DISSERTATION

BLACK BEAR FITNESS AND INTERACTIONS WITH HUMANS IN AN ANTHROPOGENIC CONTEXT

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ABSTRACT

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Multiple studies confirm that anthropogenic pressure has reshaped at least 75% of the global terrestrial biosphere, converting these areas to more anthropogenic biomes. These anthropogenic landscapes have played a key role in altering vertebrate life history strategies (e.g., shifts in breeding phenology, reduced home range, increased competition for resources, increased mortality from anthropogenic causes). Large carnivores are particularly at risk in anthropogenic landscapes because of their large home ranges, high dietary needs, and long generation times, which increases their likelihood of conflict with humans. In the northeastern U.S., populations of American black bears (*Ursus americanus*) have increased rapidly, more than any other black bear population in the country, with human-bear interactions (HBI) on the rise since the middle of the 20th century. One state in particular, New Jersey, currently sustains the highest coupled density of black bears and humans in the country. Previous research in New Jersey found anthropogenic environments supported higher cub production of female black bears than wildland conspecifics, but females also suffered higher mortality costs. Knowledge gaps remain of the specific ecological components contributing to changes in female black bear (sow) fitness and how these shifts may shape the dynamics of HBI. To bridge these knowledge gaps, I first used statewide, long-term HBI reported incidents (2001 – 2017) in New Jersey, and quantified relative risks and shifts in HBI over space (e.g., land cover types) and time (e.g., bear life cycle stages). I then used 35 years of sow den surveys (1984 – 2019) to examine the relative effects of anthropogenic change (e.g., garbage production, urban development), landscape composition and configuration, natural resource availability, harvest, and individual characteristics (e.g., prior conflict behavior) on sow reproductive components (e.g., body mass and litter size). I found HBI varied by bear life cycle stage and landcover type, and individual characteristics and the environmental context experienced by sows *both* played important roles in shaping sow fitness and reproduction. I found there were significantly lower odds of more severe HBI during denning. When bears emerge from dens in the spring, there were significantly higher odds of more nuisance HBI, and more specifically garbage complaints. During the breeding and summer activity period, there were significantly higher odds of both benign and more severe HBI occurring. During hyperphagia there were higher odds of more severe and nuisance HBI, when bears are foraging excessively to prepare for winter denning. Spatially, most conflicts occurred in anthropogenic-dominated areas, which also supported the highest odds of garbage complaints. Agricultural areas also supported the highest odds of more severe HBI. My results demonstrated sow body mass is tightly linked to agricultural and developed-low intensity land covers, likely due to the reliable food subsidies in those landscapes, but only apparent within certain sow home range extents. Yet, I found specific anthropogenic food subsides (e.g., trash and corn production) may not be as important to sows, rather increased anthropogenic stimuli (e.g., from cultivated crop and developed-low density land covers) is. I also found that a prior history of conflict with humans contributed to increased sow body mass. Litter size varied with respect to maternal condition, experience, and litter composition (e.g., same sex-female or male litters, mixed sex litters). Results failed to support the assumption of a trade-off between litter size and litter mass that is implicit in many life-history studies. Though, I found litter size and mass were more constrained in older sows compared to younger and middle-aged sows, with a similar relationship apparent in lighter sows versus medium weight and heavy sows.

Results revealed sows could be investing more into sons in male-biased triplet litters, because their litter mass exceeded litter mass in other litter types (e.g., female-biased, same sex ratio). My results demonstrate sows may be circumventing trade-offs by continually acquiring more resources for larger litter size and mass, which is likely contributing to the high abundance and success of black bears in New Jersey. My results provide valuable insight in directing management focus towards specific life cycle events and land cover types, where anthropogenic change may simultaneously influence reproductive fitness and HBI, which often results in negative outcomes for black bears in New Jersey. Between 2001 and 2015, >$12 million has been allocated to bear management in New Jersey which at current conflict levels is not economically, environmentally, or socially sustainable long term. My results help guide management so that black bears can continue to thrive in the northeastern U.S., while minimizing human-bear conflicts and cost associated with them, and thus maximizing human-black bear coexistence in this human-dominated landscape.

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fallen. Even though she will never read this, I am grateful for the constant amusement and love provided by my Maine Coon, Cleopatra.

DEDICATION

This dissertation is dedicated to my late father, Michael “Pockets” Nelson, who passed away during my dissertation research. Thank you for instilling in me a strong passion for wildlife and the outdoors. I hope your Lil’ Darlin made you proud.

