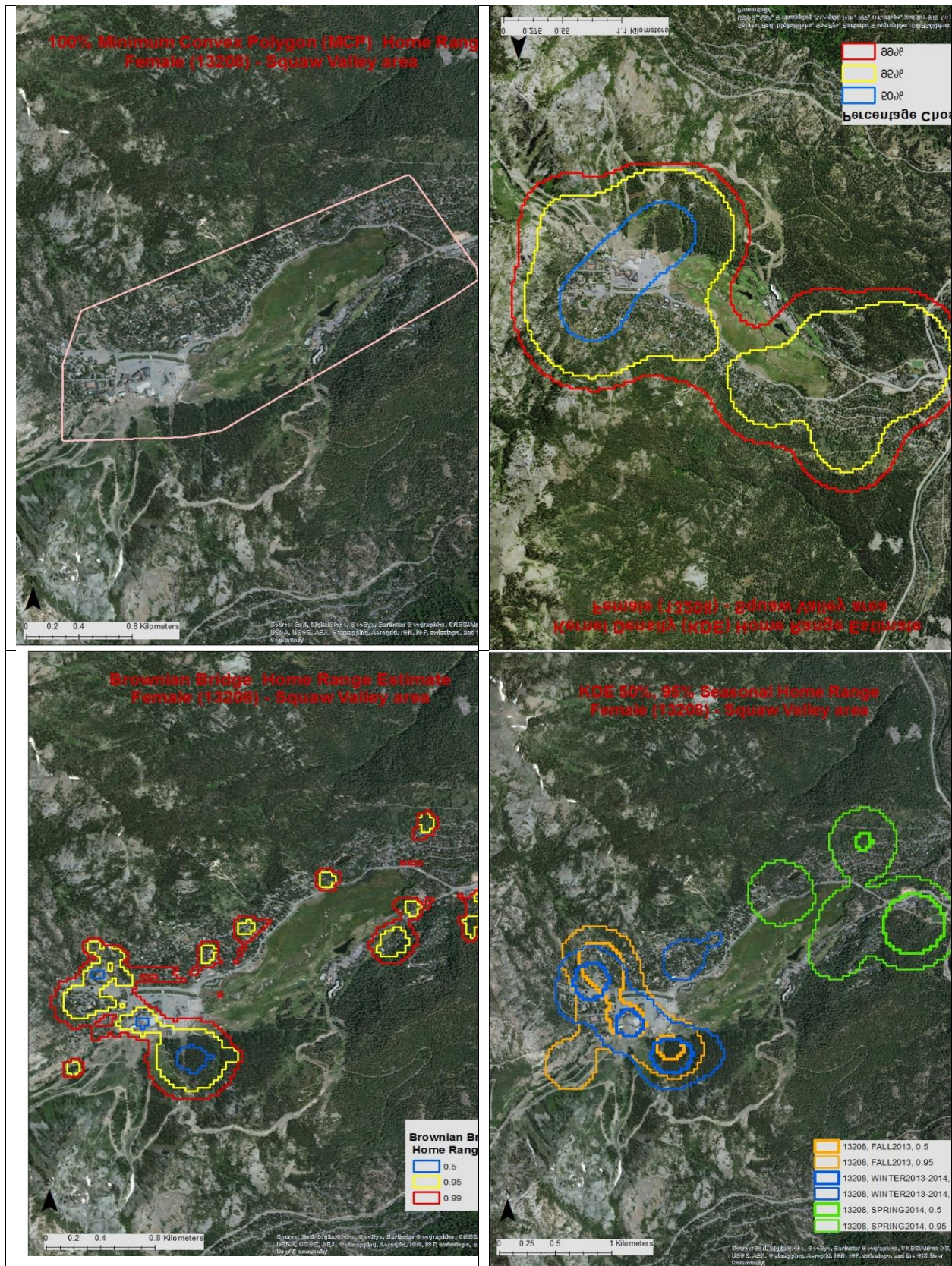


Figure 4D. Individual home ranges based on MCP, KDE, BBMM and seasonal home ranges for comparison purposes for female 13208.

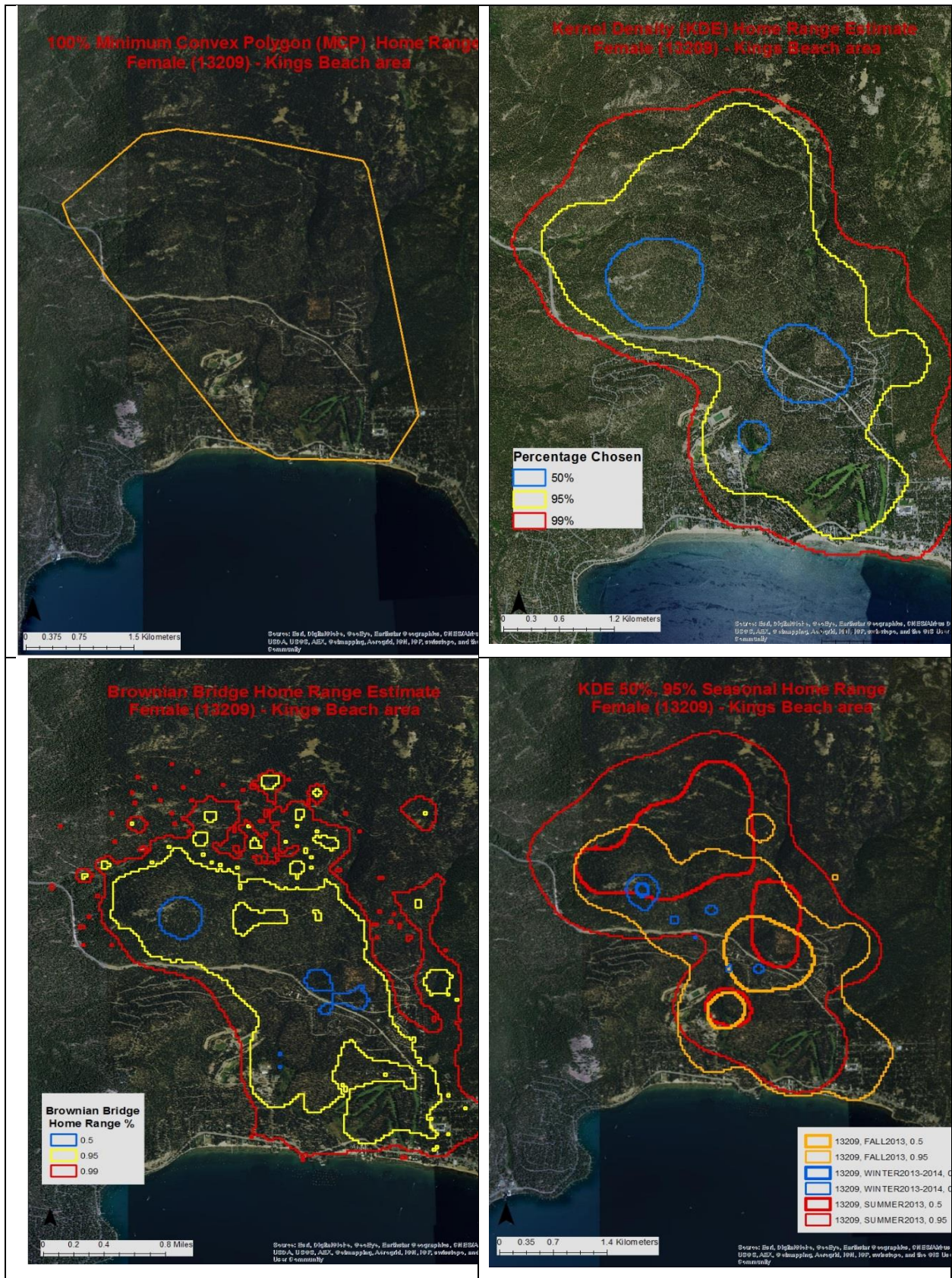


Figure 4E. Individual home ranges based on MCP, KDE, BBMM and seasonal home ranges for comparison purposes for female 13209.

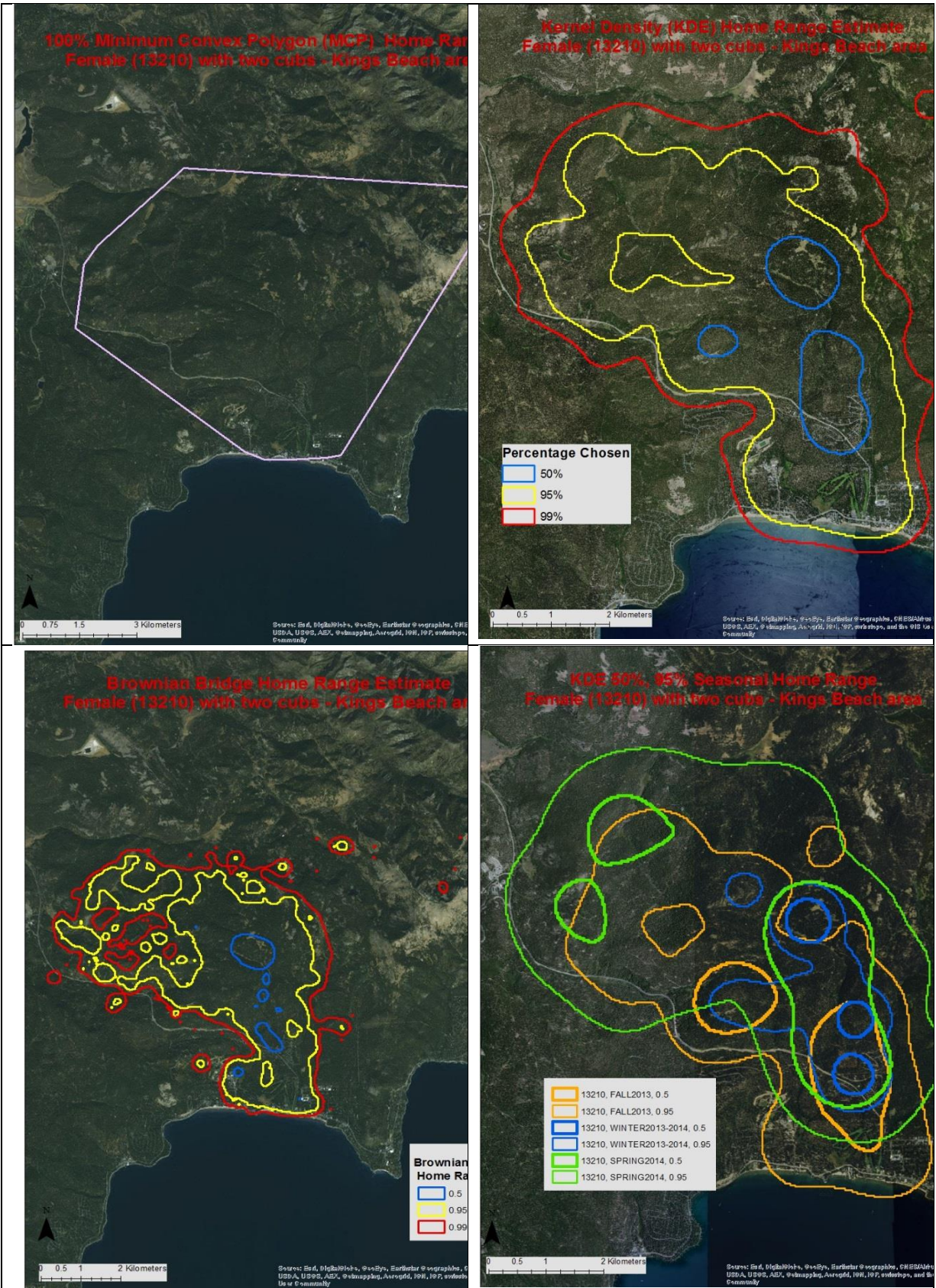


Figure 4F. Individual home ranges based on MCP, KDE, BBMM and seasonal home ranges for comparison purposes for female 13210.

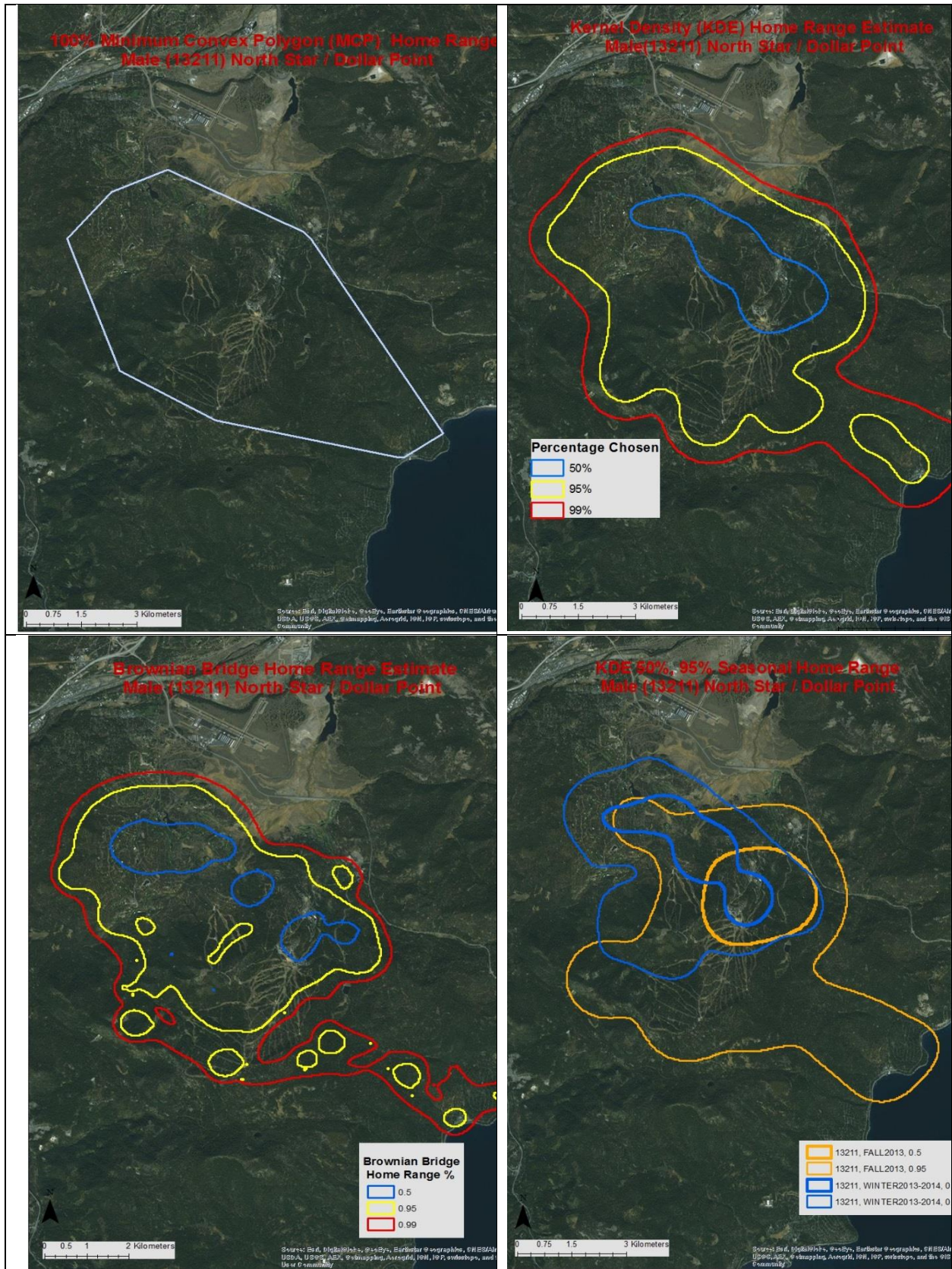


Figure 4G. Individual home ranges based on MCP, KDE, BBMM and seasonal home ranges for comparison purposes for male 13211.



Figure 4H. Individual home ranges based on MCP, KDE, BBMM and seasonal home ranges for

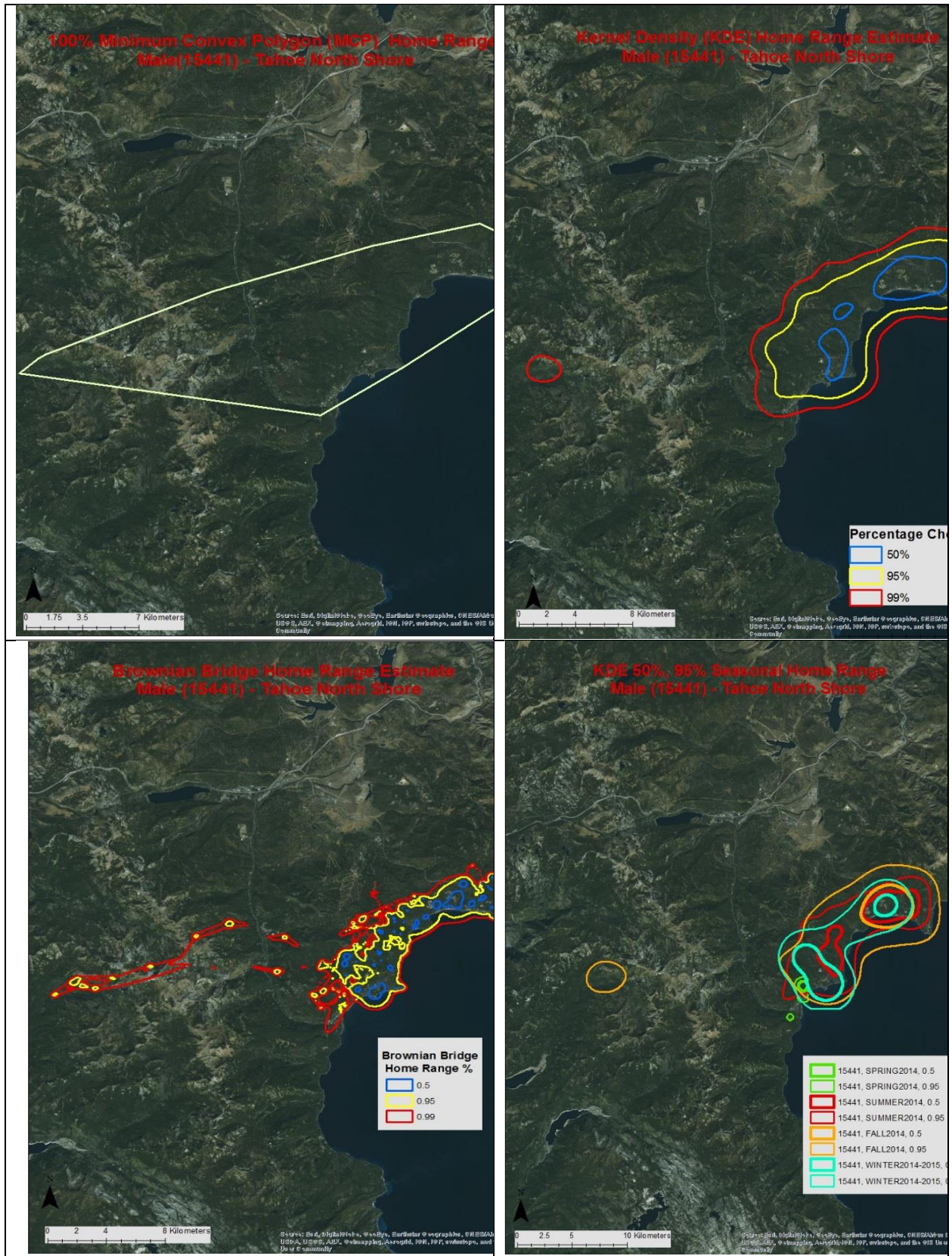


Figure 4I. Individual home ranges based on MCP, KDE, BBMM and seasonal home ranges for comparison purposes

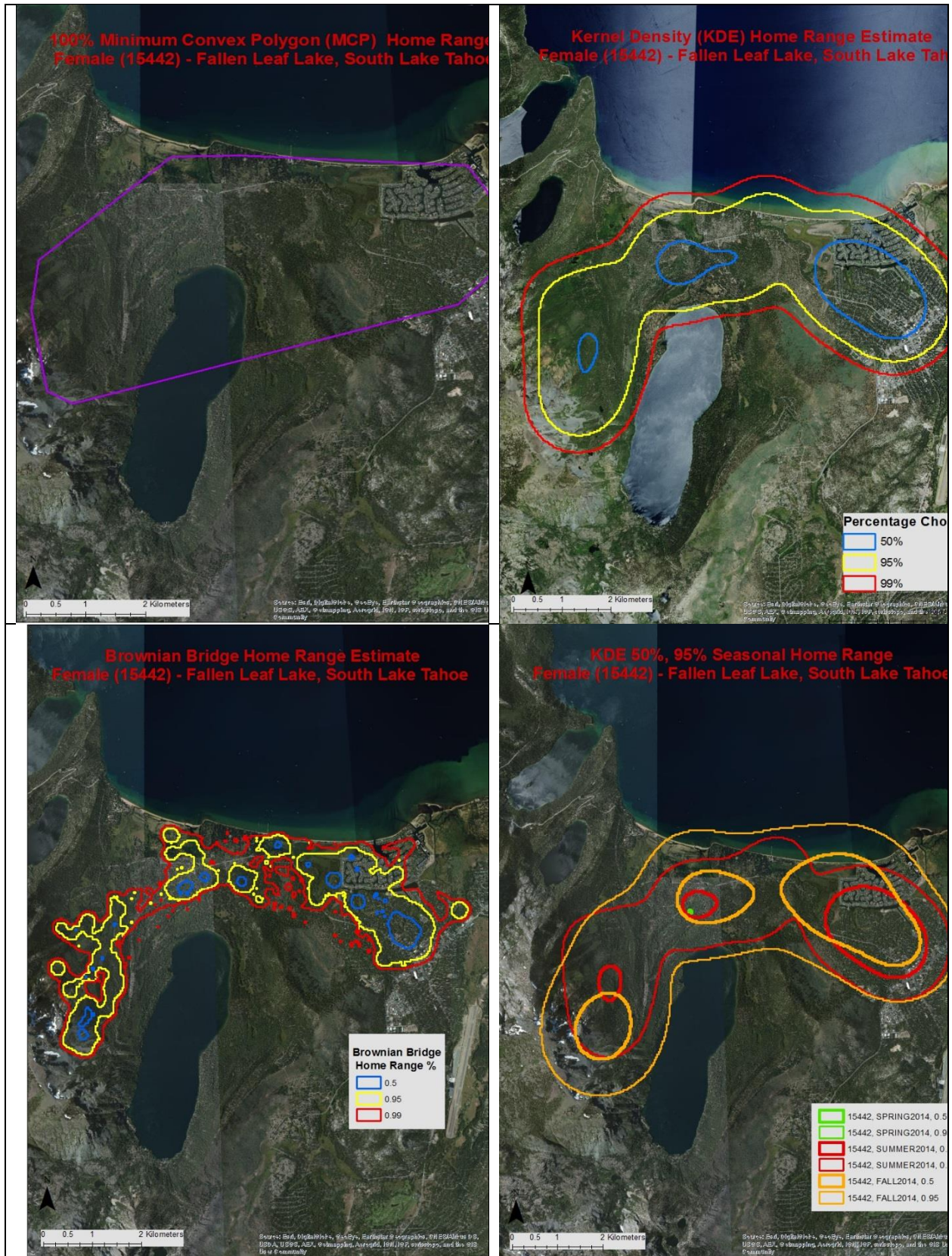


Figure 4J. Individual home ranges based on MCP, KDE, BBMM and seasonal home ranges for comparison purposes for female 15442.