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INTRODUCTION

The human footprint upon Earth's ecosystems spans an extensive gradient ranging from seminatural to (sub)urban habitats, exerting rapid and intense ecological and evolutionary forces on wildlife (Alberti 2008). This footprint and subsequent anthropogenic pressure (e.g., land conversion, habitat fragmentation and degradation, human population density, hunting) have become more pervasive in recent decades, along with accelerated human demands for resources (Woodroffe et al. 2005). Consequently, 75 to 95% of terrestrial lands have been converted to anthropogenic biomes (Ellis et al. 2021) with evolutionary and ecological forces likely to keep affecting wildlife (Ellis and Ramankutty 2008). For example, anthropogenic landscapes have played a considerable role in altering wildlife demographic processes (e.g., earlier breeding, increased reproductive performance, Rodewald and Gehrt 2014), and foraging behavior (e.g., reduced range size due to stable food resources, Prange et al. 2004, Harveson et al. 2007, Herr et al. 2009). Anthropogenic landscapes have also elicited regular competition for resources between people and wildlife, thus prompting human-wildlife conflict (Treves and Karanth 2003).

Anthropogenic effects can also manifest at any ecological scale. Yet, evolutionary theory predicts that persistent anthropogenic influence over succeeding generations can shape surviving populations' structure (Pelletier and Coltman 2018), whereby species may not be able to evolve at a similar pace to cope with changing environmental conditions (e.g., evolutionary rescue, Gomulkiewicz and Holt 1995). Large body sizes and home range requirements, limited protection, habitat alteration, and anthropogenic pressure render large mammalian carnivores extremely susceptible to local extinction in anthropogenic landscapes (Crooks 2002a, Cardillo et al. 2004, 2005). Anthropogenic landscapes have adversely affected the majority of large, mammalian carnivores in North America through habitat fragmentation (e.g., residential, energy, and agricultural development; roadways), hunting, depredation control, introduced diseases (Nowak et al. 2005), and climate change (Ripple et al. 2014). As a result, large carnivore populations have declined throughout the world, despite their high ecological value (Nowell and Jackson 1996, Woodroffe 2000, Gittleman et al. 2001, Ray et al. 2005). Thus, identifying the context in which carnivore populations respond to anthropogenic change is important to capture potential links between ecological and evolutionary dynamics, particularly given the velocity at which anthropogenic pressure has spread across the planet.

Life history traits are often shaped by ecological and evolutionary trade-offs (e.g., reproductive investment vs. survival, Stearns 1989; Fig. 1). Trade-offs are evolutionary constraints and solutions to ecological risk (e.g., mortality, food acquisition), often leading to optimal evolutionary compromise (Stearns 1992). Although life histories evolve from internal restrictions (e.g., genetics, behavioral), they also respond to temporal and environmental variability, with the pattern and extent of variation favoring specific life history strategies (van Noordwijk and de Jong 1986, de Jong and van Noordwijk 1992, Tuljapurkar et al. 2009, Snell-Rood et al. 2015). Anthropogenic effects on life history traits and fitness have been linked to habitat alteration, and resource availability and quality (Martin 1987, Vanni and Lampert 1992, Boggs and Ross 1993, Twombly et al. 1998, Cartwright et al. 2014). Organisms' life history responses to anthropogenic change may be further constrained by the life history strategy along a slow (e.g., large body size, low fecundity, long-lived) to fast (e.g., small body size, high fecundity, short-lived) continuum

(Stearns 1992). Species along the slow end of the slow-fast continuum are expected to be more susceptible to environmental stress and variation because their life history strategy does not support rapid response to changing environments (Quetglas et al. 2016). The increased rate at which anthropogenic landscapes have expanded globally (Ellis et al. 2010) has amplified concern for wildlife conservation (Pimm and Raven 2000), particularly the adaptive potential of populations to anthropogenic pressure (Cheptou et al. 2017).

Inevitably, anthropogenic landscapes will continue to expand into habitat occupied by large carnivores. Life history theory can help predict how animals respond to anthropogenic pressure (Stearns 1977). Life history traits (e.g., age, Chiyo et al. 2012, Elfström et al. 2014) and events (e.g., during the young-rearing period, Lukasik and Alexander 2011) can also contribute to understanding human-wildlife interactions and conflicts. The increased quantity of steady, reliable food subsidies from humans found within anthropogenic landscapes can influence wildlife behaviors, life histories, and fitness, (Newsome and van Eeden 2017) which can trigger increased human-wildlife interactions and conflicts (Snijders et al. 2019). Aspects contributing to human-wildlife conflict are particularly important to understand for long-lived species with extended generation times, such as large carnivores, where behavior can be mediated by life history stage (Biro and Stamps 2008). For instance, human-wildlife conflict can vary and subsequently increase across various species' life history stages and can be particularly deleterious if conveyed from parent to young (Mazur and Seher 2008). Given the increased susceptibility of large carnivores to human perturbations (Ripple et al. 2014), identifying *when* and *where* large carnivores use anthropogenic resources, as well as the fitness costs and benefits of doing so, will help implement proper management that optimizes large carnivore fitness, while minimizing human-carnivore conflicts.