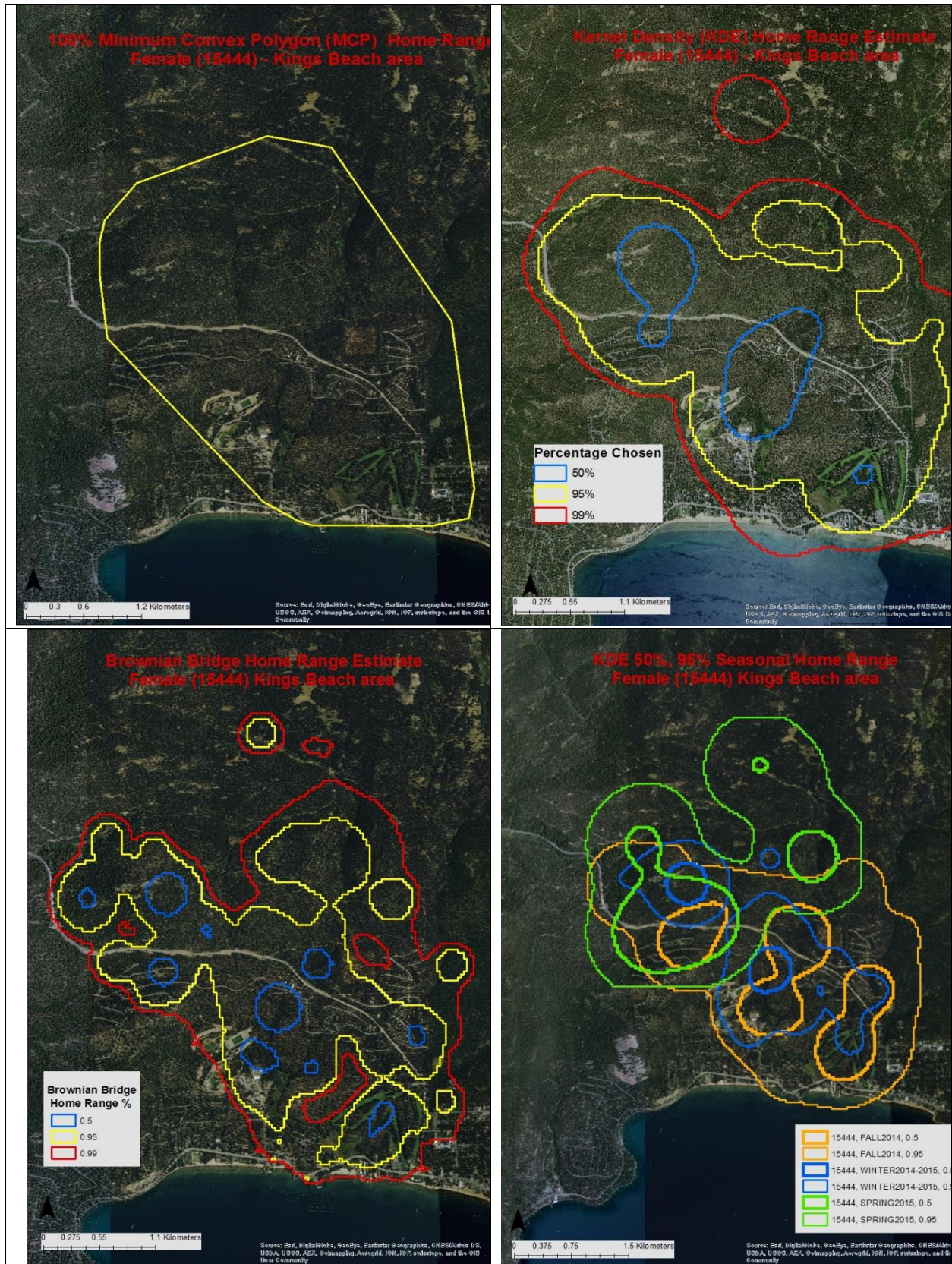


Figure 4K. Individual home ranges based on MCP, KDE, BBMM and seasonal home ranges for comparison purposes for female 15444.

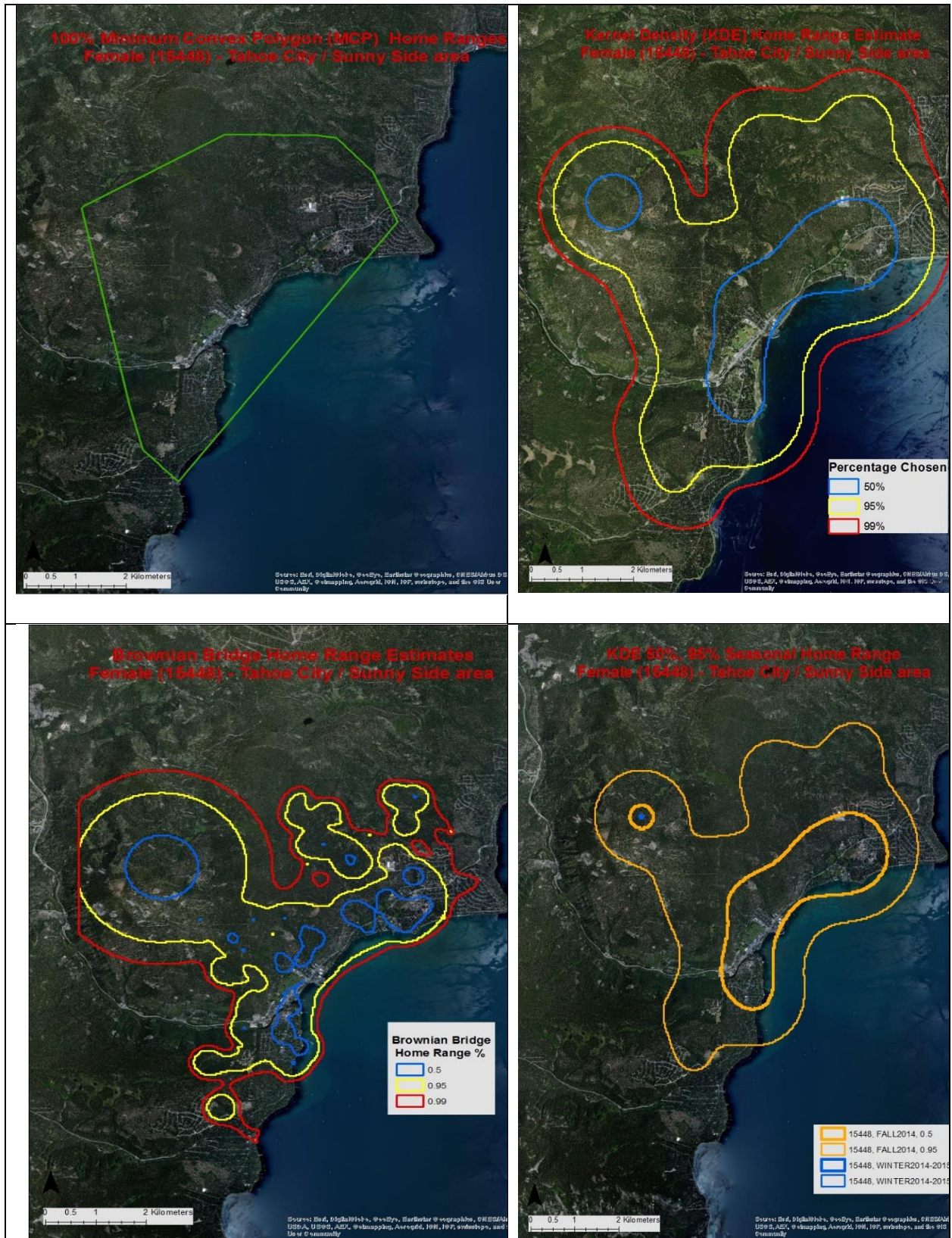


Figure 4L. Individual home ranges based on MCP, KDE, BBMM and seasonal home ranges for comparison purposes for female 15448.

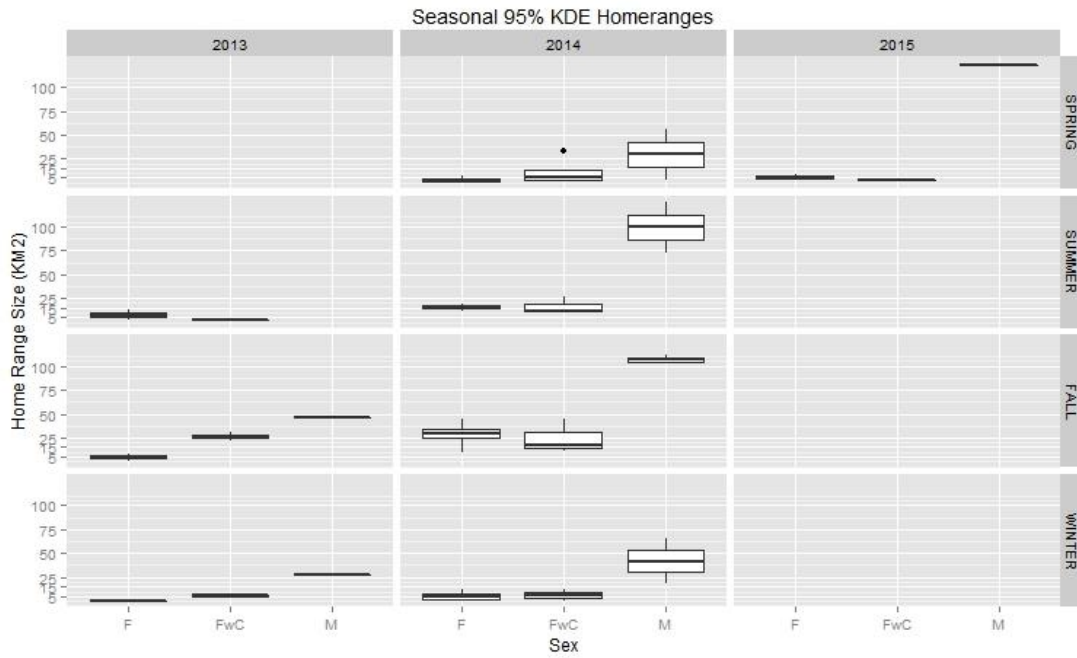


Figure 5. Seasonal home ranges by sex, year and season based on 95% KDE. Boxplots indicate the mean and the 25th percentile and 75th percentile, seasons without data did not have any collars deployed.

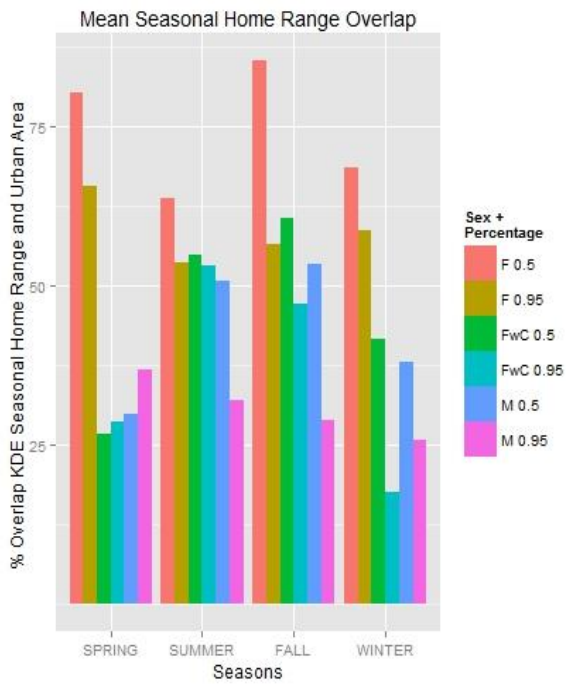


Figure 6. Mean urban home range overlap based on Kernel Density Estimates (KDE) with the urban area by season. Females (F), Females with Cubs (FwC) and Males (M).

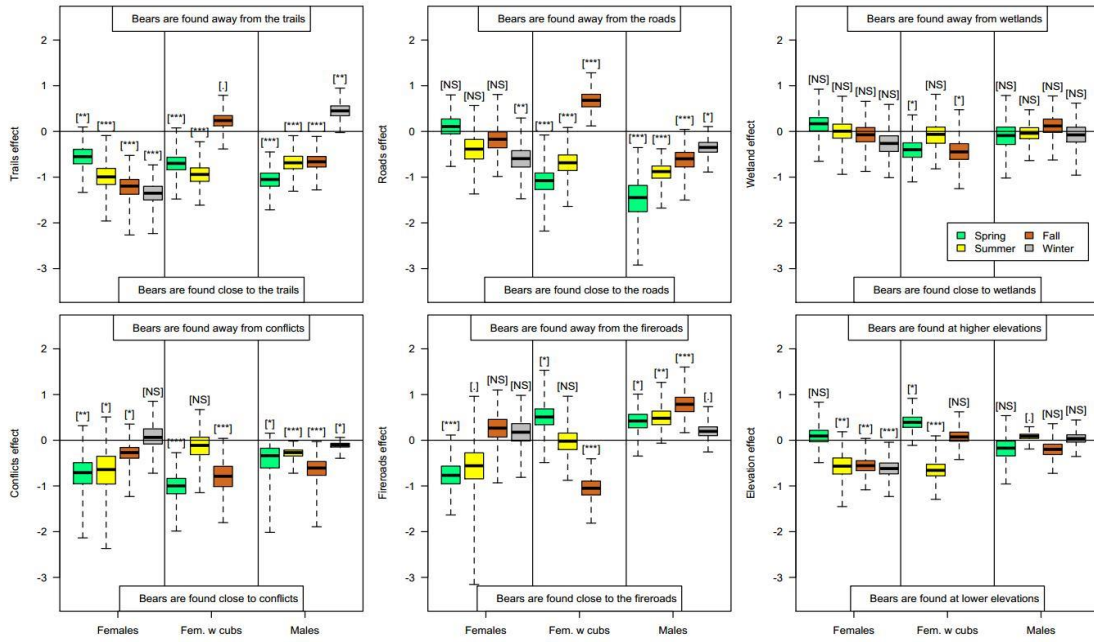


Figure 7. Resource selection function addressing temporal patterns by sex for trails, roads, wetlands, areas of known bear conflict, fire-roads and elevation. Where negative values indicate an attraction to the variable. Statistical significance is indicated on top of the error bar. Where NS refer to non-significant p value, “.” refers to a p value of < 0.1, “*” < 0.05, “**” < 0.01 and “***” < 0.001.

4. Can a bite in the butt change black bear behavior? Effects of aversive conditioning on predictors of bear-human conflict

Introduction

Conflict between humans and wildlife is growing across the globe (Decker et al. 1997, Riley et al. 2002, Breitenmoser 1998). As humans expand their global footprint, many wildlife populations are forced to live in close proximity to humans or are constrained to human-modified habitats. Human-wildlife conflict is particularly acute in areas with significant human development abutting wild lands. To coexist with humans in such areas, some species significantly alter their behavior and ecology; a process termed “synurbanization” (Luniak 2004, Adams 2005). Large predators are especially at risk of conflict with humans due to their perceived threats to humans and their pets and livestock (Gehrt, Stanley and Riley 2010). As a result, these predators are generally lethally-controlled in human dominated areas (Treves 2005). In North America, the main predators linked to human-wildlife conflict are pumas (*Felis concolor*), coyotes (*Canis latrans*), wolves (*Canis lupus*), grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*). Of these species, the black bear is arguably associated with the greatest increases in conflict in North America over the last 30 years (Spencer et al. 2007). As opportunistic omnivores, black bears are attracted to anthropogenic food sources such as garbage, bird food, backyard beehives, and chickens (Breck et al. 2006, Merkle et al. 2013). Increasing human conflict with black bears and growing public aversion towards a reliance on lethal control has prompted new studies on the efficacy of non-lethal strategies for conflict mitigation (Hunt 1984, Ternent and Garshelis 1999, Beckmann et al. 2004, Spencer et al. 2007, Homstol 2011).

The Lake Tahoe Basin in California, is a prime example of an area where growing black bear populations pursue anthropogenic food sources and consequently have caused a wave of bear-human conflict. Between 2007-2015 more than 20,000 bear incidents in this region were reported to state and local agencies and a local nonprofit organization, The Bear League (Klip, unpublished data). Incidents ranged from damaged property caused by bears gaining access to cars and homes, to garbage disturbances (i.e. tipping over garbage cans, removing trash bags from dumpsters) and bears denning underneath homes and decks. Bear-human interactions are particularly problematic when bears break into occupied dwellings because of human safety concerns (Law enforcement reports). The state agency assigned to manage this conflict, California’s Department of Fish and Wildlife (hereafter; CDFW), developed a three-pronged approach to reduce the likelihood of bear-human encounters. The first element of this effort was public education around the management of garbage, securing houses and limiting other attractants around human structures. The second element involved the “retraining” of conflict-prone bears through aversive conditioning (hereafter; AC), and the third relied on traditional lethal removal of bears associated with conflict resulting in significant monetary damage.

Lethal removal of bears engaged in conflict with people remains a commonly used management approach in California. However, while black bears are not endangered in the State, lethal bear removal often elicits negative responses from the public. This has been particularly true in the Lake Tahoe region where public pressure has mounted for the use of non-lethal management

tools such as AC. This call for non-lethal approaches in Lake Tahoe is consistent with trends across California (Koch 1994) and other U.S. states including Utah, Virginia and New Jersey (Teel et al. 2002, Lafon et al. 2003, Johnson and Sciascia 2013). Thus, many wildlife management agencies charged with managing bear-human conflict, including CDFW, have begun programs to assess the efficacy of non-lethal methods.

Aversive conditioning is a form of operant conditioning used to reduce undesirable behavior by applying physical or psychological discomfort to conflict animals (Shivik et al. 2003). AC is further defined as a learning process in which deterrents are continually and consistently administered to conflict animals to reduce the frequency of undesirable behavior (Hopkins et al. 2010). Shooting conflict animals with rubber bullets or paintballs, hazing with dogs, and exposure to loud noises are common AC stimuli applied to black bears. Generally, the stimuli stops when the bear retreats to suitable cover outside of developed areas. Several studies have examined the effectiveness of different forms of AC. For example, Gillin et al. (1997) found that hazing black bears with bear dogs was more effective than other forms of AC, and that multiple dogs were more effective than one dog. Beckman et al. (2004) reported that bears stayed away from a patch for 100 days, on average, after being treated with dogs. Similarly, a study in New Hampshire found that bears chased with hounds stayed away from release sites longer than bears treated with rubber buckshot alone (Comeau 2013). Additionally, bears conditioned to human food returned more quickly than unconditioned bears to the capture area (Mazur 2010), and bears that were exclusively night active when pursuing anthropogenic food sources were found to be less likely to return after AC (Clark et al. 2002).

While research on the effectiveness of AC for reducing bear-human conflict is not new, most published research has focused predominantly on whether treated bears returned to the area where nuisance behavior was first observed. This approach tests whether AC is a “silver bullet” that solves nuisance behavior once and for all. However, this method ignores whether treated bears were changing their behavior in more subtle ways that might ultimately reduce conflict and make bears more avoidant of human-dominated areas generally. A more nuanced understanding of the behavior of bears experiencing AC is critical to assess whether methods such as those employed by CDFW are worth the cost, risk and effort.