Roles Large Carnivores Play Within Ecosystems and Their Adaptive Potential to Anthropogenic Landscapes

Large carnivores play an integral role in ecosystems and in regulating ecological function (Terborgh 2005, Ripple et al. 2014). For example, large carnivores can enhance soil and plant communities and dynamics by providing significant nutrient impulses to the environment by spatially and temporally distributing prey carcasses (Bump et al. 2009). The utility of large carnivores in ecosystems can extend far, throughout and across ecosystems, with effects manifesting through tightly linked carnivore-prey relationships. For instance, when there is an imbalance of large carnivores and their prey (e.g., carnivore densities are low, and subsequent browsing intensity by prey are high), large carnivores can mediate drastic shifts in trophic cascades and in ecosystem structure and function simultaneously among different ecosystems (e.g., both aquatic and terrestrial, Ripple and Beschta 2006). Large carnivores can also drive behavioral decisions of their prey such as habitat selection, food acquisition, and activity patterns that could indirectly affect flora and fauna communities and structure (Terborgh 1988, Miller et al. 2001). Carnivores, particularly omnivorous ones, can also directly regulate vegetative dynamics through seed consumption and long-distance seed dispersal (Otani 2002, Jordano et al. 2007). While large carnivores are considered a keystone species in helping regulate a multitude of ecosystem processes (Terborgh et al. 1999), humans are considered a higher order, “hyperkeystone” species, also exerting constant influence that shapes ecosystem structure that cascades to other species and processes (Worm and Paine 2016).

Human influence has also restructured how large carnivores use landscapes (Laliberte and Ripple 2004) and carnivore activity patterns (Ditchkoff et al. 2006). Comparable responses among carnivores to anthropogenic pressure stem from large carnivores sharing similar life history and ecological traits with one another (Weaver et al. 2009). Although carnivore conservation within anthropogenic landscapes is of increasing concern (Penteriani et al. 2018), we have limited knowledge on how large carnivores cope with anthropogenic change to mitigate behavioral and energetic costs (Woodroffe 2000; Crooks 2002a,b; Lehrer et al. 2012). Additionally, very little is known about the individual fitness and population-level consequences of anthropogenic pressure on carnivores over generational scales. As anthropogenic landscapes become more pervasive, humans are likely to keep contributing to shifts in species' life histories, via changes in behavior that are known to affect fitness components such as body mass, reproduction, and survival, as well as shape human-wildlife interactions (Alberti et al. 2017). A comprehensive approach integrating anthropogenic pressure (e.g., development, food subsidies), ecological context (e.g., climate, habitat type), and the subsequent large carnivore responses (e.g., reproductive fitness), is necessary to understand the dynamics of potential human-carnivore coexistence.

A Large Carnivore Case Study: The American Black Bear in New Jersey

The American black bear (*Ursus americanus*, hereafter, black bear), a large carnivore, has experienced drastic population and range declines because of anthropogenic pressure (Hristienko and McDonald 2007). By the 1950s, black bears were nearly extirpated from their historic range throughout much of North America (Hall 1981). In the eastern U.S., rapid declines in black bears by this time were a result of anthropogenic conversion, timber extraction, and unregulated harvest that diminished their once relatively ubiquitous, stable populations to an estimated <100 individuals in northern New Jersey (Lund 1980, McConnell et al. 1997). In 1953, black bears were designated by the New Jersey Fish and Game Council as game animals and regulated hunting was legalized from 1958 – 1970, resulting in a reported 46 harvested black bears (Lund 1980, NJOAL 2015). However, from 1971 – 2002 the Council ceased hunting altogether to allow the populations to increase and re-stabilize (Lund 1980). During the 32-year hunting moratorium, black bear populations recovered with an estimated 450 – 550 black bears in northwestern New Jersey in 1992 (McConnell et al. 1997). Consequently, limited hunting seasons were reestablished in 2003, 2005, and 2010 to 2020, to regulate black bear populations and mitigate increasing human-bear conflict, with intermittent hunting closures due to various local, public, and legal pressures (Lund 1980, NJOAL 2015). Since the 1950s, black bear populations have significantly rebounded to an estimated 3,158 black bears in northern New Jersey in 2020, up from ~2,200 bears in 2019 (*unpublished data*, NJDFW), and their distributions have increased throughout the entire state, with bear sightings reported in all 21 New Jersey counties (Carr and Burguess 2011). Protection from hunting over the 32-year and intermittent hunting moratoriums have helped bear populations recover in New Jersey. In addition, increasing and expanding bear populations from neighboring states (e.g., New York and Pennsylvania), increased quality and protection of bear habitat, intensified management-based research, and education programs (e.g., “Bear Aware”, controlling human food sources) have all contributed to the black bear population recovery in New Jersey (McConnell et al. 1997, Carr and Burguess 2011, Hurst et al. 2012).

Although black bears are classified as large carnivores, they are better characterized as highly opportunistic omnivores, capitalizing on an assortment of available food and resources consisting of both plant and animal matter. Black bears have a large vegetative component in their diet (≈75%, NJDFW 2019), yet they are not able to digest cellulose as efficiently as meat (Larivière 2001) because they lack a cecum (Stevens and Hume 1995). Their generalist diet, however, has allowed them to adapt and thrive in anthropogenic landscapes (Ternent et al. 2001). Like many wildlife species, black bears shift and synchronize their diet in response to seasonal plant phenology and other food availability (Chapter 1 – Fig. 1.1). The seasonal variation of black bear diet in the eastern U.S., consists of skunk cabbage (*Symplocarpus foetidus*), sedges (*Carex* spp.), grasses (Graminae), forbs, tubers, bulbs, deer fawns and carcasses, and insects in spring after den emergence (NJDFW 2019). In the spring through fall, black bears forage on fruits and berries of plants such as blackberries and raspberries (*Rubus* spp.), blueberries (*Vaccinium* spp.), and wild cherries (*Prunus* spp.) (NJDFW 2019). In the fall, when black bears are preparing for winter denning (e.g., hyperphagia, Chapter 1 – Fig. 1.1), they forage on hard mast such as acorns from oaks (*Quercus* spp.), beechnuts (*Fagus grandifolia*), and hickory nuts (*Carya* spp.) (NJDFW 2019) to accumulate fat reserves to meet the energy requirements of winter denning. However, when natural food is limited, black bears supplement their diet with human-related foods (e.g., agricultural crops, garbage, birdfeed, harvest baiting), particularly when these non-natural foods are in constant supply (Rogers 1987, Baruch-Mordo et al. 2014, Lewis et al. 2015), often leading to increased human-bear interactions and conflict (Baruch-Mordo et al. 2008, 2014).

There is a paucity of information on the fitness costs and benefits of using habitat that overlaps substantially with human development, other than a few studies on habitat selection (e.g., Tri et al. 2013) in the eastern U.S., particularly in New Jersey. But recent insight regarding human-black bear conflict in the eastern U.S. (e.g., Evans et al. 2014, 2019) and in New Jersey (e.g., Raithel 2017) has furthered our understanding of the interplay between explicit spatial and temporal ecological factors shaping black bear fitness and behavior in this region. Yet, a long-term perspective on these effects and how they may shape plastic responses to changing environmental conditions, may reveal important dynamics relevant to black bear management.

Reproduction Ecology and Responses to Anthropogenic Influence

Fecundity, a key life history trait and measure of an organism's fitness (Stearns 2000), can vary widely across females with respect to age (Pianka and Parker 1975), body condition

(McNamara and Houston 1996), and even behavior (e.g., bold versus shy, Wolf et al. 2007), leading to variation in reproductive rates within and among populations (Stearns 1992). These reproductive patterns are also shaped by environmental conditions such as climate (Boyce 1988), food resource abundance (e.g., Persson 2005), and seasonality (Boyce 1979). Anthropogenic pressure can also directly affect reproductive potential and dynamics in carnivores (Fuller et al. 2010). Increased reproductive success, for example, has been attributed to increased anthropogenic food subsidies (e.g., in coyotes, *Canis latrans*, Iossa et al. 2010; raccoons, *Procyon lotor*, Prange et al. 2003; San Clemente Island foxes, *Urocyon littoralis clementae*, Gould and Andelt 2011). Conversely, decreased reproduction and genetic diversity has been linked to habitat fragmentation, which can diminish corridors and carnivores' subsequent inability to connect to other habitat patches and mates (Grilo et al. 2015). Other impacts include the reduction in recruitment of young linked to increased human activity (e.g., cheetahs, *Acinonyx jubatus*, Broekhuis 2018) and climate change (e.g., African wild dogs, *Lycaon pictus*, Woodroffe et al. 2017).

The spectrum of effects to carnivore reproduction highlights the importance of including the anthropogenic context experienced by females in quantifying reproductive outcomes and population-regulating processes. Animals are assumed to be distributed on the landscape based on resource availability that can maximize their fitness (e.g., ideal free distribution, Fretwell and Lucas 1970). For many long-lived species, such as ursids, reproductive rates are determined by food resource availability on the landscape and bear nutritional condition (e.g., Rogers 1987). Anthropogenic resources, however, generally do not allow bears to fulfill their maximum reproductive potential because of increased removal and mortality linked to human food exploitation (Beckmann and Lackey 2008). Variability in bear reproduction can further be reflective of temporal dynamics in food resource availability (Clark 2004). For example, during years when hard mast availability is low and female black bears (sows) are in poor body condition, sows can extend their reproductive cycle (Eiler 1981), exhibit delayed age of primiparity (Eiler 1981, Eiler et al. 1989), produce smaller litters (Eiler 1981), and experience reproductive failure (Eiler et al. 1989, Pelton 1989). Fluctuating reproductive rates have also coincided with variable soft mast production (e.g., huckleberry, Jonkel and Cowan 1971).