Here, I studied the behavior of black bears subjected to varying levels of AC in the Lake Tahoe region. The conditioning of bears in my study took the form of 1) simple capture and release, 2) capture and harassment with Karelian bear dogs (hereafter KBD), and 3) capture, harassment with KBD and less-lethal ammunition. I examined the traditional metric of how quickly treated animals returned to the capture area and assessed how the return is affected by season, sex and drought, but I also focused on behavioral proxies that may better reveal the likelihood that a bear will come into conflict with humans again after treatment. Specifically, I tested if the level of AC treatment was predictive of bears: a) selecting hibernacula further from urban areas, roads and homes, b) becoming less active in the winter, c) changing their daily activity patterns to become more nocturnal, d) spending less time in urban areas and e) becoming less reliant on food-waste dumpsters. By measuring these various aspects of bear behavior, I hoped to gain a deeper understanding of the efficacy and sustainability of commonly used AC methods.

Methods

Study area

The study area included the Lake Tahoe portion of El Dorado and Placer counties (Figure 1). The area encompassed approximately 850km² (528mi²) consisting of both private and public property. I worked with local businesses, homeowners, and land agencies to secure access to trapping sites, which were largely determined based on access. Additional details on the study area can be found in Chapter 2.

All bears used in this study were captured with trailer-mounted traps (Figure 2) in developed areas, and all trapping locations were close (<25m) to where bears had tried to obtain anthropogenic food sources (mostly garbage). All bears were collared and assigned to one of three AC groups, detailed below. Trapped bears were chemically immobilized using Telazol (Fort Dodge Laboratories Inc., Fort Dodge, IA) following the California Department of Fish and Wildlife (CDFW) Capture and Restraint Manual (Jessup et al. 2001). UC Berkeley's Institutional Animal Care and Use Committee (IACUC) approved all animal handling procedures (IACUC: R358-0315, Sikes 2016).

Telemetry

Bears were captured between May and November of 2011 to 2014, using a heavy-duty box trap mounted on a trailer. GPS Iridium collars were placed on captured bears to track movement and quantify habitat use. All collars were programmed to collect a position every 20 minutes during the first six weeks and thereafter every two hours. Sex classes were defined as males (n=10), females (n=12), and females with cubs (n=5). Due to sample size concerns, these categories were pooled for some analyses (details below). See below and Chapter 2 for additional details on capture methods.

Experimental design

Three aversive conditioning protocols were used in this study on a total of 27 captured bears. These were Treatment 1 – Control, soft release with no AC deployed (n=10); Treatment 2 – Dogs, two KBDs only used for AC (n=8); Treatment 3 – All, two KBDs and less-lethal ammo used for AC (n=9)

After a target bear was captured, I moved the trailer-mounted traps to the nearest safe location for release with a maximum distance of 1.5km from the capture location. When releasing a bear, the backdoor of the trap was opened (Figure 3), which allowed the bear to leave the trap. Bears in the control group (release without other AC) were released by opening the back door without additional stimuli provided. Bears that were part of treatment 2 (AC with KBDs), were chased with two dogs on release. Specifically, prior to release, an object (e.g., rock or branch) was placed 20-30 ft. from the trap and functioned as a visual cue such that the dogs were let loose when the bear reached this marked location. This translated into giving the bear a 2-5 second head start, after which the two dogs initiated their chase. The dogs barked, and nipped at the bear, and often forced bears to retreat to a tree (Figure 4).

Treatment 3 (AC with dogs and less-lethal ammo) was performed similarly to Treatment 2 with the exception that bears were first shot at with less-lethal ammo. Less-lethal ammo included

rubber bean bags, rubber balls, and rubber slugs, all fired from a shotgun. The projectile selected was based on distance to the animal. Rubber bean bags and balls were used at short range and rubber slugs at greater range (>50 ft.). The treatment protocol was to hit the bears twice with projectiles prior to releasing the dogs. Shots were not fired after the release of dogs to prevent accidentally hitting a dog.

Bears were assigned to different treatments to maintain even proportions of each treatment type. Availability of field personnel to perform AC with less-lethal ammo played a role in assigning bears to treatment groups. During all releases, a law enforcement officer was present to provide protection through lethal means, if necessary, should a dangerous situation arise (Figure 5).

Return to patch

Bear Return to Patch (BRP) was defined as the number of days before a bear returned to a defined area. I defined six different patch types which included the capture location, the release location and four different spatial extents defining human-developed areas. These four spatial extents of high human activity were measured by: 1) City Limits, 2) U.S. Census, 3) Remote Sensing and 4) a combination of the City Limits, U.S. Census, and Remote Sensing information referred to as “Combined” hereafter. U.S. Census (United States Census Bureau 2010), City Limits and Remote Sensing (USDA Forest Service Pacific Southwest Region 2010) were delineated by polygons containing the specific urban extent features bound by the study area. Additional descriptions of the spatial extents can be found in Chapter 2. A bounding polygon around the spatial extent of each patch was used to record return to the area. In some situations, the release of a bear occurred at the capture location, and, thus, these two patches were identical. In most cases, a bear was transported to the nearest suitable habitat that allowed for a safe release. Both the capture location and release location were buffered by 100m. This distance was selected to allow detection and account for any GPS error. The number of days to return was calculated based on GPS locations from the time the bear was released to the time it returned to the relevant patch. Once the bear’s GPS location was recorded within the patch polygon, the bear was considered to have “returned to patch”. If a bear was released within a developed patch area, then I assessed whether it left the patch within the first three days and would then count from this date until its return to the patch of concern. If it did not leave the urban patch area at all, the number of days to return was recorded as zero. Additionally, I investigated how BRP metrics were affected by season, sex classes and drought. Seasons were defined as follows: Spring as March 16th till June 15th, Summer as June 16th till August 31st, Fall as September 1st till 30th of November 30th, Winter as 1st of December 1st till March 15th. Seasons were selected to align with snowfall in the Lake Tahoe Area. Drought was based on precipitation during the year, and all study years were considered drought years except for 2011 which was considered a “wet” year (Jones 2015).

Behavioral proxies for bear-human conflict

Another goal of this research was to identify behavior proxies for bear-human conflict; that is, behaviors that were thought to impact the potential future bear-human conflict for animals captured and treated in this study. I focused on the following behavioral proxies detailed below (see also Table 1).

Hibernaculum selection. To test if levels of AC affected the proximity of presumed hibernation sites to human infrastructure, hibernacula were mapped by identifying clusters of 3-D GPS locations after Julian Day 300 (around the 27th of November) and before Julian Day 150 (around the 30th of May) the following year, reflecting the approximate start and end dates of the hibernation season. Clusters of GPS locations were visually inspected at two different scales, first at 100m and then at 10m to detect movement and further pinpoint the hibernaculum location. The hibernacula locations were assessed (ANOVA) relative to distance to: a) roads, b) roads with speed limits greater than 35mph, c) fire roads, d) trails, and e) the four measures of developed area (City Limits, U.S. Census, Remote Sensing and Combined). Additionally, the sex of collared bears and the interaction of sex with treatment type were assessed (ANOVA) in relation to hibernation location. Hibernacula locations were not verified on the ground. Females with cubs were grouped with other adult females for this analysis due to limited sampling of hibernacula locations for females with cubs.

Winter activity. Winter movement of bears was defined as movement during the hibernation season (defined as above, i.e., between Julian dates 300 – 150). Movement was recorded through a minimum displacement of 60m between subsequent GPS locations. I expected limited GPS locations during the hibernation period because bears would enter a hibernacula which prevented the transmission of GPS locations. Winter movement was measured in active events, where multiple activities during one day would be counted as one active event. The 60m minimum movement threshold was selected to account for GPS error and allow for shallow or above ground dens that would allow for a GPS location to be transmitted while the bear was not actually moving (Immell et al. 2013). If fewer than 5% of the points within a given week showed a minimum displacement of 60m the bear was considered inactive for that period.

Nocturnality. Daylight hours were based on the daylight calendar for South Lake Tahoe (Thorsen 2018), and bears were assessed for the first six weeks after release because data were gathered at 20 minute intervals during that time period (versus every two hours thereafter). Nocturnality was assessed within the urban envelope using the Combined extent because this is the most conservative definition for the developed area. Nocturnality was defined as the total number of nocturnal GPS fixes divided by total number of urban GPS fixes, expressed as a percentage. To supplement findings from the GPS data, nocturnality was also assessed from August 2013 until May 2014 through trail cameras (RECONYX PC900) in South Lake Tahoe. The focal area, Taylor Creek (Figure 6), included the home range of several bears included in this study. The area adjacent to the creek is heavily used by humans and dogs during the day and home to the largest campground in the region (Fallen Leaf Lake Campground). Over 40,000 photos were assessed as part of this analysis. I recorded time capture and photos were sorted based on the day light calendar. Photos taken between sunset and sunrise were considered “nocturnal” activity photos.

Time spent in urban area. The amount of time that individual bears spent in urban areas was assessed for each bear and each of the four urban spatial extents (City Limits, U.S. Census, Remote Sensing, and Combined). Intersections, defined as the GPS fixes found within the selected spatial extent, were created to understand use of the urban patch types. The number of GPS locations for each individual bear within the urban extent was divided by the total number of locations for that bear. Analysis was completed for the first 20, 60 and 100 days after release.

Total number of locations within the extent types was divided by the total number of GPS locations for the animal to calculate the percentage use of the urban spatial extent. Additionally, I assessed whether sex classes and season affected time spent in urban areas.

Food-waste dumpster reliance. Reliance on human-generated food resources was measured by examining the frequency of GPS fixes near dumpster locations specifically intended to gather food waste from restaurants. Dumpster locations were obtained from Tahoe Truckee Sierra Disposal. Locations were geocoded and buffered by 100m. If a GPS location was found within the buffered dumpster location it was considered a visit to the food-waste dumpster. Bears with home ranges that did not overlap with the dumpster locations or whose home ranges were further away than 3 km were removed from this analysis.

Software utilized. All spatial analyses were completed in ArcGIS 10.2 (ESRI 2015, ArcGIS Desktop, Redlands, CA, Environmental Systems Research Institute) and R (version 3.1.3 R Core Team 2014, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>). Graphs were made in GGPLOT2 (Wickham 2009) or base R. Data reorganization and manipulations were done using the following R packages: PLYR (Wickham 2011), STRINGI (Gagolewski 2015), RESHAPE (Wickham 2007) and doBy (Hojsgaard and Halekoh 2014).

Results

A total of 27 bears were radio collared (Table 2). Collars collected 80,443 GPS locations, including an average of 2694 (\pm SD 2287; range 27-7875) locations per bear.

Bears returning to patch (BRP)

For all three treatments employed, Control, Dogs, and All (dogs and less-lethal ammo), results varied based on the capture and release locations and each of the four spatial extents (City Limits, U.S. Census, Remote Sensing and Combined). Of the 27 bears monitored, six (22%) did not return to the capture location, of which two were treated with Dogs, three were treated with All and one was a Control bear. On average, bears treated with dogs returned to the capture site after 150 (\pm SD 167) days versus 130 (\pm SD 189) days for All treated animals and 28 (\pm SD 65) days for Control bears. The difference among treatments was not significant (ANOVA, $P > 0.05$; Figure 7). In contrast, differences between treatments for return to the release location were significant (ANOVA; $F_{2,21} = 5.36$, $p < 0.05$; Figure 8), with the greatest effect associated with exposure to Dogs. Nine (33%) bears did not return to the release location, of which five were treated with Dogs, three were treated with All, and two were Control animals. Bears that returned to the release location did so on average after 242 (\pm SD 214) days for Dogs, 64 (\pm SD 97) days for All, and 33 (\pm SD 65) days for Control animals. Interactions between season and treatment for the capture site were not significant but showed a trend in which Control animals returned to the urban spatial extent sooner than the other treatments (Figure 9). The interaction between season and release site was significant (ANOVA; $F_{4,19} = 3.86$, < 0.05 ; Figure 10), and BRP was highest during the summer. Interactions between BRP and sex, drought, and season were not significant, nor did BRP differ significantly between the three treatments for Census, City Limits, Remote Sensing, and Combined urban extents.

Behavioral proxies for bear-human conflict

Hibernaculum selection. Eighteen bears were assessed for hibernacula selection; the remaining nine bears were removed from this analysis because their data ended prior to October 27th or they did not hibernate. Bears selected a hibernaculum between the 1st of November and 24th of January (Table 3). The average hibernation start date within the Combined urban extent was the 2nd of December (\pm SD 22 days) and in the wild area (outside of urban extent) was the 4th of December (\pm SD 24 days). Hibernation locations are shown in Figure 11. Of the 18 bears assessed, two hibernated within City Limits, and four established hibernacula within the Census and Remote Sensing spatial extents. The distance of hibernacula from City Limits varied from 314m to over 10km. Distance of hibernacula to roads varied between 24m and 3236m. Distance from fire roads was between 114m and 4166m.

None of the variables tested significantly predicted hibernacula location with the exception of sex; distances to human spatial extent differed significantly between males and females for several of the spatial extents considered. Females denned closer to the Combined urban extent (linear mixed-model, $F_{1,16} = 4.30$, $p < 0.05$) on average 811 (\pm SD 751m) away, whereas males were on average 3,245 (\pm SD 3594m) away. A similar trend was found for the Remote Sensing extent, for which females hibernated closer to urban areas (1,158 \pm SD 1053m) than males (4,135 \pm SD 4,201m; linear mixed-model, $F_{4,20.3} = 4.72$, $p > 0.05$). Differences for the extent based on U.S. Census and City Limits were not significant but showed a similar pattern of females denning closer to urban areas. Females denned 1,021 (\pm SD 997m) away from the U.S. Census urban extent, whereas males denned 3,426 (\pm SD 3,821m) away, and females denned 3,875 (\pm SD 2,789m) and males 5,262 (\pm SD 4,271m) away from the City Limits extent. While not statistically significant, females trended to select a hibernacula closer to roads with speeds greater than 35 miles per hour, closer to all roads, and closer to fire roads in comparison to males (Table 3). AC treatments did not appear to influence the location of hibernacula.

Winter activity. Fifteen bears were assessed for winter activity; 12 bears were removed from the data set because their data ended prior to the hibernation season (seven bears) or because they did not hibernate (five bears). Although winter activity for bears treated with Dogs (0.78 \pm SE 0.69 winter active events) and All (2.01 \pm SE 0.87) tended to be less than that for Control bears (2.15 \pm SE 0.48), these differences were not statistically significant (ANOVA: $F_{2,12} = 2.92$, $p = 0.09$; Figure 12, 13). Winter activity also did not differ among sex classes (males, females, females with cubs).

Nocturnality. Twenty-four bears were assessed for nocturnal behavior. Two bears did not have enough data to allow analysis and one bear did not show any nighttime activity in the Combined urban extents. Mean (\pm SE) percent nocturnal activity was highest (67.5% \pm 5%) for bears treated with Dogs for the Combined spatial extent, followed by bears treated with All (63.1% \pm 4.8%) and Control bears (60.2% \pm SE 3.3%; Figure 14). There was no difference in nocturnality among sexes (males, females, females with cubs). Direct comparison on a weekly basis suggested that bears treated with Dogs and All were more nocturnal than the Control group for all weeks assessed (Figure 15). Photos obtained through trail cameras at Taylor Creek, a human impacted area, indicated that 58% of the bear photos were taken after dark.

Time spent in the urban area. Bears that did not have 20, 60 or 100 days of data within the urban extent were removed from the corresponding analysis. The resulting sample sizes were 20

days = 24 bears; 60 days = 23 bears; 100 days = 21 bears. While time spent in urban areas did not differ significantly across treatments, bears treated with Dogs or All recorded the lowest urban visitation except when urban extent was measured by the City Limits method (Figure 16). Bears in the Control group used the urban areas most intensively for all spatial extents and all three durations (20, 60 and 100 days). Females treated with Dogs spent less time in urban areas than males or females with cubs (e.g., at 60 days in Combined; ANOVA: $F_{8,12} = 1.79$, $p < 0.05$; Table 4).

Food-waste dumpster reliance. A total of 22 bears were assessed for use of dumpster sites; five bears were removed from the data set because their home ranges did not overlap with the dumpster area or their home ranges were at least 3km away from the dumpster location. Visitation of human food resources was higher for bears in the All ($9 \pm \text{SD } 5$) treatment and Dogs ($7.8 \pm \text{SD } 5$) treatments in comparison to Control ($4.1 \pm \text{SD } 4$; Figure 17). The difference in dumpster reliance among sexes was marginally significant (ANOVA: $F_{2,18} = 3.92$, $p = 0.056$), with females visiting dumpsters least often (mean = 5 ± 5 visits per animals), followed by males (6 ± 4 visits per individual) and highest for females with cubs (mean = 12 ± 3 visits per individual).

Discussion

My study on the impact of three levels of aversive conditioning (AC) on the behavior of black bears in the Lake Tahoe Region revealed several important trends. Contrary to expectation, some bears did not return to their capture or release locations. The majority of these individuals had experienced AC, with AC with Dogs appearing to have the greatest effect. Additionally, the return to patch time (BRP) for bears treated with Karelian bear dogs (KBD) was greater than bears in the Control group for their return to both capture and release locations. Dogs also had the greatest effect on all behavioral proxies examined and bears treated with Dogs seemed to become more nocturnal, less winter active and spent less time in urban areas. These impacts of bear behavior may ultimately reduce the level of conflict with humans. Below I address these findings in more detail.

Captured conflict bears were expected to return within days or weeks to the areas where they were captured and released based on the results of previous research (McCullough 1982, Beckmann et al. 2004, Mazur 2010, Northeast Wildlife DNA Laboratory 2010, Homstol 2011). As a result, longer times to return to these locations have often been interpreted as a measure of the success of AC protocols. In my study, treatment with Dogs kept bears away from the capture and release sites for the longest period of time, which was consistent with other studies (Gillin et al. 1997, Beckmann et al. 2004). Dogs appeared to yield the strongest effect during the summer months; this may be because, in contrast to spring and fall, bears are less nutritionally stressed during the summer. In spring, right after hibernation, bears are hungry and male bears may come into urban areas to pursue females during the breeding season. During the fall period, bears are in hyperphagia and seeking additional calories, often in the form of anthropogenic sources (Ditmer et al. 2015, Johnson et al. 2015). In both spring and fall seasons, these nutritional demands may result in bears returning more quickly to areas in which they had been successful in finding food. Traps were located close to garbage receptacles that were replenished reliably. If bears did not return to their capture location, I interpreted this as an indication that they associated this

location with an experience negative enough to forego utilizing this food source. Foregoing visits to these areas suggested that bears at minimum located alternative food sources and might be responding to a landscape of fear (Laundré et al. 2001), i.e., some locations were associated with higher levels of risk and discomfort for bears and were therefore avoided.

I found that AC with Dogs had a positive effect in terms of reducing the potential for future bear-human conflict based on several of the behavioral proxies examined. For example, both telemetry and photos from camera traps indicated that bears treated with Dogs tended to be more nocturnal than the other treatments. Nocturnal behavior is common for species living in close proximity to humans (Ditchkoff et al. 2006) and has been observed in coyotes (Grinder and Krausman 2001), bobcats (*Lynx rufus*, George and Crooks 2006) and pumas (Dickson and Beier 2002) as well as in black bears (Beckmann and Berger 2003b, Matthews et al. 2006, Baruch-Mordo et al. 2014). Human presence has previously been reported to make bears more nocturnal, and I interpreted my findings regarding increased nocturnality after AC in this context (Reimchen 1998). The study area is heavily visited by humans and nocturnal bears presumably limited their interactions with humans. Bears treated with Dogs appeared to become more nocturnal in comparison to the other treatments, possibly reflecting an association with humans and dogs. This is consistent with findings from Yosemite, California where bears subject to AC became more elusive (Madison 2008) and in Whistler, Canada, where bears were more wary after AC treatments (Homstol 2011). In Austria, brown bears were more nocturnal as a result of AC (Rauer et al. 2003) and in Yellowstone, brown bears became more nocturnal and were described as becoming “sneaky” as a result of AC (Gillin et al. 1994). While I found, as did other studies, that bears continued to use developed areas, the result that bears are apparently more wary/nocturnal after AC is preferable from a human safety perspective, because it reduces the potential for conflict.

Aversive conditioning with Dogs also seemed to impact winter activity, with activity during the winter lowest for bears treated with Dogs. Several bears remained winter active, which may be due to the large amounts of food waste during the ski season in some areas, which may increase the potential for bears to come into close contact with people. Anecdotally, winter activity in Tahoe’s bear population seems to be increasing. Bears are often quick to take advantage of anthropogenic food sources (Spencer et al. 2007), and food availability may influence when bears start denning (Baldwin and Bender 2010). Although LeCount (1983) found that bears will den regardless of sustained food availability. Many other factors may influence winter activity, and conflicting impacts on hibernation have been reported. For example, in Colorado and western Oregon, precipitation appeared to have an effect on timing of den entrance and winter activity (Baldwin and Bender 2010, Immell et al. 2013). However, in New York state, environmental factors did not play a role in the timing of black bear hibernation (O’Pezio et al. 1983). Winter activity may also be a result of disturbance at the den site (Goodrich and Berger 1994, Immell et al. 2013). Temporal patterns of denning have been found to be dependent on sex (Johnson and Pelton 1980, O’Pezio et al. 1983); however little is known about how sex or food availability affect intermittent winter activity. These relationships should be investigated further, especially if bears become increasingly active during winter. While the full suite of factors affecting winter activity remains to be determined, AC appeared to reduce winter activity, which should reduce the likelihood of bear-human conflict.