To cope with environmental stressors, such as reduced resource availability, bears have also evolved physiological mechanisms through delayed implantation of embryos and facultative hibernation in winter dens (Hellgren 1998). These mechanisms and others, such as less reduction in body temperature during winter denning, help distinguish bears from true, obligate hibernators (Hissa 1997, Hellgren 1998, Evans et al. 2016). Additionally, bears are capital breeders, where they rely on stored reserves acquired from resources prior to reproduction (Varpe et al. 2009). This storage of resources and subsequent increased body growth is an investment in future reproduction (Ejsmond et al. 2010) and population recruitment (Inman 1997). Thus, the source(s) of variability in resources and ecological conditions leading up to reproduction should be considered to assess potential population-level fitness consequences and gains in sows (Fig. 1).

Bear reproduction has also benefitted from land conversion through constant availability of anthropogenic foods, where urban bears have experienced higher age-specific fecundity compared to wildland populations (Beckmann and Lackey 2008, Raithel 2017). Increased reproduction in bears has also been attributed to the coupled availability of anthropogenic (e.g., crops) and natural foods (Garshelis et al. 2013, Ditmer 2014). Bears exhibit high behavioral plasticity, where they can mitigate deleterious effects of poor natural forage years by shifting to anthropogenic environments and foods (e.g., trash, Baruch-Mordo et al. 2014, Johnson et al. 2017). This plasticity supports the optimal foraging theory (MacArthur and Pianka 1966, Schoener 1971), in that bears can efficiently and strategically select optimal food resources that maximizes their energy return, fitness, and subsequent contribution to future generations (Bunnell and Trait 1981). Because this plastic behavior can be a part of bears' and other large carnivores' optimal foraging strategy, it is inherent this behavior will play a strong role in human-carnivore interactions. However, other behaviors described below can surface to help carnivores cope with increasing anthropogenic pressure and are also important to consider. Such behavioral responses may be important drivers of ecological and evolutionary change (Blumstein and Fernández-Juricic 2004) and may also add to the complexity behind human-carnivore interactions in anthropogenic landscapes.

Behavioral Responses to Anthropogenic Influence

While constant availability of anthropogenic food subsidies (e.g., bird feeders, crops, trash, livestock) may influence individual and population level parameters (Oro et al. 2013), anthropogenic pressure can also induce evolutionary change via behavioral shifts (Sih et al. 2011, Tuomainen and Candolin 2011). Yet, carnivores' plastic behavior may help mitigate some negative impacts associated with anthropogenic change. For example, large carnivores can shift their temporal activity from crepuscular to more nocturnal in response to anthropogenic pressure (e.g., livestock grazing and spotted hyenas, *Crocuta crocuta*, Holekamp and Dloniak 2010; human presence and tigers, *Panthera tigris*, Carter et al. 2012). Carnivores may also demonstrate a bold temperament (Lowry et al. 2012). This boldness can cause the animal to take more risks by using areas or protecting territories and resources in anthropogenic landscapes (Elfström et al. 2014), which can in turn contribute to human-carnivore conflicts. Understanding where and when human-carnivore conflicts arise in anthropogenic landscapes is essential to not only determine if carnivores might be adapting behaviorally to anthropogenic change, but also in providing managers the information necessary to target individuals exhibiting behaviors detrimental to humans (Blackwell et al. 2016).

Behavioral plasticity in bears may contribute to their adaptability to anthropogenic change, and thus success within converted landscapes. Anthropogenic pressure can displace bears during important stages of their life cycle, resulting in behavioral shifts to cope with such pressure. For instance, bears can shorten their denning periods due to constant and abundant anthropogenic food subsidies (e.g., supplemental feeding of grizzly bears, *Ursus arctos*, Krofel et al. 2017; black bears in warmer temperatures with human food use, Johnson et al. 2017). This behavioral shift can ultimately influence reproductive potential and survival, and subsequently increase the likelihood of human-bear conflicts (Servheen and Cross 2010).

Additional anthropogenic pressure, such as roadways, acts as a major influence on bear behavior, with bears using roads as paths of least resistance, or roads impeding bear movement – particularly on roads with higher traffic volume and during high traffic times (Brandenburg 1996). Nonetheless, anthropogenic landscapes may provide many benefits to bears. For example, brown bears relying on trash experienced annual sedentary bouts with reduced migration, whereas brown bears that did not visit dumps travelled extended migration distances to acquire food resources (Cozzi et al. 2016). Bears relying more on anthropogenic landscapes could experience more niche overlap among conspecifics and humans and could also grow to larger sizes that cannot be maintained by natural forage alone (Robbins et al. 2005). This reliance can adaptively alter bear behavior, as demonstrated by the habituation of bears to anthropogenic landscapes (Gunther et al. 2018). Yet, research has shown that habituation may not have the opportunity to manifest and be retained, particularly during good natural forage years, where bears opt for natural forage over anthropogenic resources (e.g., Baruch-Mordo et al. 2014)

Along with behavioral plasticity, vigilance in bear behaviors may offset the many costs of anthropogenic pressure and of an increased likelihood of conflict with humans (Penteriani et al. 2018). For example, brown bears increased their nocturnal foraging during the hunting season such that the cost of harvest mortality was low (Ordiz et al. 2012). Increased bear vigilance, however, may not keep up with the pace of land conversion, as evidenced by the number of human-bear conflicts around the country. Human-bear interactions and conflicts correspond with the trajectories of rapid human and black bear population growth in the U.S., particularly in northeastern states such as New Jersey (Southwick 2007). This concurrent growth has resulted in ~29,000 reported human-black bear interactions in New Jersey from 2001 to 2017. Further, >$12 million has been allocated to black bear management by the New Jersey Department of Fish and Wildlife (NJDFW) between 2001 and 2015, which included $2.3 million to enhance education, $2.3 million to law enforcement, and $7.5 million for control, monitoring, and research (NJOAL 2015). As human populations continue to expand and convert natural habitats into anthropogenic landscapes, human-black bear conflict at this current scale is not economically and ecologically sustainable long-term (NJOAL 2015). Thus, identifying areas of greater spatial risk in human-carnivore interactions may help limit future conflicts, by pointing to appropriate mitigation strategies that focus on areas where conflict is highest, based on spatial scale and ecological context (Rostro-García et al. 2016).

Spatial Patterns of Human-Carnivore Conflict in Response to Anthropogenic Change

Human-carnivore conflicts can vary across scales, manifest at some scales but not others, and exhibit spatially non-random patterns (Soulsbury and White 2015). For example, wolves (*Canis lupus*) in the midwestern U.S. selected areas of livestock prey with limited croplands, coniferous forests, herbaceous wetlands, and open water, but also areas that included abundant pastureland and natural prey densities at the township scale (Treves et al. 2004). In contrast, at the individual farm scale, wolves selected habitats with the same features, but also areas based on farm size and road density (Treves et al. 2004). Conversely, spatial analyses can also point to where human-carnivore conflicts are negligible, and where carnivores are more likely to coexist with humans, as seen with tigers in Nepal (Carter et al. 2012). Spatial analyses may also reveal if anthropogenic landscapes superimpose a "landscape of fear" onto carnivores, where carnivores choose not to spatially intersect with humans (Gaynor et al. 2019). Human-wildlife interactions and conflicts can range from nuisance interactions (e.g., raiding trash/birdfeeders), agricultural damage and livestock predation, wildlife-vehicle collisions, to rare direct attacks on humans (Nyhus 2016). Therefore, conflict is a byproduct of interactions negatively impacting humans and (or) wildlife (Madden 2004).

While human-wildlife conflict is already inclusive of numerous dimensions, spatial aspects contributing to human-wildlife conflict should be considered to gain a more comprehensive perspective of conflict (e.g., Nyhus 2016). Multiple black bear studies have established a link between anthropogenic habitat use and conflict, where bears selected areas rich in anthropogenic foods (e.g., fruit trees in Colorado, Lewis et al. 2015, and in Montana, Merkle et al. 2013). Other spatial analyses of human-bear conflict, such as livestock depredation, identified habitats near livestock grazing areas as more likely to experience grizzly depredation, particularly when near beehives, quality bear habitat, and areas where livestock raise young (Wilson et al. 2005). Similarly, spatial analyses in Colorado revealed black bear-livestock depredation was spatially clustered around higher farm and sheep densities, and bear-vehicle collisions were clustered in prime bear habitat (Baruch-Mordo et al. 2008). Spatiotemporal variation in human-wildlife conflicts can further assist wildlife officials and local governments in planning cost-effective mitigation measures to direct management actions accordingly. Additionally, analyses that temporally connect bear life history stages (e.g., reproduction) to anthropogenic change and ecological context are important in fully understanding how human-bear conflicts may fluctuate over time.

CONCLUSION

Extensive and ubiquitous anthropogenic change drive significant variation in large carnivore behaviors and life history traits. As a result, effective management of large carnivores requires knowledge of the spatiotemporal dynamics of human-black bear interactions (e.g., bear life cycle stage, land cover type) to mitigate human-carnivore conflict, particularly because of the wide-ranging nature and longevity of carnivore species. In this dissertation, I connected black bear behavioral (e.g., categorized human-bear interactions) and demographic (e.g., reproductive fitness) responses to ecological context and anthropogenic pressure in a human-dominated and highly fragmented landscape: New Jersey.