Bears treated with Dogs did not stop visiting urban areas but appeared to reduce their presence in these areas compared to bears subject to other treatments. However, bears subjected to AC treatments tended to show more of a reliance on food waste dumpsters. This was somewhat counter intuitive, especially given that bears treated with Dogs used the urban environment less than other treatments. Food waste dumpster locations were only available for a portion of the study area and consequently the effects of dumpsters was assessed for a smaller number of bears. This reduction in sample size might be responsible for this result. Future research should examine the time budgets of bears in greater detail. If bears treated with AC spend less time in urban areas but utilize areas with food waste dumpsters more, then it would be interesting to understand whether treated bears come in to feed but do not linger before retreating to wild patches after each foraging bout.

In addition to noting behavioral effects based on AC treatment, I also observed differences in response among sex classes. In particular, females with cubs appeared to use areas with food waste dumpster more than males or females without cubs. Personal observations suggest that some of the “worst” conflict bears were sows with cubs - “worst” in the sense that they would be active during the day and breaking into homes on a regular basis. Additionally, I found that females denned closer to urban areas than males, leading to a higher potential for interaction with humans. Future research should explore factors associated with denning underneath houses and human structures, since it is likely that these bears are responsible for the majority of conflict during the hibernation season.

One item that remains to be addressed is why the All treatment, which included AC with less-lethal bullets as well as dogs, was less effective in some situations than AC with dogs only. I propose that Karelian bear dogs may be more effective than the combined stimuli because the dogs were held back until after the less-lethal rounds were fired. Although this delay was typically short (5-10 seconds), it often resulted in the dogs not making any physical contact with the bear because the bear was able to climb a tree before the dogs were able to nip the bear. Future studies should further examine whether dogs alone, particularly when they make physical contact with bears, are indeed more effective in changing bear behavior than more commonly deployed, mixed stimuli methods.

Management implications

Resolving bear-human conflict has challenged bear managers and scientists for at least forty years (Graber and White 1978, 1983), with various methods employed to address bear nuisance behavior by wildlife agencies and scientists. Approaches used over the years include relocation (Hopkins and Kalinowski 2013), taste aversion (Ternent and Garshelis 1999, Homstol 2011), diversionary feeding (Nolte et al. 2001, Rogers 2011, Garshelis et al. 2017), electro-shocking (Breck et al. 2006), and aversive conditioning with dogs and other stimuli (Hunt 1984, Spencer et al. 2007).

While trying to solve nuisance wildlife issues is not a new issue, it is relatively new for agencies, especially in urban or suburban areas, to be confronted with significant opposition from groups advocating for animal rights and against lethal measures. This movement may influence elected officials in local, county, and state government to act against lethal control. Lethal control has

also caused significant human-to-human conflict, a problem that is of concern to the Tahoe recreational industry. The industry is keenly aware that a bear trap on their property will garner unwanted attention in the age of social media and may have an effect on their bottom line, or put them at odds with their employees. As a result, lethal control, for some, will only be resorted to as a final effort. It is not uncommon for law enforcement and security personnel at the various resorts and neighborhoods to have an idea of which individual bears are “bad” and to monitor their behavior daily. The same applies to residential neighborhoods, where people are concerned about the views of their neighbors and prefer not to be known as the person who lethally removed a bear. As a result, conflict-bears remain in the population.

Different strategies of dealing with nuisance wildlife have been tested, but this study challenges researchers to rethink what defines success. Often wildlife management programs, or their constituents, have higher expectations than can be delivered by the program. Achieving success requires managing divergent - even conflicting - stakeholder expectations. Inflated public expectations may lead to the pursuit of a “silver bullet” solution that is not realistic. In addition, when agencies look at success, they may look at the problem in a transactional sense. Is this bear likely to become a nuisance again? If so, when can it be removed? Stakeholder concerns may result in meetings to discuss other approaches besides lethal removal or require managers to respond to media attention. Collectively, these demands generate a significant drain on resources, which should be considered as part of the total management cost when weighing management options.

A shift in paradigm is required away from a “silver bullet” permanent solution to a focus on solutions that, though more temporary in nature, define success based on stakeholder expectations and provide an economic analysis of options considered. Temporary solutions and meeting stakeholder expectations do not need to be mutually exclusive and temporary solutions can be considered successful. For example, temporary reductions in bear presence that give communities a respite from an ongoing issue, reduce risk during the six weeks of high tourist season, or minimize contact during the period before a bear starts its hibernation would all be valuable temporary “solutions”. Conversely, lethal control can also be viewed as temporary because open home ranges in Tahoe are quickly recolonized by other bears. In many areas, lethal control options can still be implemented without invoking significant human-to-human conflict; however, there appears to be a undeniable trend toward people expecting wildlife agencies to employ solutions other than just killing the conflict animal (Decker and Chase 1997, Manfredo et al. 2003, Koval and Mertig 2004).

Aversive conditioning alone cannot resolve human-wildlife conflict, and public education beyond strategies for garbage and food storage needs to be part of the strategy (Gore et al. 2006). The general public does not realize that the black bear population in California is robust and growing. The general public may have the impression that all large carnivores are struggling to survive, but black bears in California are an exception to this narrative. In some areas, black bears may even be overabundant. This information needs to be shared with the general public. In addition, enforcement needs to play a more prominent role in changing people’s behavior as it pertains to leaving food out for bears. Results in Colorado found that enforcement yielded much better compliance with food storage regulations than education (Baruch-Mordo et al. 2011) and increased implementation of existing laws is specifically needed in the Tahoe Basin, where

enforcement is a patchwork of different jurisdictions. However, even with increased education and enforcement, lethal removal may continue to cause ethical concerns for some people, especially when the bear that is removed may not be the offending animal, or when small cubs are involved.

How does AC with dogs play into all of this? AC with Karelian bear dogs (KBD) may alleviate a situation temporarily. In many cases this would be seen as meeting community expectations. Besides short term gains, KBDs have impacts on bear behavior that makes bears less inclined to interact with people in the first place. In terms of furthering education of and outreach to stakeholder communities, KBDs are generally people friendly and make law enforcement and uniformed biologists more approachable to members of the public. Dogs in their uniform provide a great opportunity to perform educational programs at festivals, schools, and local organizations. Personal observation suggests that the presence of dogs allows for a change in narrative from “people are told what to do with their trash” to “what do the dogs do and how can people help make the dogs more successful”? Education becomes easier when people have an interest in the topic and dogs facilitate this. Inviting decision makers such as community leaders to participate in bear releases where they can see the dogs at work offers a unique opportunity to build relations, excite members of the public, and mobilize the decision makers to take action relevant to local enforcement and implementation of ordinances. This approach is cost effective, as the total cost for food, veterinary care, and supplies for one KBD is less than 5,000 dollars per year. Allowing for in kind and monetary donations should cover these expenses because AC is something many people support and feel good about. More challenging is to find biologists or wildlife managers who are willing to keep a KBD as their working dog. While they make great companions, the dogs’ high prey drive and energy level may give some potential dog handlers pause. Finally, plans would need to be developed to support a dog once it retires from active “bear” duty.

The role of KBDs in wildlife management is not constrained to AC of bears. In addition, the dogs can play a critical role in locating wildlife, for example locating animals injured in traffic collisions. Using dogs to locate bears injured in this way makes it easier to assess a bear’s range of movement and to determine if it is able to fend for itself. The dogs can also help locate cubs orphaned as a result of traffic collisions to allow for capture and rehabilitation. When partnered with an active bear manager or biologist, KBDs are an instrumental component of the toolkit needed for dealing with urban bear populations, and use of AC by dogs adds significant synergistic effects to traditional approaches for addressing human-wildlife conflict.

Tables and Figures

Proxy	Question asked / Reason used	Method
Usage of the urban area	Does AC affect usage of urban area?	The percentage of GPS fixes for each bear in urban area during the first 20, 60 and 100 days. The percentage was calculated by dividing total urban gps fixes by total number of fixes per bear.
Return to urban	Does AC change the return rates to capture, release site and developed areas?	Number of days from release day to a bear's GPS location intersecting with 100m buffer around capture or release site, or within four developed spatial extents*.
Nocturnality in urban area	Does AC affect nocturnality?	Percentage of nocturnal urban activity during first six weeks after release. Measured by the The percentage of GPS fixes for each bear during night hours (based nocturnal location/total urban locations) in the urban areas (defined by sunrise and set times for each season).
Hibernacula Selection	Does AC make bears select hibernaculas further away from four urban extents, roads, roads > 35mph and fire roads?	Hibernation location for each bear defined as area where bear does not move from for more than a three days during the hibernation season (Julian date 300-151), and the distance of that location to each urban area definition and other spatial variable.
Usage of known bear conflict areas	Does AC affect bear usage of areas with recorded known historical bear conflict?	Tabulate the total number of GPS fixes within conflict area buffered by 100m
Winter Activity	Does AC affect bears winter activity levels?	GPS fixes during the hibernation season (Julian day 300-151) that showed movement >60m were categorized as active, and active days were categorized as days that had >5% of points as active during that week. The ratio of active and inactive days were compared between bears.
Reliance of food waste dumpsters	Does AC affect the reliance on food waste dumpsters	The number of GPS fixes within a 100m buffer around the dumpster locations. CA1:C10

Table 1. This table describes the behavioral proxies selected to understand the effects of aversive conditioning on bear behavior. Behaviors selected were considered proxies for potential nuisance activities or creating bear-human conflict. * refers to four urban extents uses; City Limits, U.S. Census, Remote Sensing (eVeg) and a Combined an aggregate of the three urban extents.

Bear Summary

Bear ID	Sex	Total Positions	Start Date	End Date	Number of Days
13205	Female with Cubs	4749	2014-05-15	2014-11-21	190
13206	Male	4552	2014-05-23	2015-04-01	313
13207	Female with Cubs	4293	2014-05-24	2015-04-02	313
13208	Female	1047	2013-11-07	2014-04-04	148
13209	Female	3367	2013-08-05	2014-03-06	213
13210	Female with Cubs	7875	2013-10-22	2015-03-05	499
13211	Male	567	2013-11-15	2014-01-15	61
13212	Female with Cubs	4541	2013-09-28	2014-03-03	156
15441	Male	5078	2014-06-14	2015-03-05	264
15442	Female	4372	2014-06-14	2014-11-27	166
15544	Female	2212	2014-09-07	2015-03-24	198
15448	Female	706	2014-09-07	2015-02-15	161
10611	Male	61	2012-09-21	2013-06-11	263
12643	Female	386	2012-11-04	2012-11-09	5
12644	Male	6087	2013-07-09	2015-03-24	623
12645	Male	2361	2013-06-13	2013-12-26	196
12647	Male	1189	2013-07-30	2013-11-07	100
12648	Female	7543	2013-07-29	2015-04-01	611
13207saw	Female	27	2013-08-23	2013-08-25	2
30579	Female	333	2011-07-22	2011-11-17	118
30581	Female	2176	2011-10-20	2012-04-03	166
30582	Female	2933	2011-11-04	2012-09-28	329
30583	Female	175	2011-10-14	2011-10-18	4
30584	Male	1482	2011-09-04	2011-11-03	60
30585	Male	1853	2011-08-18	2012-08-19	367
30586	Male	897	2011-09-30	2011-11-10	41
30587	Female with Cubs	1884	2011-08-20	2012-10-05	412

Table 2. This table shows individual bears, their sex, the total number of position collected through GPS collars, when the collar was deployed when the collar was no longer sending data and the number of days the collar collected GPS fixes.

Hibernation Summary

Bear ID	Protocol	Sex	Hibernation Date	All Urban Combined	City Limits	U.S. Census	Remote Sensing	All Roads	Roads >35 mph	Fire Roads
13207sugar	Control	F Cubs	2014-12-23	1379	3654	1379	2917	1569	23721	406
13208*	Control	Female	2013-12-02	0	6007	0	0	535	14475	2122
13209*	All	Female	2013-12-06	274	314	675	274	552	13211	396
13210	All	F Cubs	2014-01-02	1511	1733	2263	1511	285	13422	367
13212*	Control	F Cubs	2013-12-12	2226	9127	3064	2226	2422	11255	2508
15441*	All	Male	2014-11-30	0	0	0	0	17229	17229	2439
15444*	Control	Female	2014-11-02	0	0	0	114	24	14744	526
10611	Dogs	Male	2012-11-22	291	1051	291	889	1162	16738	200
12644	Dogs	Male	2013-11-30	0	1116	0	0	189	15324	921
12645	Dogs	Male	2013-12-04	2775	8109	2775	6014	1891	9512	1825
12648	Dogs	Female	2013-12-02	842	3438	842	2151	430	12944	376
13206	All	Male	2014-12-01	402	3680	744	402	437	14293	534
30581*	Dogs	Female	2012-01-24	880	5941	880	1390	729	7953	618
30582	Dogs	Female	2012-01-02	0	4895	106	0	128	13455	1045
30584	Control	Male	2011-11-01	7476	10092	7476	9570	3236	26921	789
30585	All	Male	2011-11-06	7685	10221	9035	7685	602	21606	4166
30586	All	Male	2011-11-11	7086	7824	7086	8514	2603	22985	1229
30587	Control	F Cubs	2011-11-18	996	3633	1002	996	1227	18989	114

*= bears that ended before Julian day 151

F Cubs= Female with Cubs

Table 3. This table shows the distances(m) of the hibernacula to four spatial extents for urban; City Limits, Remote Sensing, U.S. Census and an aggregate of these three (Combined), to roads, roads with speeds limits exceeding 35mph and fire roads. Estimated hibernation dates are reported. The treatments (Protocol) are indicated here; Treatment 1 – (C) Control, soft release with no aversive conditioning deployed (n=10); Treatment 2 – (D) Dogs, two KBDs only used for aversive conditioning (n=8); Treatment 3 – (A) All - two KBDs and less-lethal ammo used for aversive conditioning (n=9).

CollarID	Sex	Treatment Combined	City Limits			US Census			Remote Sensing			Season			
			20	60	100	20	60	100	20	60	100				
10611	M	DOGS	0.82	0.74	0.73	0.81	0.71	0.70	0.57	0.53	0.52	0.56	0.45	0.44	Fall
12644	FwC	DOGS	0.77	0.83	0.85	0.65	0.72	0.78	0.30	0.29	0.36	0.45	0.63	0.72	Summer
12645	M	DOGS	0.17	0.22	0.27	0.13	0.19	0.26	0.15	0.16	0.18	0.14	0.17	0.18	Spring
12647	M	CONTROL	0.70	0.26	0.15	0.65	0.22	0.13	0.40	0.15	0.09	0.49	0.18	0.11	Summer
12648	F	DOGS	0.59	0.41	0.47	0.51	0.36	0.43	0.28	0.19	0.22	0.31	0.23	0.26	Summer
13205	FwC	ALL	0.27	0.35	0.39	0.13	0.26	0.30	0.02	0.04	0.08	0.14	0.11	0.14	Spring
13208	F	CONTROL	0.80	0.78	0.69	0.00	0.00	0.00	0.47	0.54	0.53	0.80	0.78	0.69	Fall
13209	F	ALL	0.31	0.46	0.56	0.31	0.45	0.56	0.09	0.15	0.24	0.16	0.28	0.40	Summer
13210	F	ALL	0.54	0.44	0.40	0.54	0.44	0.40	0.34	0.33	0.29	0.30	0.33	0.30	Fall
13211	M	DOGS	0.48	0.44	0.00	0.03	0.01	0.00	0.17	0.20	0.00	0.43	0.38	0.00	Fall
13212	FwC	CONTROL	0.18	0.27	0.25	0.01	0.00	0.00	0.02	0.07	0.07	0.16	0.20	0.18	Fall
15441	M	ALL	0.60	0.68	0.67	0.57	0.65	0.64	0.25	0.34	0.33	0.42	0.52	0.51	Spring
15442	F	CONTROL	0.65	0.59	0.58	0.62	0.55	0.54	0.63	0.57	0.56	0.57	0.52	0.51	Spring
15444	F	CONTROL	0.90	0.93	0.90	0.90	0.90	0.87	0.33	0.30	0.29	0.57	0.68	0.66	Summer
15448	F	ALL	0.52	0.73	0.67	0.44	0.63	0.58	0.33	0.35	0.50	0.46	0.63	0.58	Summer
30579	F	ALL	0.45	0.25	0.17	0.40	0.23	0.15	0.10	0.07	0.05	0.14	0.08	0.06	Summer
30581	F	DOGS	0.02	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.02	Fall
30582	F	DOGS	0.71	0.44	0.45	0.43	0.24	0.25	0.45	0.26	0.27	0.56	0.38	0.39	Fall
30584	M	CONTROL	0.14	0.11	0.00	0.00	0.00	0.00	0.10	0.08	0.00	0.13	0.10	0.00	Summer
30585	M	ALL	0.28	0.15	0.14	0.20	0.10	0.10	0.15	0.08	0.08	0.19	0.10	0.09	Summer
30586	M	ALL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	Fall
30587	FwC	CONTROL	0.42	0.41	0.43	0.21	0.08	0.07	0.15	0.21	0.23	0.31	0.23	0.22	Summer

Table 4: This table shows the amount of time spent in time in urban areas by sex, season and treatment for 20, 60 and a 100 days after release. Treatment 1 – Control, soft release with no aversive conditioning deployed (n=10); Treatment 2 – Dogs, two KBDs only used for aversive conditioning (n=8); Treatment 3 – All - two KBDs and less-lethal ammo used for aversive conditioning (n=9).

List of Figures

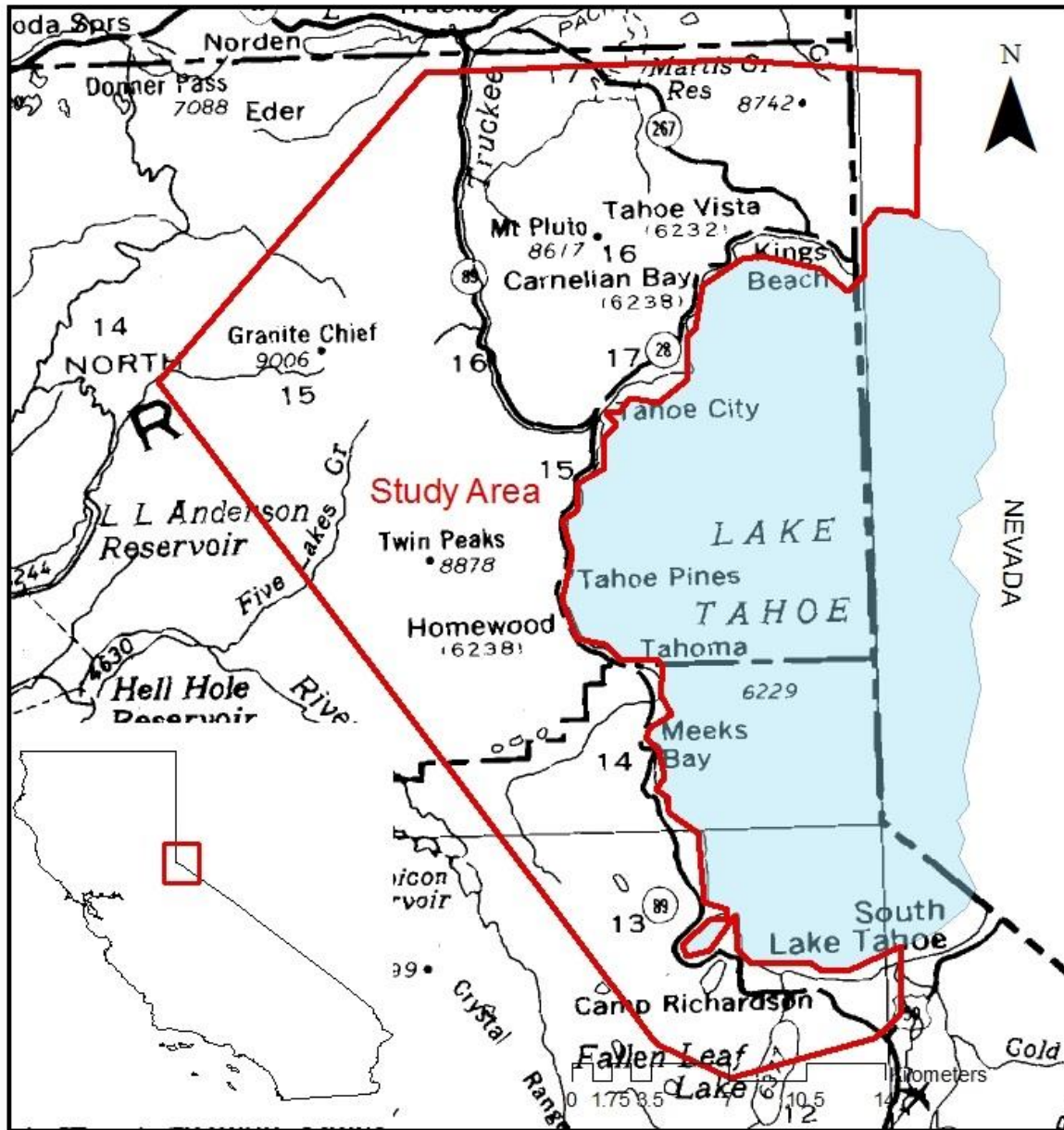


Figure 1. This map shows the study area consisting of western portion of Lake Tahoe, including El Dorado, Placer and Nevada counties, including part of the city of Truckee and the area east of Truckee to Nevada state border.