In Chapter 1, I used nearly two decades (2001 – 2017) of human-black bear interaction (HBI) data to assess and quantify the spatiotemporal dynamics of HBI across New Jersey. I evaluated how HBI varied across distinct bear life cycle stages (e.g., during denning, den emergence, summer breeding and activity, hyperphagia) and land cover types. In Chapter 2, I examine the shared roles of climate, anthropogenic pressure (e.g., human food subsidies, harvest), bear characteristics (e.g., age, history of human-bear conflict), habitat composition and configuration, and natural resource availability (e.g., hard mast production) in explaining variability in female (sow) black bear body mass – an important determinant of successful reproduction, across 35 years (1984 – 2019) in New Jersey. In Chapter 3, I quantified how maternal characteristics (e.g., age, body mass, den type selection, legacy of human-bear conflict), litter characteristics (e.g., sex ratio, mass, composition) environmental context (e.g., trash generated, hard mast production, bear management zone, county), hunting pressure, and bear population size influenced litter size across 35 years. In the final chapter of this dissertation, I briefly outline potential directions for black bear research and management in New Jersey, to better understand and protect a large carnivore living in landscapes shared with humans.

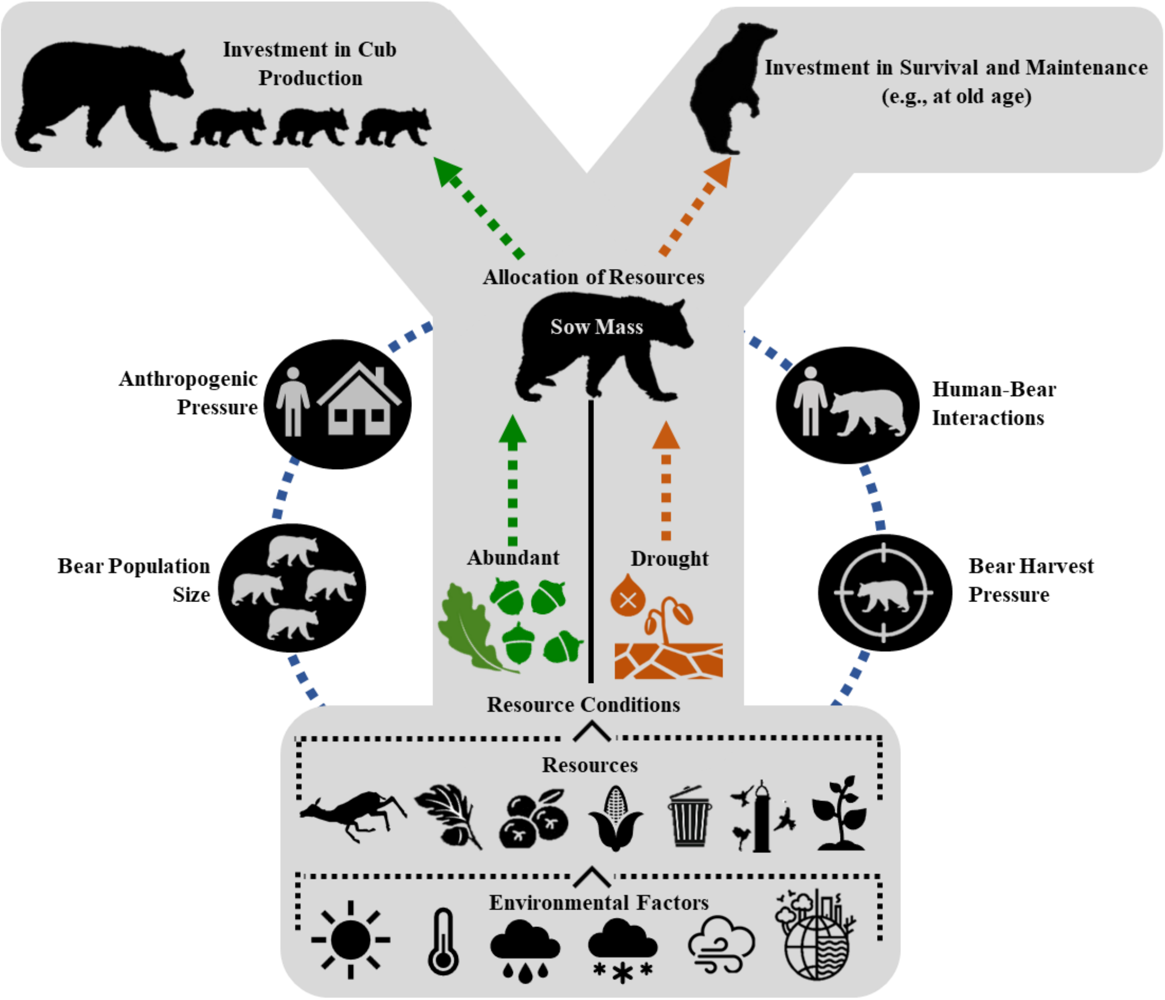

Figure 1. Classic “Y” model of life history trade-offs of a large carnivore, the American black bear (*Ursus americanus*), modified from Snell-Rood et al. (2015). Depicted are the resources available to a bear (e.g., roadkill, hard mast such as acorns, soft mast such as blueberries, corn, trash, birdfeeder, other vegetation), the conditions of the resources in the environment, and the subsequent life history trade-offs between reproduction and survival ultimately shaped by environmental factors (e.g., temperature, precipitation, climate), anthropogenic pressure (e.g., human population size, development intensity), bear population size, bear harvest pressure, and human-bear interactions.

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CHAPTER 1: SPATIOTEMPORAL DYNAMICS OF HUMAN-BLACK BEAR (*URSUS AMERICANUS*) INTERACTIONS IN A FRAGMENTED LANDSCAPE

SUMMARY

Human-wildlife interactions, which can result in conflict, are a prevalent issue often attributed to the expansion of urbanization into wild habitats and the ability of opportunistic species to exploit anthropogenic resources. In the northeastern U.S., black bears (*Ursus americanus*) are particularly prone to interactions with humans. We examined how different temporal and spatial factors impact the frequency and severity of human-black bear interactions (HBI) in New Jersey using data from 2001 to 2017 (n = 28,811), where each HBI is identified as either Category I: bear is a threat to public safety; Category II: nuisance bear that caused property damage; or Category III: bear sighted exhibiting non-threatening behavior. Temporally, the frequency of HBI varied widely across bear life cycle stage, with most HBI occurring during breeding and summer activity (1 June – 31 August), followed by den emergence (1 April – 31 May), hyperphagia (1 September – 30 November), then denning (1 December – 31 March). There were significantly lower odds of more severe HBI (Category I) occurring during