Figure 2: This figure shows box shaped trailer mounted bear trap, allowing for movement of bears to nearest possible habitat for release (Photo credit: Mario Klip).



Figure 3: This figure illustrates the release process. The back door swings up to allow bear to exit the trap (Photo credit: Go Pro Camera)



Figure 4: This photo illustrates the treatment where Karelain bear dogs are used only, where the dog barking and nipping at bears behind. (Photo credit: Marguerite Sprague)

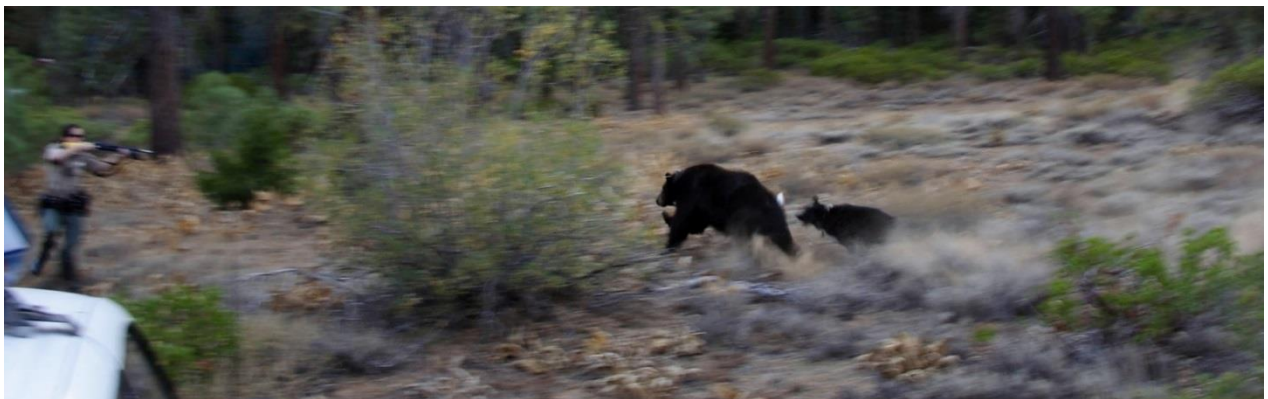


Figure 5. This figure shows law enforcement officer providing back up support in case it was needed. Lethal support for safety reasons involving bears was never necessitated and lethal ammo while present during all bear releases was never fired during the course of this study (Photo credit: Lisa Fields).



Figure 6. This map shows area where trail cameras were located and is adjacent to Taylor Creek, located between Fallen Leaf Lake and Lake Tahoe. Trail cameras were placed in 2013 and 2014 within 800m of Highway 89 in an area utilized heavily by people and dogs in an effort to understand whether bears were using the area during night or daylight hours.

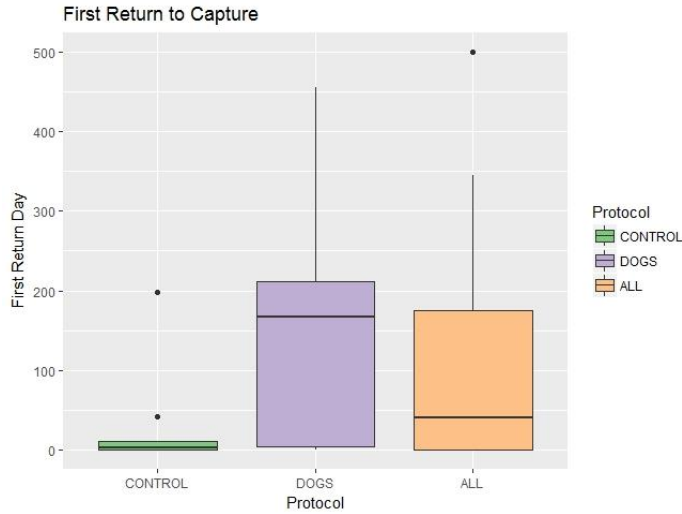


Figure 7. This figure shows a comparison for three aversive conditioning treatment for the capture location. Treatment 1 - Control, soft release with no aversive conditioning (AC) deployed (n=10); Treatment 2 – Dogs, two KBDs only used for AC (n=8); Treatment 3 – All - two KBDs and less-lethal ammo used for AC (n=9). Differences between AC treatments: Control, Dogs and All were not significant, however Dogs trend higher than all other treatments and bears stay away the longest under this treatment.

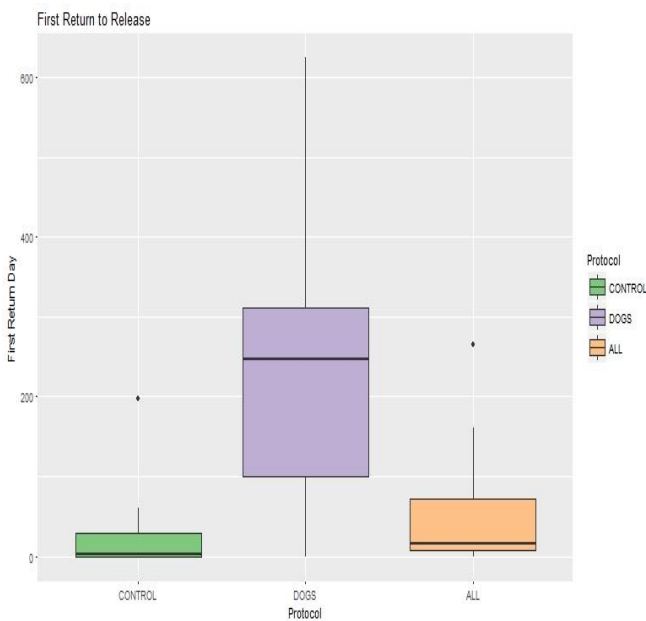


Figure 8. This figure shows a comparison for three aversive conditioning treatment for the release location. Treatment 1 – Control, soft release with no aversive conditioning (AC) deployed (n=10); Treatment 2 – Dogs, two KBDs only used for AC (n=8); Treatment 3 – All - two KBDs and less-lethal ammo used for AC (n=9). Results between treatments for return to release site was significant and bears stayed away the longest when AC was performed with dogs.

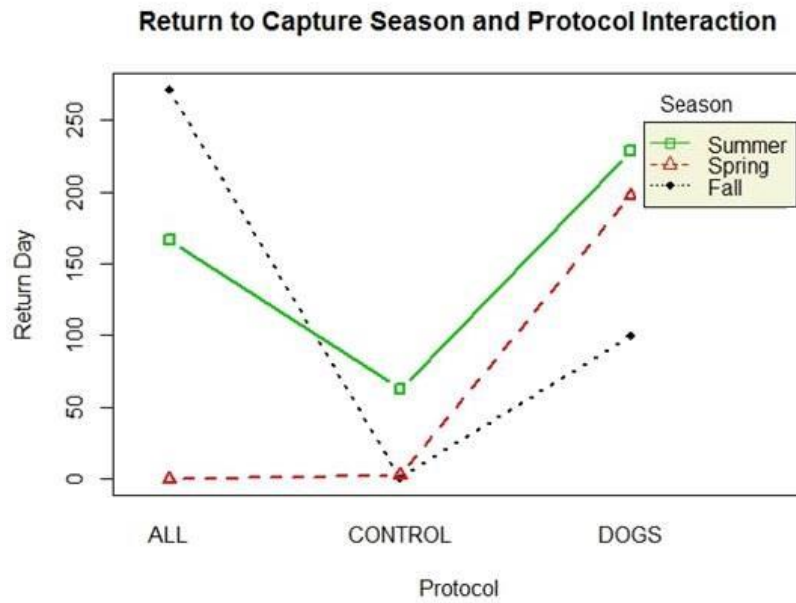


Figure 9. This figure shows a comparison for three aversive conditioning (AC) treatments and interaction with season for the capture location. Treatment 1 – Control, soft release with no AC deployed (n=10); Treatment 2 – Dogs, two KBDs only used for AC (n=8); Treatment 3 – All - two KBDs and less-lethal ammo used for AC (n=9). Results for AC interaction with season were not significant.

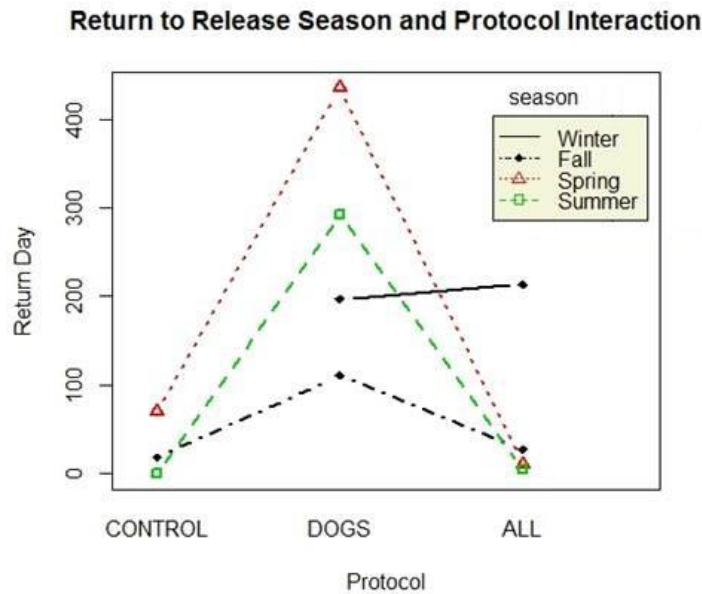


Figure 10. This graph shows a comparison for three aversive conditioning (AC) treatments and interaction with season for the capture location. Treatment 1 – Control, soft release with no AC deployed (n=10); Treatment 2 – Dogs, two KBDs only used for AC (n=8); Treatment 3 – All - two KBDs and less-lethal ammo used for AC (n=9). Interaction of treatment with season was statistically significant for the summer.

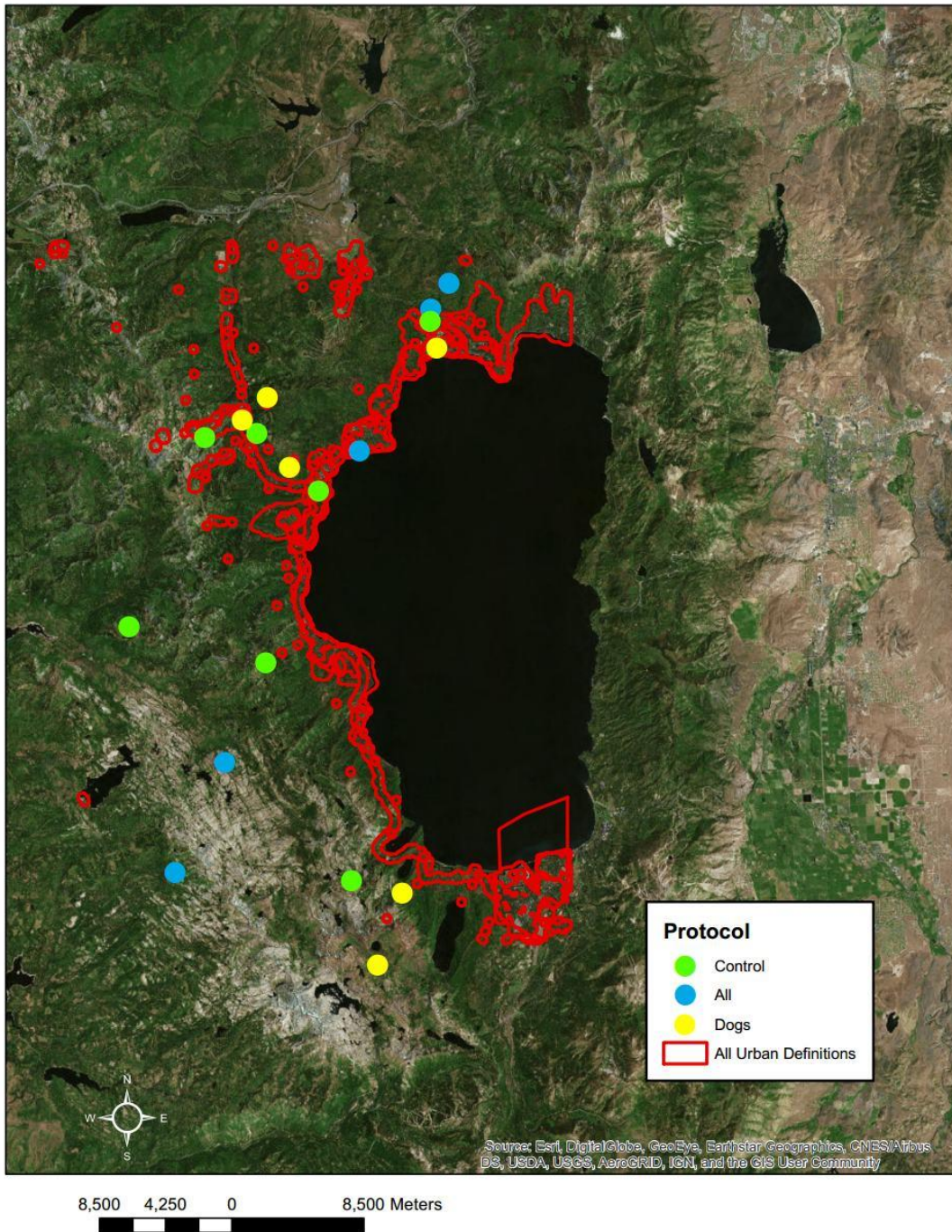


Figure 11. This map illustrates the west side of Lake Tahoe, and the hibernation locations located based on three aversive conditioning (AC) protocols. The treatments were; Treatment 1 – Control, soft release with no AC deployed (n=10); Treatment 2 – Dogs, two KBDs only used for AC (n=8); Treatment 3 – All - two KBDs and less-lethal ammo used for AC (n=9).

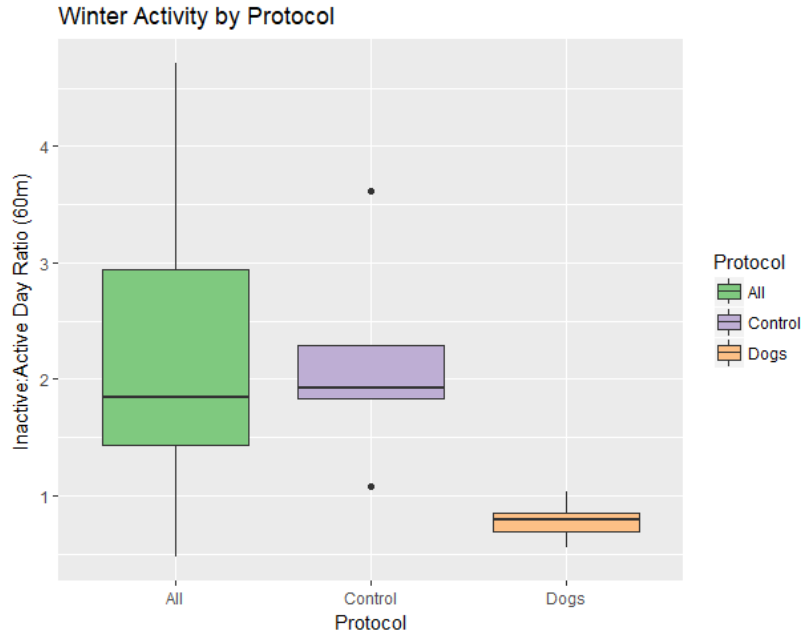


Figure 12. This graph represents winter activity by aversive conditioning (AC) treatment. The treatments were; Treatment 1 – Control, soft release with no AC deployed (n=10); Treatment 2 – Dogs, two KBDs only used for AC (n=8); Treatment 3 – All - two KBDs and less-lethal ammo used for AC (n=9). The figure suggests that females with cubs may be more winter active than females and males, however these results were not statistically significant.

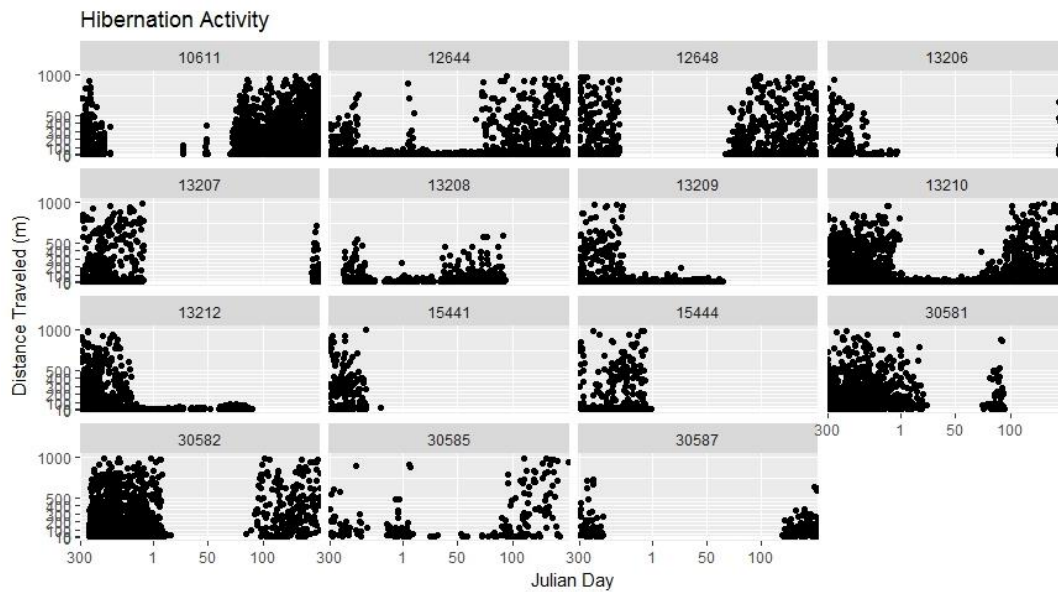


Figure 13. This graph shows winter activity, some bears do not appear to be active at all some appear to have spikes at activity whereas others appear to sustain a low level of activity throughout the winter.

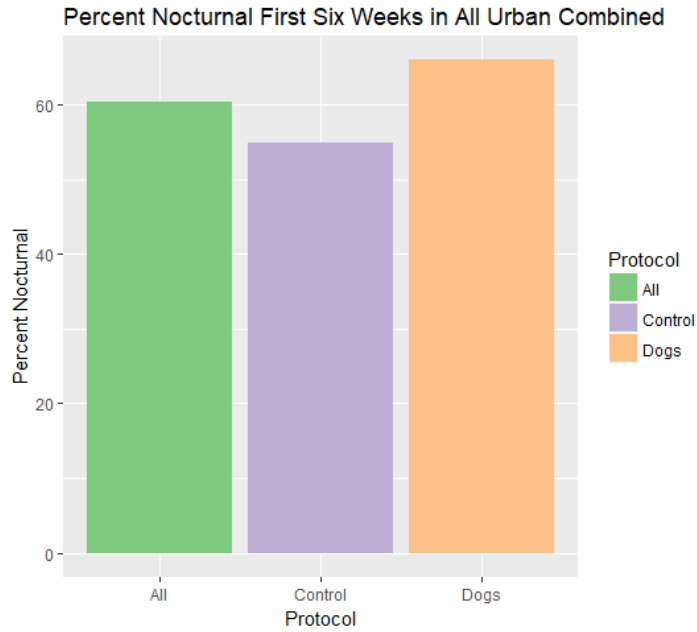


Figure 14. This graph represents the nocturnal behavior by treatment group, suggesting that All and Dogs are more nocturnal than Control, results are not statistically different from each other. The following treatments were used; Treatment 1 – Control, soft release with no AC deployed (n=10); Treatment 2 – Dogs, two KBDs only used for AC (n=8); Treatment 3 – All - two KBDs and less-lethal ammo used for AC (n=9).

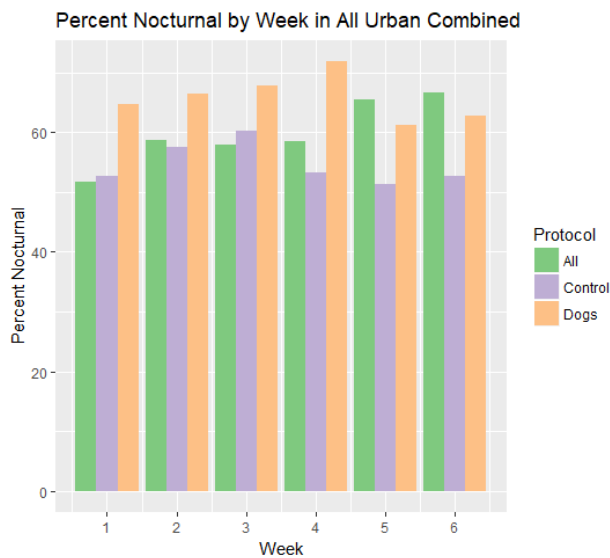


Figure 15. This figure shows the nocturnal behavior during the first six weeks after release. Control is generally lower than All and always lower than Dogs, however comparisons were not statistically significant. The following treatments were used; Treatment 1 – Control, soft release with no AC deployed (n=10); Treatment 2 – Dogs, two KBDs only used for AC (n=8); Treatment 3 – All - two KBDs and less-lethal ammo used for AC (n=9).

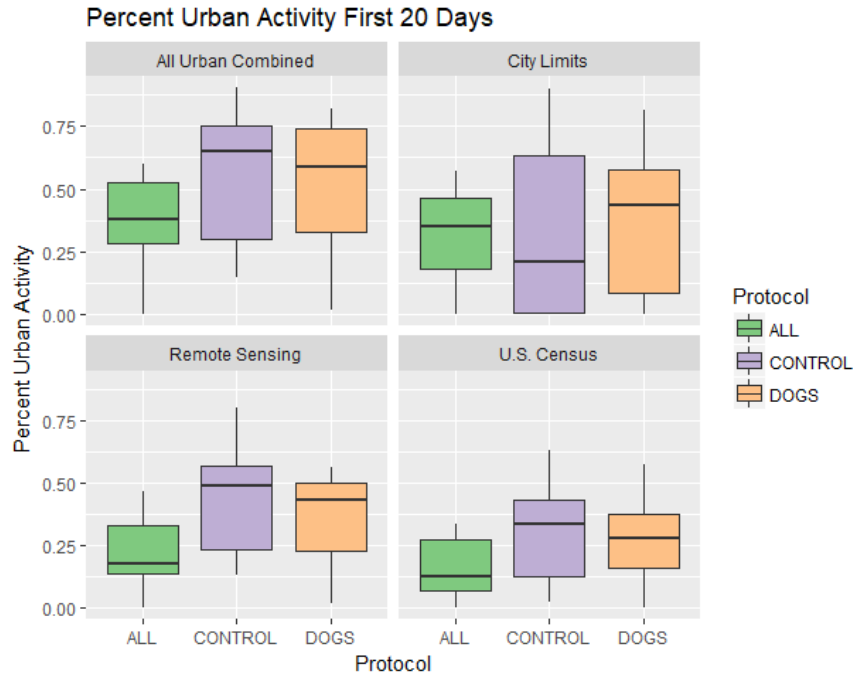


Figure 16. This graphs shows the urban activity by aversive conditioning (AC) treatment for four different urban spatial extents (City Limits, Remote Sensing and U.S. Census and combination of these three definitions). Treatment 1 – Control, soft release with no aversive conditioning (AC) deployed (n=10); Treatment 2 – Dogs, two KBDs only used for AC (n=8); Treatment 3 – All - two KBDs and less-lethal ammo used for AC (n=9). While results were not significant, urban use trends higher for the Control.

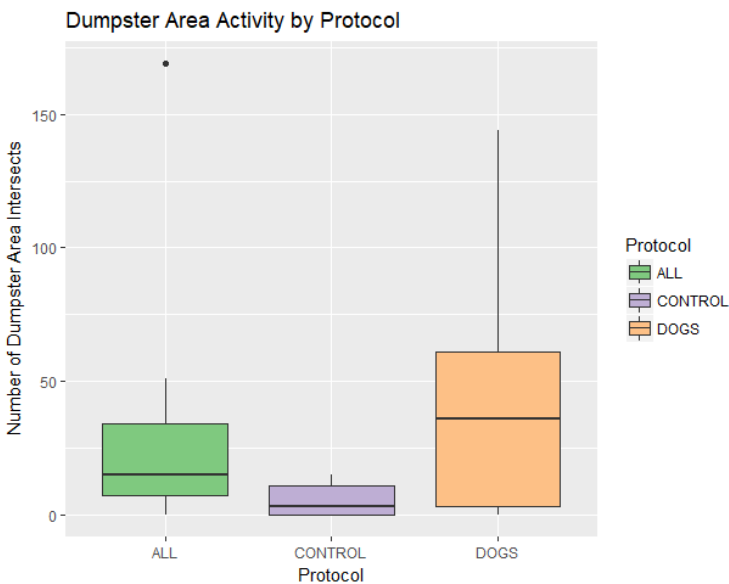


Figure 17. This graph shows reliance on food-waste dumpster by aversive conditioning (AC) treatment. Treatment 1 – Control, soft release with no AC deployed (n=10); Treatment 2 – Dogs, two KBDs only used for AC (n=8); Treatment 3 – All - two KBDs and less-lethal ammo used for AC (n=9). Results between treatments were not statistically significant.

5. Conclusion

Human-wildlife conflict continues to expand as a result of growing human populations and possibly wildlife adapting to living in close proximity to anthropogenic environments (Luniak 2004). Adapting to conditions close to humans is a process that seems to favor generalist species that in turn may be acting as subsidized predators and competitors. These beneficiaries of human-altered landscapes likely have negative impacts on species that are less adaptable, effectively creating ecological losers. Understanding behavioral traits of generalists is a starting point in painting a larger conservation picture, and is especially useful when traits can be identified in an area where conflict is not directly threatening people's livelihoods. Lake Tahoe (CA) is such an area and an ideal study location due to intense human-wildlife conflict experienced by a generally affluent population. This dissertation examined the behavior and ecology of black bears (*Ursus americanus*) living in and around the heavily human-modified landscapes of Lake Tahoe. In so doing, it highlighted novel behavioral changes in bears as a result of human employed stimuli.

Key Findings

Chapters 2-4 of this dissertation summarize my research on bear-human interactions in the Lake Tahoe Basin and include several key findings. My second chapter demonstrated that the spatial definition of "urban" used in analyses has a great effect on how a bear's habitat use is characterized. Thus, urban extents should be defined clearly when describing "urban" behavior. Estimates for use of the urban area were divergent enough that the same bear could be identified as urban under one definition and identified as wild in another. Here, it was clear that after assessing black bear spatial data, bears were not exclusively using the urban envelope. They also could be found in wild areas during large portions of the year, and the majority of bears spent more than 50% of their time in wild areas. While not tested specifically, bears did not appear to sustain themselves exclusively on anthropogenic food sources. Additionally, habitat partitioning was evident between males and females with cubs and between adult males and sub adult males. For example, females with cubs did not use the urban envelope during the first four months of the year, a time when adult males were using the urban envelope heavily. When bears were in the urban areas, they generally preferred habitats that more closely resembled wild land features. Finally, urban usage increased during the time of drought and developed habitats were used more than during the wet year (2011) in this study. This indicated that drought played a role in bears seeking out anthropogenic food sources in urban areas.

In my third chapter, I applied three commonly used home range estimators to study bear distributions and behavior in the Lake Tahoe region. The estimators yielded very different home range sizes. Home range analyses and their use have changed over the years. These analyses were harder to obtain 10-15 years ago, in part because gathering animals' positions was much more arduous in comparison to current GPS technology. Home ranges are now frequently used as an intermediary step in more complex analyses. When using home ranges as part of multi-step

analyses, it is important to be aware that different methods may affect the overall analysis significantly. I also assessed the home range overlap with the urban area. Season was an important covariate for home range overlap and the fall period recorded the greatest overlap. Additionally, during 2014 this was even more pronounced as a result of a drought that affecting the area. Finally, the resource selection function generally reported that known areas of bear conflict were increasing the likelihood of bears spending time in these areas. Females with cubs selected for these areas the strongest.

My fourth chapter focused on testing whether aversive conditioning with Karelian bear dogs had an effect on bear behavior and spatial patterns. I found that bears stayed away longer from the capture and release location when treated with Karelian bear dogs in comparison to the control. Additionally, I assessed whether behavioral proxies considered to place the animal in more conflict with people were influenced through aversive conditioning. I assessed hibernacula selection, winter activity, nocturnality, time spent in the urban area and food dumpster reliance. Bears treated with Karelian bear dogs were more nocturnal, less winter active, and spent less time in urban areas. These changes in bear behavior indicated that Karelian bear dog programs were a valuable addition to programs focused on dealing with bears in the wildlife-urban interface.

Throughout my research I emphasize that there is not one solution to address human-wildlife conflict. Below, I offer recommendations on how to better address bear-human conflict issues in the Lake Tahoe locale and suggest that these approaches may be applicable elsewhere.

Recommendations for the Lake Tahoe context and beyond

As addressing human-wildlife conflict will likely become more and more important in the future, wildlife agencies will likely spend more time fielding concerns from animal advocacy groups, elected officials, and the general public. Dealing with people requires a different personnel skill set for the traditional wildlife biologist. It requires a comfort with media, giving presentations and an understanding of viewpoints that may be more value-based and less science-based. Awareness of divergent values and training on understanding that different values are not categorized as right or wrong is key if agencies want to be considered a partner. Active listening and at least understanding these values is important when looking for community support of inherently divisive policies, such as choosing when to lethally remove nuisance wildlife.

Community support does not come easy; wildlife-human conflict is often a localized event with many stakeholders and divergent opinions. All too often, agency representatives have limited community interaction beyond the meeting they are invited to. Inserting yourself as the agency representative into a situation without understanding the players and perspectives hampers your ability to drive support. For example, at the beginning of my study, most bear traps were closed overnight by concerned citizens. They were likely worried that bears would be euthanized, since trapping bears for depredating activities is a common management practice. Trap tampering by

the public did not stop until a local bear advocacy group addressed this on their Facebook page, and informed the general public that these traps were intended to gather scientific information and not for killing bears. This is a simple example of how a management action became ineffective without communicating with local interests. A much greater effort will be needed to garner support on a bear policy that describes what management action to take when a bear is involved in a certain depredating activity, especially when it involves lethal control.

State resources agencies generally have the legal authority to manage bears, in California this is CDFW. Articulating wildlife management directives for field implementation requires stakeholder feedback to be effective. Moreover, management actions in the field are now even more scrutinized as a result of cell phones with cameras and a direct connection to social media. Executing wildlife management in areas such as Lake Tahoe requires agencies to work with constituents to garner a basis of support. Working closely with constituents may sometimes be perceived by some as giving up some authority, especially when the viewpoints are divergent. Giving up authority may be true in some cases; however in most instances acute bear conflict involving human safety at Lake Tahoe is addressed by local police and sheriff's departments. Their leadership consists of elected officials who are sensitive to bad press and will therefore be hesitant to take action that upsets their constituents.

Local law enforcement is frequently involved when human safety concerns present themselves; e.g., bears enter human occupied homes by breaking down doors and/or windows. Once the bear has left the scene, the human safety concern has abated, and lethal force is no longer considered, despite the fact that the bear in question is likely to repeat this behavior. People who sustain bear damage, such as broken windows or doors, may request a depredation permit. Generally, a Department representative verifies the damage. It is not uncommon that a few days have passed between the actual incident and a trap being delivered at the location in an attempt to catch the offending bear. This is when the trap is even delivered in the first place because people are very concerned about the "neighborhood" and potential conflict with humans. If the trap is delivered and set up, it frequently leads to discussions on which bear should be removed and whether the right bear is killed. Local law enforcement often knows which bears are "bad" and are the first responders in the majority of the cases. With this intelligence, the appropriate management action can be taken without a concern of future public safety issues, additional damage or whether the correct bear was taken. In order to make this work, local law enforcement needs to feel supported in making these unpopular decisions.

A first step to effective community partnership in dealing with wildlife conflict is to develop an agreed upon protocol on bear management. This protocol describes what management action is warranted in specific situations. This approach necessitates a community supported approach on what bear behavior is acceptable and what action to take in clearly defined situations. The community would include all local stakeholders including local law enforcement, local nonprofits and when decisions are made a reference can be made to the agreed policy. This is

especially important when lethal removal is required. Currently, however, bear management is mostly based on assessing individual situations, and similar situations may have different outcomes.

Aversive Conditioning (AC) is no longer programmatically practiced at Lake Tahoe after conclusion of this study. There can be a myriad of benefits to a program involving Karelian bear dogs. AC offers a solution that is in-between “handing out a brochure” on living in bear country and lethal removal. Karelian bear dogs can temporarily reduce nuisance behavior, and are often the only feasibly management strategy if lethal control is not possible. Finally, outreach and education events are much more powerful when dogs are present and they offer fantastic opportunities to engage with local leadership about bear-related concerns.

People visiting Tahoe need to be prepared for bear-human conflict. Every tourist coming to the area should be educated and expect that damage to their belongings will occur if they do not take precautions. There are actually only two roads into the Tahoe Basin and signs on the roads alerting people could be easily implemented. Tahoe has been a tourist destination for many years, however the rental market appears to be very different now. In the age of VRBO and Airbnb, a new wave of tourists naïve to wildlife behavior arrive every weekend. Educating tourists to improve bear-human conflict readiness, coupled with enforcement coordinated by a single point of accountability will drive change. The Tahoe Regional Planning Agency supersedes county and even state boundaries and is uniquely positioned to fulfil this role. TRPA can be the guiding entity to drive a comprehensive Lake Tahoe bear management plan with stakeholder engagement and agreed upon enforcement protocols for people leaving food accessible to bears.

Finally, forget about that “silver bullet” solution, there is no such thing in wildlife management or any complex problem, for that matter. Managing problematic encounters between people and wildlife is complicated, and solutions are multi-disciplinary. Successes can certainly be accomplished, but inevitably there will also be setbacks. The issue will continue to require management attention, and if problems are ignored any progress will quickly deteriorate.

Academic-agency partnerships

Wildlife agencies generally make decisions, at least when possible, on the basis of science. Much of that science comes from work by and partnerships with the academic community. Science is, however, not a fast process, and PhD studies in wildlife ecology often take more than five years. During this time, there likely will be changes in agency personnel, leadership and possible reorganizations. These changes sometimes go hand-in-hand with changes in priorities and science that seemed very relevant five years ago is less relevant today. Due to these fluctuating priorities, it is important for successful academic-agency partnerships that research contracts are established that guarantee completion of the project and detail support to accomplish set objectives. Additionally, shared long term objectives, independent of regime changes, should be

articulated and documented. These observations come in part from my own challenges of completing a project during a period when agency priorities changed.

Future Research

Research traditionally has focused on wild areas and urban areas and refer to wildlife in a binary fashion, either urban or wild. As the world becomes increasingly human-dominated, more wildlife will need to live in areas that they at least share part time with us. As a result, we need to start thinking about urban wildlife in a way that is less binary. Future research should focus on how to adequately refer to wildlife that employ mixed space strategies.

As generalist omnivores and animals using the wildlife-urban interface extensively, black bears may be ecological winners and may have an impact on species with less behavioral plasticity. Some generalists may effectively become subsidized predators as a result of anthropogenic food sources and depress species that are having a hard time living in human-dominated landscapes. In considering key areas for future research, I suggest researchers compare historically occupied species' habitats to current habitat trends to illuminate behavioral plasticity in habitat selection. Additionally, I propose researchers identify which species may potentially be affected by an increased number of subsidized predators. Focusing our conservation efforts on these species may be of high priority.

Specific to bears, I suggest future research identifies important natural food sources and document the sex and age classes utilizing these sources, specifically focusing on the use of wild land resources. During the fall season it was very difficult to capture mature males within the urban envelope, while at the same time sub adult males were captured disproportionately during the entire season. Anecdotally, young males seem to disappear from the urban area after about four years of age, where previously they were omnipresent. Might this be that they need a certain body size before they can actively compete with resident males for wild food sources? Additionally, females with cubs may be disproportionately destructive when caring for cubs. Personal observations suggest that once the cubs disperse, the females appear to spend less time in urban areas than when they are accompanied with cubs. It would be fascinating to understand how resource partitioning and avoidance of male bears by females with cubs could generate more conflict in urban environments.

Bear-human conflict has two components. Traditionally, the "bear" component has been addressed with biological and ecological approaches. The "human" component often remains under-investigated, while the problem clearly requires a multi-disciplinary approach. Social sciences specifically should look into the social carrying capacity of bears and other urban wildlife species. Social carrying capacity in this context would be defined as the level of bear damage and nuisance tolerated by stakeholders before action is demanded. Additionally, an agency could check what kinds of management options would be supported by the local stakeholders. A wider survey beyond traditional stakeholders is important because advocacy

groups may have a disproportionate amount of sway, while potentially representing a small cross section of the population.

Taken together, these suggestions for future research emphasize the biological and social challenges we need to address if we are to make progress in our management of human-wildlife conflict and coexistence.

Literature Cited

- Adams, C. E. 2016. Urban wildlife management. CRC press.
- Adams, L. W. 2005. Urban wildlife ecology and conservation: a brief history of the discipline. *Urban Ecosystems* 8:139–156.
- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.
- Alt, G. L., F. W. Alt, and J. S. Lindzey. 1976. Home range and activity patterns of black bears in northeastern Pennsylvania. *Proceedings of the Northeast Section of the Wildlife Society* 33:45–56.
- Alt, G. L., G. J. Matula, F. W. Alt, and J. S. Lindzey. 1980. Dynamics of home range and movements of adult black bears in northeastern Pennsylvania. *Ursus* 4:131–136.
- Amstrup, S. C., and J. Beecham. 1976. Activity patterns of radio-collared black bears in Idaho. *The Journal of Wildlife Management* 40:340–348.
- Artinuzzi, S. M., V. C. R. Adloff, J. V. H. Iggins, D. P. H. Elmers, and A. J. P. Lantinga. 2013. Key areas for conserving United States' biodiversity likely threatened by future land use change. *Ecosphere* 4(5):58.
- Atwood, T. C., and S. W. Breck. 2012. Carnivores, conflict, and conservation: defining the landscape of conflict. *Page Species, Conservation, and Management*.
- Baker, P. J., and S. Harris. 2007. Urban mammals : what does the future hold? An analysis of the factors affecting patterns of use of residential gardens in Great Britain. *Mammal Review* 37:297–315.
- Baldwin, R. A., and L. C. Bender. 2010. Denning chronology of black bears in Eastern Rocky Mountain National Park, Colorado. *Western North American Naturalist* 70:48–54.
- Baruch-Mordo, S., S. W. Breck, K. R. Wilson, and J. Broderick. 2011. The carrot or the stick? Evaluation of education and enforcement as management tools for human-wildlife conflicts. *PLoS ONE* 6.
- Baruch-Mordo, S., S. W. Breck, K. R. Wilson, and D. M. Theobald. 2008. Spatiotemporal distribution of black bear-human conflicts in Colorado, USA.

The Journal of Wildlife Management 72:1853–1862.

- Baruch-Mordo, S., C. T. Webb, S. W. Breck, and K. R. Wilson. 2013. Use of patch selection models as a decision support tool to evaluate mitigation strategies of human-wildlife conflict. *Biological Conservation* 160:263–271.
- Baruch-Mordo, S., K. R. Wilson, D. L. Lewis, J. Broderick, J. S. Mao, and S. W. Breck. 2014. Stochasticity in natural forage production affects use of urban areas by black bears: Implications to management of human-bear conflicts. *PLoS ONE* 9.
- Beasley, J. C., T. L. Devault, M. I. Retamosa, and O. E. Rhodes Jr. 2007. A hierarchical analysis of habitat selection by raccoons in Northern Indiana. *Journal of Wildlife Management* 71:1125–1133.
- Beausoleil, R. A. 1999. Population and spatial ecology of the Louisiana black bear in a fragmented bottomland hardwood forest. University of Tennessee, Knoxville, Tennessee, USA.
- Beckmann, J. P., and J. Berger. 2003a. Using black bears to test ideal-free distribution models experimentally. *Journal of Mammalogy* 84:594–606.
- Beckmann, J. P., and J. Berger. 2003b. Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. *Journal of Zoology*:207–212.
- Beckmann, J. P., and C. W. Lackey. 2008. Carnivores, urban landscapes, and longitudinal studies: a case history of black bears. *Human–Wildlife Conflicts* 2:168–174.
- Beckmann, J. P., C. W. Lackey, and J. Berger. 2004. Evaluation of deterrent techniques and dogs to alter behavior of “nuisance” black bears. *Wildlife Society Bulletin* 32:1141–1146.
- Beecham, J. J., and J. Rohlman. 1994. A shadow in the forest: Idaho’s black bear. Northwest Naturalist Books, Moscow.
- Beeman, L. E. 1975. Population characteristics, movement, and activities of the black bear (*Ursus americanus*). University of Tennessee, Knoxville, Tennessee, USA.
- Belant, J. L. 2002. Sampling considerations for American black and brown bear home range and habitat use. *Ursus* 13:299–315.

- Ben-David, M., K. Titus, and L. R. Beier. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia* 138:465–474.
- Benson, J. F., and M. J. Chamberlain. 2007. Space use and habitat selection by female Louisiana black bears in the Tensas River Basin of Louisiana. *Journal of Wildlife Management* 71:117–126.
- Benson, J. F., J. A. Sikich, and S. P. D. Riley. 2016. Individual and population level resource selection patterns of mountain lions preying on mule deer along an urban-wildland gradient. *PLoS ONE* 11:1–16.
- Beringer, J. 1986. Habitat use and response to roads by black bears in Harmon Den, Pisgah National Forest, North Carolina. University of Tennessee, Knoxville, Tennessee, USA.
- Bingham, G., R. Bishop, M. Brody, D. Bromley, E. (Toby) Clark, W. Cooper, R. Costanza, T. Hale, G. Hayden, S. Kellert, R. Norgaard, B. Norton, J. Payne, C. Russell, and G. Suter. 1995. Issues in ecosystem valuation: improving information for decision making. *Ecological Economics* 14:73–90.
- Bivand, R., and L.-K. Nicholas. 2016. Maptools: tools for reading and handling spatial objects.
- Bivand, R., and E. J. Pebesma. 2018. Package “sp.”
- Bivand, R. S., and C. Rundel. 2017. rgeos: interface to geometry engine - open source (GEOS).
- Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* 75:1393–1405.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Breck, S. W., N. Lance, and P. Callahan. 2006. A shocking device for protection of concentrated food sources from black bears. *Wildlife Society Bulletin* 34:23–26.
- Brody, A. J. 1984. Habitat use by black bears in relation to forest management in Pisgah National Forest, North Carolina. University of Tennessee, Knoxville, Tennessee, USA.

- Brody, A. J., and M. R. Pelton. 1989. Effects of roads on black bear movements in western North Carolina. *Wildlife Society Bulletin* 17:5–10.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346–352.
- Cadenasso, M. L., S. T. A. Pickett, and K. Schwarz. 2007. Spatial heterogeneity in urban ecosystems: Reconceptualizing land cover and a framework for classification. *Frontiers in Ecology and the Environment* 5:80–88.
- Cahill, S., F. Llimona, L. Cabañeros, and F. Calomardo. 2012. Characteristics of wild boar (*Sus scrofa*) habituation to urban areas in the collserola natural park (Barcelona) and comparison with other locations. *Animal Biodiversity and Conservation* 35:221–233.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.
- Carr, P. C. 1983. Habitat utilization and seasonal movements of black bears in the Great Smoky Mountains National Park. University of Tennessee, Knoxville, Tennessee, USA.
- Carter, N. H., D. G. Brown, D. R. Etter, and L. G. Visser. 2010. American black bear habitat selection in northern Lower Peninsula Michigan, USA, using discrete-choice modeling. *Ursus* 21:57–71.
- Chaulk, K. 2001. Black bears (*Ursus americanus*) in northeastern Labrador. Acadia University, Wolfville, Nova Scotia, Canada.
- Ciarniello, L. M., M. S. Boyce, D. R. Seip, and D. C. Heard. 2009. Comparison of grizzly bear demographics in wilderness mountains versus a plateau with resource development. *Wildlife Biology* 15:247–265.
- Clark, J. E., F. T. Van Manen, and M. R. Pelton. 2002. Correlates of success for on-site releases of nuisance black bears in Great Smoky Mountains National Park 30:104–111.
- Clevenger, A. P. 1986. Habitat and space utilization of black bears in Cherokee National Forest, Tennessee. University of Tennessee, Knoxville, Tennessee, USA.
- Cohn, J. P. 2005. Urban wildlife. *BioScience* 55:201–205.

- Coleman, T. H., C. C. Schwartz, K. a. Gunther, and S. Creel. 2013. Human dimensions grizzly bear and human interaction in Yellowstone National Park: An evaluation of bear management areas. *Journal of Wildlife Management* 77:1311–1320.
- Comeau, N. A. 2013. Evaluation of two methods of aversive conditioning on nuisance activity levels of New Hampshire black bear.
- Conover, M. R. 1997. Wildlife management by metropolitan residents in the United States, practices, perceptions, costs and values. *Wildlife Society Bulletin* 25:306–311.
- Cooper, A., and J. J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. *Ecology* 80:566–575.
- Costello, C. M. 1992. Black bear habitat ecology in the central Adirondacks as related to food abundance and forest management. State University of New York, Syracuse, New York, USA.
- Costello, C. M. 2008. The spatial ecology and mating system of black bears (*Ursus americanus*) in New Mexico. Montana State University, Bozeman, Montana, USA.
- Costello, C. M., S. I. Cain, R. M. Nielson, C. Servheen, and C. C. Schwartz. 2013. Response of American black bears to the non-motorized expansion of a road corridor in Grand Teton National Park. *Ursus* 24:54–69.
- Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* 16:488–502.
- Czetwertynski, S. M., M. S. Boyce, and F. K. Schmiegelow. 2007. Effects of hunting on demographic parameters of American black bears. *Ursus* 18:1–18.
- D'Eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. *Journal of Applied Ecology* 43:383–388.
- DeBruyn, T. D. 1997. Habitat use, food habits and population characteristics of female black bears in the central upper peninsula of Michigan: a geographic information system approach. Michigan Technological University, Houghton, Michigan, USA.
- Decker, D. J., and L. C. Chase. 1997. Human dimensions of living with wildlife - a management challenge for the 21st century. *Wildlife Society Bulletin* 25:788–

795.

- Dellinger, J. A., C. Proctor, T. D. Steury, M. J. Kelly, and M. R. Vaughan. 2013. Habitat selection of a large carnivore, the red wolf, in a human-altered landscape. *Biological Conservation* 157:324–330.
- DeStefano, S., and R. M. DeGraaf. 2003. Exploring the ecology of suburban wildlife. *Frontiers in Ecology and the Environment*:95–101.
- Dickson, B. G., and P. Beier. 2002. Home-range and habitat selection by adult cougars in southern California. *The Journal of Wildlife Management* 66:1235–1245.
- Ditchkoff, S. S., S. T. Saalfeld, and C. J. Gibson. 2006. Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosystems* 9:5–12.
- Ditmer, M. A., T. E. Burk, and D. L. Garshelis. 2015. Do innate food preferences and learning affect crop raiding by American black bears? *Ursus* 26:40–52.
- Dobey, S., D. V Masters, B. K. Scheick, J. D. Clark, M. R. Pelton, and M. E. Sunquist. 2005. Ecology of Florida black bears in the Okefenokee-Osceola ecosystem. *Wildlife Monographs* 158:1–41.
- Duquette, J., J. L. Belant, W. M. Clay, N. Fowler, B. W. Waller, D. E. Beyer, N. J. Svoboda, S. L. Simek, and J. Beringer. 2016. Black bear functional resource selection relative to intraspecific competition and human risk. *Canadian Field-Naturalist*:36.
- Early, D. A. 2010. Intraspecific black bear spatial patterns and interactions at a small spatio-temporal scale. Humboldt State University, Arcata, California, USA.
- Edwards, A. S. 2002. Status of the black bear in southwestern Alabama. University of Tennessee, Knoxville, Tennessee, USA.
- Ellis, E. C., K. K. Goldewijk, S. Siebert, D. Lightman, and N. Ramankutty. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* 19:589–606.
- Etter, D. R. 2002. Black bear population management techniques. Michigan.
- Eubanks, A. L. 1976. Movements and Activities of the Black Bear (*Ursus americanus*) in the Great Smoky Mountains National Park.

- Evans, M. J., T. A. G. Rittenhouse, J. E. Hawley, and P. W. Rego. 2017. Black bear recolonization patterns in a human-dominated landscape vary based on housing: new insights from spatially explicit density models. *Landscape and Urban Planning* 162:13–24.
- Eveland, J. F. 1973. Population dynamics, movements, morphology, and habitat characteristics of black bears in Pennsylvania. Pennsylvania State University, State College, Pennsylvania, USA.
- Fersterer, P., D. L. Nolte, G. J. Ziegltrum, and H. Gossow. 2001. Effect of feeding stations on the home ranges of American black bears in western Washington. *Ursus* 12:51–54.
- Fieberg, J. 2007. Kernel density estimators of home range: smoothing and the autocorrelation red herring. *Ecology* 88:1059–1066.
- Fieberg, J., and L. Börger. 2012. Could you please phrase “home range” as a question? *Journal of Mammalogy*:890–902.
- Fimbel, C. C. 1990. Characteristics of black bears in a residential area of New Jersey. The State University of New Jersey, New Brunswick, New Jersey, USA.
- Forman, R. T. T., D. S. Friedman, D. Fitzhenry, J. D. Martin, A. S. Chen, and L. E. Alexander. 1997. Ecological effects of roads; Toward three summary indices and an overview for North America. Pages 39–54 *Habitat Fragmentation & Infrastructure*.
- Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6.
- Fuller, D. 1993. Black bear population dynamics in western Massachusetts. University of Massachusetts, Amhurst, USA.
- Fuller, T. K., and L. B. Keith. 1980. Summer ranges, cover-type use, and denning of black bears near Fort McMurray, Alberta. *Canadian Field-Naturalist* 94:80–83.
- Gagolewski, M. 2015. Package ‘stringi’: Character String Processing Facilities.
- Gaines, W. L., A. L. Lyons, J. F. Lehmkuhl, and K. J. Raedeke. 2005. Landscape evaluation of female black bear habitat effectiveness and capability in the North Cascades, Washington. *Biological Conservation* 125:411–425.

- Garneau, D. E., T. Boudreau, M. Keech, and E. Post. 2008. Habitat use by black bears in relation to conspecifics and competitors. *Mammalian Biology* 73:48–57.
- Garner, N. P. 1986. Seasonal movements, habitat selection, and food habits of black bears (*Ursus americanus*) in Shenandoah National Park, Virginia. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.
- Garris, R. 1983. Habitat utilization and movement ecology of black bears in Cherokee National Forest. University of Tennessee, Knoxville, Tennessee, USA.
- Garrison, E. P., J. W. McCown, and M. K. Oli. 2007. Reproductive ecology and cub survival of Florida black bears. *Journal of Wildlife Management* 71:720–727.
- Garshelis, D. L., S. Baruch-Mordo, A. Bryant, K. A. Gunther, and K. Jerina. 2017. Is diversionary feeding an effective tool for reducing human – bear conflicts? Case studies from North America and Europe. *Ursus* 28:31–55.
- Garshelis, D. L., and H. Hristienko. 2006. State and provincial estimates of American black bear numbers versus assessments of population trend. *Ursus* 17:1–7.
- Garshelis, D. L., and C. R. McLaughlin. 1995. Review and evaluation of breakaway devices for bear radiocollars. Pages 459–465 *A Selection of Papers from the tenth International Conference on Bear Research and Management*, Fairbanks, Alaska, July 1995, and Mora, Sweden, September 1995.
- Garshelis, D. L., and K. V Noyce. 2006. Discerning biases in a large scale mark–recapture population estimate for black bears. *Journal of Wildlife Management* 70:1634–1643.
- Garshelis, D. L., and M. R. Pelton. 1980. Activity of black bears in the Great Smoky Mountains National Park. *Journal of Mammalogy* 61:8–19.
- Gehrt, Stanley, D., and S. P. D. Riley. 2010. Urban carnivores: Ecology, conflict, and conservation. Page (B. L. Cypher, Ed.). Baltimore, MD.
- George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. *Biological Conservation*:107–117.
- Gilbert, F. F. 1982. Public attitudes toward urban wildlife: A pilot study in Guelph,

- Ontario. Wildlife Society Bulletin 10:245–253.
- Gillin, C. M., I. Chestin, P. Semchenkov, and J. Claar. 1997. Management of bear-human conflicts using Laika dogs. Pages 133–137 A Selection of Papers from the Ninth International Conference on Bear Research and Management, Grenoble, France, October 1992.
- Gillin, C. M., F. M. Hammond, and C. M. Peterson. 1994. Evaluation of an aversive conditioning technique used on female grizzly bears in the Yellowstone ecosystem. Pages 503–212 International Conference on Bear Research and Management. Missoula, Montana.
- Goodrich, J. M., and J. Berger. 1994. Winter recreation and hibernating black bears *Ursus americanus*. *Biological Conservation* 67:105–110.
- Gore, M. L., B. A. Knuth, P. D. Curtis, and J. E. Shanahan. 2006. Education programs for reducing American black bear–human conflict: indicators of success? *Ursus* 17:75–80.
- Graber, D. M., and M. White. 1978. Management of black bears and humans in Yosemite National Park. *Transaction Western Section Wildlife Society* 14:42–51.
- Graber, D. M., and M. White. 1983. Black bear food habits in Yosemite National Park. *International Conference on Bear Research and Management* 5:1–10.
- Graham, K., A. P. Beckerman, and S. Thirgood. 2005. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation*:159–171.
- Greer, S. Q. 1987. Home range, habitat use, and food habits of black bears in south-central Montana. Montana State University, Bozeman, Montana, USA.
- Grenfell, W. E., and A. J. Brody. 1986. Black bear habitat use in Tahoe National Forest, California. Pages 65–72 *Bears: Their Biology and Management*, Vol. 6, A selection of papers from the sixth international conference on bear research and management, February 1983. Grand Canyon, Arizona, USA.
- Grinder, M. I., and P. R. Krausman. 2001. Home range, habitat use, and nocturnal activity of coyotes in an urban environment. *The Journal of Wildlife Management* 65:887–898.
- Grubbs, S. E., and P. R. Krausman. 2009. Observations of coyote-cat interactions. *The Journal of Wildlife Management* 73:683–685.

- Hammond, F. M. 2002. The effects of resort and residential development on black bears in Vermont.
- Harris, A. S., G. C. Smith, B. Y. S. Harris, and G. C. Smith. 1987. Demography of two urban fox (*Vulpes vulpes*) populations. *Journal of Animal Ecology* 24:75–86.
- Harris, S. 1981. An estimation of the number of foxes (*Vulpes vulpes*) in the city of Bristol, and some possible factors affecting their distribution. *Journal of Applied Ecology* 18:455–465.
- Hayne, D. W. 1949. Calculation of size of home range. *Journal of Mammalogy* 30:1–18.
- Hechtel, J. L. 1991. Population dynamics of black bear populations, Fort Wainwright, Alaska.
- Hellgren, E. C. 1988. Ecology and physiology of a black bear (*Ursus americanus*) population in Great Dismal Swamp and reproductive physiology in the captive female black bear. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.
- Hellgren, E. C., D. W. Carney, N. P. Garner, and M. R. Vaughan. 1988. Use of breakaway cotton spacers on radio collars. *Wildlife Society Bulletin* 16:216–218.
- Hellgren, E. C., and M. R. Vaughan. 1987. Home range and movements of winter-active black bears in the Great Dismal Swamp. Pages 227–234 *International Conference on Bear Research and Management*. Williamsburg, Virginia and Plitvice Lakes, Yugoslavia.
- Hellgren, E. C., M. R. Vaughan, and F. Stauffer. 1991. Macrohabitat Use by Black Bears in a Southeastern Wetland 55:442–448.
- Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley, and D. McDonald. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology* 74:455–463.
- Herrero, S. 1980. Social behaviour of black bears at a garbage dump in Jasper National Park. Pages 54–70 *Bears: Their Biology and Management, Vol. 5, A Selection of Papers from the Fifth International Conference on Bear Research and Management, February 1980*. Madison, Wisconsin, USA.

- Heyden, M. V., and E. C. Meslow. 1999. Habitat selection by female black bears in the central Cascades of Oregon. *Northwest Science* 73:283–294.
- Higgins, J. . 1997. Survival, home range and spatial relationships of Virginia’s exploited black bear population. *Population (English Edition)*:100.
- Hijmans, R. E. 2015. *Geographic data analysis and modeling*.
- Hiller, T. L., J. L. Belant, J. Beringer, and A. J. Tyre. 2015. Resource selection by recolonizing American black bears in a fragmented forest landscape. *Ursus* 26:116–128.
- Hirsch, J. G., L. C. Bender, and J. B. Haufler. 1999. Black bear, *Ursus americanus*, movements and home ranges on Drummond Island, Michigan. *The Canadian Field-Naturalist* 113:221–225.
- Hisano, M., E. G. Raichev, S. Peeva, H. Tsunoda, C. Newman, R. Masuda, D. M. Georgiev, and Y. Kaneko. 2016. Comparing the summer diet of stone martens (*Martes foina*) in urban and natural habitats in Central Bulgaria. *Ethology Ecology and Evolution* 28:295–311.
- Hogan, N. F. 1984. Home range and habitat preferences of female black bears (*Ursus americanus*) in the San Bernardino Mountains of southern California. California State Polytechnic University, Pomona, California, USA.
- Hojsgaard, S., and U. Halekoh. 2014. Package ‘doBy’: groupwise Statistics, LSmeans, linear contrasts, utilities.
- Holm, G. W., F. G. Lindzey, and D. S. Moody. 1999. Interactions of sympatric black and grizzly bears in northwest Wyoming. *Ursus* 11:99–108.
- Homer, C. G., J. A. Dewitx, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States—representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing* 81:345–354.
- Homstol, L. 2011. Applications of learning theory to human-bear conflict: the efficacy of aversive conditioning and conditioned taste aversion. University of Alberta, Edmonton, Alberta, Canada.
- Hopkins, J. B., and S. T. Kalinowski. 2013. The fate of transported American black bears in Yosemite National Park. *Ursus* 24:120–126.

- Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. *Ecology* 88:2354–2363.
- Hunt, C. 1984. Vol. 1. Behavioral responses of bears to tests of repellents deterrents and aversive conditioning Vol. 2. Deterrents aversive conditioning and other practices: An annotated bibliography to aid in bear management. University of Montana, Missoula, Montana, USA.
- Immell, D., D. H. Jackson, and M. C. Boulay. 2013. Denning ecology of American black bears in the Cascade Mountains of western Oregon. *Ursus* 24:1–12.
- Immell, D., D. H. Jackson, and M. C. Boulay. 2014. Home-range size and subadult dispersal of black bears in the Cascade Range of western Oregon. *Western North American Naturalist* 74:343–348.
- Irwin, L. L., and F. M. Hammond. 1985. Managing black bear habitats for food items in Wyoming. *Wildlife Society Bulletin* 13:477–483.
- Jansen, A., E. Luge, B. Guerra, P. Wittschen, A. D. Gruber, C. Loddenkemper, T. Schneider, M. Lierz, D. Ehlert, B. Appel, K. Stark, and K. Nöckler. 2007. Leptospirosis in urban wild boars, Berlin, Germany. *Emerging Infectious Diseases* 13:739–742.
- Jessup, D. A., W. A. Clark, and M. A. Fowler. 2001. *Wildlife restraint handbook*, California Fish and Game. 8th edition.
- Johnson, B. B., and J. Sciascia. 2013. Views on black bear management in New Jersey. *Human Dimensions of Wildlife* 184:249–262.
- Johnson, H. E., S. W. Breck, S. Baruch-Mordo, D. L. Lewis, C. W. Lackey, K. R. Wilson, J. Broderick, J. S. Mao, and J. P. Beckmann. 2015. Shifting perceptions of risk and reward: dynamic selection for human development by black bears in the western United States. *Biological Conservation* 187:164–172.
- Johnson, K. G., and M. R. Pelton. 1980. Environmental relationships and the denning period of black bears in Tennessee. *Journal of Mammalogy* 61:653–660.
- Jones, J. 2015. California’s most significant droughts: comparing historical and recent conditions.
- Jones, M. D., and M. R. Pelton. 2003. Female American black bear use of managed forest and agricultural lands in coastal North Carolina. *Ursus*

14:188–197.

- Jones, M. D., A. N. Tri, J. W. Edwards, and H. Spiker. 2015. Home-range dynamics of female *Ursus americanus* (Pallas) (American black bear) in a recovering population in western Maryland. *Notheastern Naturalist* 22:830–841.
- Jonkel, C. J., and I. Cowan. 1971. The black bear in the spruce-fir forest. *Wildlife Monographs* 27:6–54.
- Joshi, A. R., D. L. Garshelis, and J. L. D. Smith. 1995. Home ranges of sloth bears in Nepal: Implications for conservation 59:204–214.
- Karelus, D. L., J. W. McCown, B. K. Scheick, M. van de Kerk, and M. K. Oli. 2016. Home ranges and habitat selection by black bears in a newly colonized population in Florida. *Southeastern Naturalist* 15:346–364.
- Kasworm, W. F., and T. L. Manley. 1989. Road and trail influences on grizzly bears and black bears in northwest Montana. *Bears: Their Biology and Management* 8:79–84.
- Kellert, S. R. 1984. Urban American perceptions of animals and the natural environment. *Urban Ecology* 8:209–228.
- Kelleyhouse, D. G. 1980. Habitat Utilization by Black Bears in Northern California. Pages 221–227 *Bears : Their Biology and Management , Vol . 4 , A Selection of Papers from the Fourth International Conference on Bear Research and Management. Kalispell , Montana , USA.*
- Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Page (J. M. Marzluff, Ed.) *Radio Tracking and Animal Populations. Academic Press Inc., San Diego.*
- Kie, J. G., J. Matthiopoulos, J. Fieberg, R. A. Powell, F. Cagnacci, M. S. Mitchell, J.-M. Gaillard, and P. R. Moorcroft. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*:2221–2231.
- Kilpatrick, H. J., A. M. LaBonte, J. S. Barclay, and G. Warner. 2004. Assessing strategies to improve bowhunting as an urban deer management tool. *Wildlife Society Bulletin* 32:1177–1184.
- Klenner, W. 1987. Seasonal movements and home range utilization patterns of the

- black bear, *Ursus americanus*, in western Manitoba. *The Canadian Field-Naturalist* 101:558–568.
- Koch, D. B. 1994. Biopolitical management of mountain lions, tule elk, and black bears in California. *International Conference on Bear Research and Management* 9:561–566.
- Koehler, G. M., and D. J. Pierce. 2003. Black bear home-range sizes in Washington: climatic, vegetative, and social influences. *Journal of Mammalogy* 84:81–91.
- Koval, M. H., and A. G. Mertig. 2004. Attitudes of the Michigan public and wildlife agency personnel toward lethal wildlife management. *Wildlife Society Bulletin* 32:232–243.
- Krausman, P. R. 1999. Some basic principles of habitat use. *Grazing Behavior of Livestock and Wildlife*:85–90.
- Kuznetsova, A. B., P. B. Brockhoff, and R. H. B. Christensen. 2016. lmerTest: tests in linear mixed effects models.
- Lackey, C. W., and R. A. Beausoleil. 2010. Tenth Western Black Bear Workshop. Page 191 in C. W. Lackey and R. A. Beausoleil, editors. *The Changing Climate for Bear Conservation and Management in Western North America*. Reno.
- Lafon, N. W., S. L. McMullin, and D. E. Steffen. 2003. Knowledge and opinions of stakeholders of black bear management in Virginia. *Ursus* 14:55–64.
- Landers, J., R. J. Hamilton, S. A. Johnson, and R. Larry. 1979. Foods and habitat of black bears in southeastern North Carolina. *The Journal of Wildlife Management* 43:143–153.
- Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* 79:1401–1409.
- Laver, P. N., and M. J. Kelly. 2008. A critical review of home range studies. *Journal of Wildlife Management* 72:290–298.
- Lecount, A. L. 1980. Some aspects of black bear ecology in the Arizona chaparral. *Bears : Their Biology and Management* 4:175–179.
- LeCount, A. L. 1983. Denning ecology of black bears in Central Arizona. *Bears:*

- Their Biology and Management 5:71–78.
- Lee, D. J., and M. R. Vaughan. 2004. Black bear family breakup in western Virginia. *Northeastern Naturalist* 11:111–122.
- Leigh, J. 2007. Effects of aversive conditioning on behavior of nuisance Louisiana black bears. Louisiana State University.
- Leopold, A. 1933. Game management. Charles Scribner's Sons, New York.
- Lewis, D. L., S. Baruch-Mordo, K. R. Wilson, S. W. Breck, J. S. Mao, and J. Broderick. 2015. Foraging ecology of black bears in urban environments: guidance for human-bear conflict mitigation. *Ecosphere* 6:1–18.
- Lewis, J. S., J. L. Rachlow, J. S. Horne, E. O. Garton, W. L. Wakkinen, J. Hayden, and P. Zager. 2011. Identifying habitat characteristics to predict highway crossing areas for black bears within a human-modified landscape. *Landscape and Urban Planning* 101:99–107.
- Lindzey, F. G., and E. C. Meslow. 1977. Home range and habitat use by black bears in southwestern Washington. *The Journal of Wildlife Management* 41:413–425.
- Lukasik, V. M., and S. M. Alexander. 2012. Spatial and temporal variation of coyote (*Canis latrans*) diet in Calgary, Alberta. *Cities and the Environment (CATE)* 4.
- Luke, V. 2013. Black bear encounters in the wildland-urban interface of upstate South Carolina. Clemson University.
- Luniak, M. 2004. Synurbization - adaptation of animal wildlife to urban development. Pages 50–55 in Shaw et al., editor. *Proceedings 4th International Urban Wildlife Symposium*.
- Lyda, S. B., E. C. Hellgren, and D. M. Leslie. 2007. Diurnal habitat selection and home-range size of female black bears in the Ouachita Mountains of Oklahoma. *Proc. Okla. Acad. Sci.* 87:55–64.
- Lyons, A. J. 2005. Activity patterns of urban American black bears in the San Gabriel Mountains of southern California. *Ursus* 16.
- Lyons, A. J., W. C. Turner, and W. M. Getz. 2013. Home range plus: a space-time characterization of movement over real landscapes. *Movement Ecology* 1.
- Lyons, A. L., W. L. Gaines, and C. Servheen. 2003. Black bear resource selection

- in the northeast Cascades, Washington. *Biological Conservation* 113:55–62.
- Mace, R. D., and J. S. Waller. 1997. Spatial and temporal interaction of male and female grizzly bears in northwestern Montana. *Journal of Wildlife Management* 61:39–52.
- Mack, J. A. 1988. Ecology of black bears on the Beartooth Face, south-central Montana. Montana State University, Bozeman, Montana, USA.
- Madison, J. S. 2008. Yosemite National Park: The continuous evolution of human – black bear conflict management. *Human-Wildlife Conflicts* 2:160–167.
- Maehr, D. S. 1996. Comparative ecology of bobcat, black bear, and Florida panther in south Florida. University of Florida, Gainesville, Florida, USA.
- Maehr, D. S., J. S. Smith, M. W. Cunningham, M. E. Barnwell, J. L. Larkin, and M. A. Orlando. 2003. Spatial characteristics of an isolated Florida black bear population. *Southeastern Naturalist* 2:433–446.
- Manen, F. T. Van. 1994. Black bear habitat use in Great Smoky Mountains National Park. University of Tennessee, Knoxville, Tennessee, USA.
- Manfredo, M., T. Teel, and A. Bright. 2003. Why are public values toward wildlife changing? *Human Dimensions of Wildlife* 8:287–306.
- Manly, B. F. J., L. L. McDonald, and D. L. Thomas. 1993. Examples of the use of resource selection functions. Pages 14–31 *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Chapman & Hall, London.
- Manville, A. M. I. 1983. Human impact on the black bear in Michigan's lower peninsula. *Bears : Their Biology and Management* 5:20–33.
- Marchington, F. B. 1995. Movement ecology of black bears in a fragmented bottomland hardwood habitat in Louisiana. University of Tennessee, Knoxville, Tennessee, USA.
- Massé, S., C. Dussault, C. Dussault, and J. Ibarzabal. 2014. How artificial feeding for tourism-watching modifies black bear space use and habitat selection. *The Journal of Wildlife Management* 78:1228–1238.
- Massopust, J. L. 1984. Black bear homing tendencies, response to being chased by hunting dogs, reproductive biology, denning behavior, home range, diel movements, and habitat use in northern Wisconsin. University of Wisconsin, Stevens Point, Wisconsin, USA.

- Matt, C. 2012. 4th International Human-Bear Conflicts Workshop Summary. Page 85.
- Matthews, S. M., J. J. Beecham, H. Quigley, S. S. Greenleaf, and H. M. Leithead. 2006. Activity patterns of American black bears in Yosemite National Park. *Ursus* 17:30–40.
- Mayer, K. E., and W. F. Laudenslayer. 1988. A guide to wildlife habitats, State of California. Sacramento.
- Mazaika, K. 2013. Beyond the bear necessities: a mixed methods analysis of the conflicts arising in human-bears encounters. George Mason University.
- Mazur, R. L. 2010. Does aversive conditioning reduce human–black bear conflict? *The Journal of Wildlife Management* 74:48–54.
- Mccullough, D. R. 1982. Behavior, bears, and humans. *Wildlife Society Bulletin* 10:27–33.
- Mckee, J. K., P. W. Sciulli, C. D. Fooce, and T. A. Waite. 2003. Forecasting global biodiversity threats associated with human population growth. *Biological Conservation* 115:161–164.
- McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. *BioScience* 52.
- McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127:247–260.
- McKinney, M. L. 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems* 11:161–176.
- Merkle, J. A. 2011. Human-black bear interactions in Missoula, Montana. University of Montana, Missoula.
- Merkle, J. A., H. S. Robinson, P. R. Krausman, and P. Alaback. 2013. Food availability and foraging near human developments by black bears. *Journal of Mammalogy* 94:378–385.
- Miller, J. R., and R. J. Hobbs. 2002. Conservation where people live and work. *Conservation Biology* 16:330–337.
- Miller, S. D., E. F. Becker, and W. B. Ballard. 1987. Black and brown bear density estimates using modified capture-recapture techniques in Alaska. *Bears : Their Biology and Management* 7:23–35.

- Mitchell, B. R. 2007. Comparison of programs for fixed kernel home range analysis. Page wildlife.org.
- Mitchell, M. S., and R. A. Powell. 2007. Optimal use of resources structures home ranges and spatial distribution of black bears. *Animal Behaviour* 74:219–230.
- Modafferi, R. D. 1979. Black bear movements and home range study. Juneau, Alaska.
- Montgomery, R. A., G. J. Roloff, J. J. Millspaugh, and M. Nylen-Nemetchek. 2014. Living amidst a sea of agriculture: predicting the occurrence of Canada lynx within an ecological island. *Wildlife Biology* 20:145–154.
- Morgan Henderson, M. J., M. Hebblewhite, M. S. Mitchell, J. B. Stetz, K. C. Kendall, and R. T. Carlson. 2015. Modeling multi-scale resource selection for bear rubs in northwestern Montana. *Ursus* 26:28–39.
- Mowat, G., D. C. Heard, and C. J. Schwarz. 2013. Predicting grizzly bear density in western North America. *PLOS ONE* 8:13–17.
- Moyer, M. A., J. W. McCown, and M. K. Oli. 2007. Factors influencing home-range size of female Florida black bears. *Journal of Mammalogy* 88:468–476.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. Movement research. *PNAS* 105:19052–19059.
- Nolte, D. L., T. J. Veenendaal, G. J. Ziegltrum, and P. Festerer. 2001. Bear behavior in the vicinity of supplemental feeding stations in Western Washington. *Western Black Bear Workshop* 7:106–111.
- Northeast Wildlife DNA Laboratory. 2010. New Jersey black bear aversive conditioning report. East Stroudsburg.
- Novick, H. J., and G. R. Stewart. 1982. Home range and habitat preferences of black bears in the San Bernadino Mountains of southern California. *California Fish and Game Journal* 67:32–35.
- Noyce, K. V, D. L. Garshelis, and P. L. Coy. 2001. Differential vulnerability of black bears to trap and camera sampling and resulting biases in mark-recapture estimates. *Ursus* 12:211–226.
- O’Pezio, J., S. H. Clarke, and C. Hackford. 1983. Chronology of black bear denning in the Catskill region of New York. *Bears: Their Biology and Management, Vol. 5, A Selection of Papers from the Fifth International*

- Conference on Bear Research and Management, Madison, Wisconsin, USA, February 1980 (1983) 5:87–93.
- Oli, M. K., H. a Jacobson, and B. D. Leopold. 2002. Pattern of space use by female black bears in the White River National Wildlife Refuge, Arkansas, USA. *Journal for Nature Conservation* 10:87–93.
- Onorato, D. P., E. C. Hellgren, F. Mitchell, and J. Skiles. 2003. Home range and habitat use of American black bears on a desert montane island in Texas. *Ursus* 14:120–129.
- Orlando, A. M. 2008. Impacts of rural development on puma ecology in California's Sierra Nevada. University of California, Davis.
- Pacas, C. J., and P. C. Paquet. 1994. Analysis of black bear home range using a Geographic Information System. Pages 419–425 *Bears: Their Biology and Management, Vol. 9, A selection of papers from the ninth international conference on bear research and management, Missoula, Montana, February 23-28, 1992 (1994), pp. 419-425.*
- Peirce, K. N., and L. J. Van Daele. 2006. Use of a garbage dump by brown bears in Dillingham, Alaska.
- Powell, K. A., J. W. Zimmerman, and D. E. Seaman. 1997. Ecology and behaviour of North American black bears: home ranges, habitat and social organization. Chapman & Hall, London.
- Powell, R. A. 2000. Animal home ranges and territories and home range estimators, research techniques in animal ecology: controversies and consequences. Page (F. L. Boitani, T.K, Ed.). Columbia University, New York.
- Powell, R. A., and M. S. Mitchell. 2012. What is a home range? *Journal of Mammalogy* 93:948–958.
- Quigley, H. B. 1982. Activity patterns , movement ecology , and habitat utilization of black bears in the Great Smoky Mountains National Park , Tennessee. University of Tennessee, Knoxville, Tennessee, USA.
- Radeloff, V. C., R. B. Hammer, S. I. Stewart, J. S. Fried, S. S. Holcomb, and J. F. McKeefry. 2005. The wildland-urban interface in the United States. *Ecological Applications* 15:799–805.
- Rainbolt, R. E., M. T. Wegan, C. A. Dobony, and P. D. Curtis. 2011. Black bear project on Fort Drum military installation Oct 2004 – Apr 2007.

- Rauer, G., P. Kaczensky, and F. Knauer. 2003. Experiences with aversive conditioning of habituated brown bears in Austria and other European countries. *Ursus* 14:215–224.
- Reimchen, T. E. 1998. Nocturnal foraging behaviour of black bears, *Ursus americanus*, on Moresby Island, British Columbia. *Canadian Field Naturalist* 112:446–450.
- Reynolds, D. G., J. J. Beecham, and J. Wu. 1980. Home Range activities and reproduction of black bears in West-Central Idaho. Pages 181–190 *Bears : Their Biology and Management* , Vol . 4 , A selection of Papers from the Fourth International conference on bear research and management , Kalispell , Montana , USA.
- Rieffenburger, J. C. 1973. Range and movements of West Virginia black bears during summer and autumn 1973. *Proceedings of the Eastern Black Bear Workshop* 2:139–142.
- Riley, S. P. D., R. M. Sauvajot, T. K. Fuller, E. C. York, D. A. Kamradt, C. Bromley, and R. K. Wayne. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conservation Biology* 17:566–576.
- Riley, S. P., J. Hadidian, and D. a Manski. 1998. Population density, survival, and rabies in raccoons in an urban national park. *Canadian Journal of Zoology* 76:1153–1164.
- Robbins, C. T., C. C. Schwartz, and L. A. Felicetti. 2004. Nutritional ecology of ursids: a review of newer methods and management implications.
- Rogers, L. L. 1977. Social relationships, movements, and population dynamics of black bears in northeastern Minnesota. University of Minnesota, Minneapolis, Minnesota, USA.
- Rogers, L. L. 2011. Does diversionary feeding create nuisance bears and jeopardize public safety? *Human-Wildlife Interactions* 5:287–295.
- Rogers, L. L., D. W. Kuehn, A. W. Erickson, E. M. Harger, L. J. Verme, and J. J. Ozoga. 1974. Characteristics and management of black bears that feed in garbage dumps, campgrounds or residential areas. Pages 169–175 *Bears: Their Biology and Management IUCN publications new series, Vol. 3, A selection of papers from the third international conference on bear research and management, June 1974. Binghamton, New York, USA, and Moscow,*

U.S.S.R.

- Rondeau, D., and M. Conrad, Jon. 2003. Managing urban deer. *American Journal Agricultural Economics* 85:266–281.
- Rosenzweig, R., and E. Blackmar. 1992. *The park and the people: a history of Central Park*. Cornell University Press.
- Roth, J. K., P. N. Manley, M. M. Mckenzie, and M. D. Schlesinger. 2004. Multiple-species inventory and monitoring 2002 monitoring report.
- Ruell, E. W., S. P. D. Riley, M. R. Douglas, J. P. Pollinger, and K. R. Crooks. 2009. Estimating bobcat population sizes and densities in a fragmented urban landscape using noninvasive capture–recapture sampling. *Journal of Mammalogy* 90:129–135.
- Sager-Fradkin, K. A., K. J. Jenkins, P. J. Happe, J. J. Beecham, R. G. Wright, and R. A. Hoffman. 2008. Space and habitat use by black bears in the Elwha Valley prior to dam removal. *Northwest Science* 82:164–178.
- Samson, C., and J. Huot. 1998. Movements of female black bears in relation to landscape vegetation type in southern Québec. *The Journal of Wildlife Management* 62:718–727.
- Sawyer, S. C., and J. S. Brashares. 2013. Applying resource selection functions at multiple scales to prioritize habitat use by the endangered Cross River gorilla. *Diversity and Distributions* 19:943–954.
- Scheick, B. K., and W. McCown. 2014. Geographic distribution of American black bears in North America. *Ursus* 25:24–33.
- Schindler, S. B. 2012. Of backyard chickens and front yard gardens, the conflict between local governments and locavores 87:1–296.
- Schrage, M. W. 1994. Influence of gypsy moth induced oak mortality on black bear population. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.
- Schwartz, C. C., and A. W. Franzmann. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. *The Journal of Wildlife Management* 56:426–431.
- Seaman, D. E. 1993. Home range and male reproductive optimization. North Carolina State University, Raleigh, North Carolina, USA.

- Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1998. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management*:739–747.
- Shivik, J. A., A. Treves, and P. Callahan. 2003. Nonlethal techniques for managing predation: primary and secondary repellents. *Conservation Biology* 17:1531–1537.
- Sikes, R. S. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- Smith, T. R., and M. R. Pelton. 1990. Home ranges and movements of black bears in a bottomland hardwood forest in Arkansas. *Bears: Their Biology and Management* 8:213–218.
- Spencer, R. D., R. A. Beausoleil, and D. A. Martorello. 2007. How agencies respond to human–black bear conflicts: a survey of wildlife agencies in North America. *Ursus* 18:217–229.
- Spencer, W. D. 2012. Home ranges and the value of spatial information. *Journal of Mammalogy* 93:929–947.
- Stephens, D. W., and C. J. Krebs. 1986. *Foraging theory*. Princeton University Press, New York.
- Stillfried, M., J. L. Belant, N. J. Svoboda, D. E. Beyer, and S. Kramer-Schadt. 2015. When top predators become prey: black bears alter movement behaviour in response to hunting pressure. *Behavioural Processes* 120:30–39.
- Storlid, S. A. 1995. *Spring and summer habitat use and food habits of black bears in northern Wisconsin*. University of Wisconsin, Stevens Point, Wisconsin, USA.
- Stratman, M. R. 1998. *Habitat use and effects of prescribed fire on black bears in northwestern Florida*. University of Tennessee, Knoxville, Tennessee, USA.
- Stratman, M. R., C. D. Alden, M. R. Pelton, and M. E. Sunquist. 2001. Habitat use by American black bears in the Sandhills of Florida. *Ursus* 12:109–114.
- Teel, T. L., R. S. Krannich, and R. H. Schmidt. 2002. Utah stakeholders' attitudes toward selected cougar and black bear management practices. *Wildlife Society Bulletin* 30:2–15.

- Ternent, M. A., and D. L. Garshelis. 1999. Taste-aversion conditioning to reduce nuisance activity by black bears in a Minnesota military reservation. *Wildlife Society Bulletin* 27:720–728.
- The Urban Wildlife Working Group. 2012. . <http://urbanwildlifegroup.org/urban-wildlife-information/>.
- Thompson, M. J., and R. E. Henderson. 1998. Elk habituation as a credibility challenge for wildlife professionals. *Wildlife Society Bulletin* 26:477–483.
- Thorsen, S. 2018. Time and Date. <https://www.timeanddate.com/sun/usa/south-lake-tahoe>.
- Treves, A., and K. U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17:1491–1499.
- Treves, A., L. Naughton-Treves, E. K. Harper, D. J. Mladenoff, R. A. Rose, T. A. Sickley, and A. P. Wydeven. 2004. Predicting Human - Carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. *Conservation Biology* 18:114–125.
- Tri, A. N., J. W. Edwards, M. P. Strager, J. T. Petty, C. W. Ryan, C. P. Carpenter, M. A. Ternent, and P. C. Carr. 2016. Habitat use by American black bears in the urban–wildland interface of the Mid-Atlantic, USA. *Ursus* 27:45–56.
- TRPA. 2017. No Title. <http://data-trpa.opendata.arcgis.com/>.
- Ulrey, W. A. 2008. Home range, habitat use, and food habits of the black bear in south-central Florida. University of Kentucky, Lexington, Kentucky, USA.
- Unger, D. E. 2007. Population dynamics, resource selection, and landscape conservation of a recolonizing black bear population. University of Kentucky, Lexington, Kentucky, USA.
- United States Census Bureau. 2010. 2010 Census. <http://www.census.gov/2010census/data/>.
- Unsworth, J. W., J. J. Beecham, and L. R. Irby. 1989. Female black bear habitat use in west-central Idaho. *The Journal of Wildlife Management* 53:668–673.
- USDA Forest Service Pacific Southwest Region. 2010. CalvegTiles_Ecoregions07_4. Remote Sensing Lab, McClellan, California.
- Villarrubia, C. R. 1982. Movement ecology and habitat utilization of black bears in Cherokee National Forest, Tennessee. University of Tennessee, Knoxville,

Tennessee, USA.

- Wall, J. 2014. Movement ecology tools for ArcGIS ® (ArcMET).
- Wall, J., G. Wittemyer, V. Lemay, I. Douglas-Hamilton, and B. Klinkenberg. 2014. Elliptical time-density model to estimate wildlife utilization distributions. *Methods in Ecology and Evolution* 5:780–790.
- Walter, D. W., J. W. Fischer, S. Baruch-Mordo, and K. C. Vercauteren. 2011. What Is the proper method to delineate home range of an animal using today's advanced GPS telemetry systems: the initial step. USDA National Wildlife Research Center, Lincoln.
- Warburton, G. S. 1984. An evaluation of a black bear sanctuary in western North Carolina. North Carolina State University, Raleigh, North Carolina, USA.
- Weaver, K. M. 1999. The ecology and management of black bears in the Tensas River Basin of Louisiana. University of Tennessee, Knoxville, Tennessee, USA.
- White, C., B. Moore, and D. Smith, editors. 2012. Back to the basics: the monitoring and muddling of bear management. Page Proceedings of the eleventh western black bear workshop.
- White, T. H. 1996. Black bear ecology in the forested wetlands of the Mississippi Alluvial Valley. Mississippi State University, Starkville, Mississippi, USA.
- Wickham, H. 2007. Reshaping data with the reshape package. *Journal of Statistical Software* 21:1–20.
- Wickham, H. 2009. *Elegant graphics for data analysis*. Springer-Verlag, New York.
- Wickham, H. 2011. The split-apply-combine strategy for data analysis. *Journal of Statistical Software* 40:1–29.
- Wooding, J. B., and T. S. Hardinsky. 1994. Home range, habitat use, and mortality of black bears in north central Florida. *Bears: Their Biology and Management* 9:349–356.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.
- Xie, Y. 2018. A general-purpose package for dynamic report generation in R.

Young, B. F., and R. L. Ruff. 1982. Dynamics of home range and movements of adult black bears in northeastern Pennsylvania. *Journal of Wildlife Management* 46:845–860.

Young, D. D., and J. J. Beecham. 1986. Black bear habitat use at Priest Lake, Idaho. *Bears: Their Biology and Management* 6:73–80.

Zhu, H. 2018. Construct complex table with “kable” and Pipe syntax.