denning. When bears emerge from dens in the spring, there were significantly higher odds of more nuisance HBI (Category II), and more specifically garbage complaints. During the breeding and summer activity period, there were significantly higher odds of both benign HBI (Category III) and more severe HBI (Category I) occurring. During hyperphagia, there were significantly higher odds of Category I and II HBI, when bears are foraging excessively to prepare for winter denning. Spatially, most conflicts occurred in anthropogenic-dominated areas, with agricultural land cover supporting the

highest odds of Category I HBI. Anthropogenic areas also sustained the highest odds of garbage complaints. Our results indicate that current management strategies, particularly the educational campaign, combined with established hunting seasons, will likely be effective in reducing HBI. However, management efforts should focus on securing garbage in bear proof containers, providing monetary assistance for residential bear proof containers particularly in anthropogenic areas, and when natural forage is scarce during den emergence to reduce the likelihood of HBI. Though management would likely benefit from stricter law enforcement of reducing attractants and administering fines, which may help offset the costs of other proactive HBI reduction measures.

INTRODUCTION

Human-wildlife interactions (HWI) have become an increasingly relevant issue worldwide. Particularly worrisome are interactions that arise when top predators encounter humans as anthropogenic pressure intensifies and expands into natural landscapes, which can result in a conflict with negative repercussions on either side of the interaction.

The human footprint upon earth spans an extensive gradient of ecosystems that has become more pervasive (Goldewijk et al. 2017). Consequently, 75 to 95% of the global terrestrial biosphere has experienced anthropogenic pressure to some extent (Ellis et al. 2010, 2021, Kennedy et al. 2019, Williams et al. 2020), and ~18,000 terrestrial vertebrates have experienced intense pressure from this human footprint (O’Bryan et al. 2020). The upsurge of top predators using more urbanized areas poses an additional concern (Blecha et al. 2018), especially in countries experiencing rapid levels of development. For example, in Brazil, the expansion of human settlements, agricultural lands, and recreational areas have given rise to concerning levels of interactions between humans and jaguars (*Panthera onca*), as well as humans and pumas (*Puma concolor*) (Marchini and Crawshaw 2015). In India, forests fragmented by agriculture have led to increased HWI involving humans, tigers (*Panthera tigris*) and leopards (*Panthera pardus*) (Sundriyal and Dhyani 2014), ultimately leading to substantial reciprocal mortalities. Globally, urbanization and land use change are key factors contributing to increased HWI (Soulsbury and White 2015). This growing issue has the potential to pose significant challenges pertaining to the economics and safety concerns surrounding HWI (Soulsbury and White 2015), particularly when such interactions involve large carnivores (Morehouse et al. 2018). To address these challenges, wildlife managers and policymakers have been forced to take action in mitigating any damages experienced by humans – a task that involves time, money, controversy, and contentious politics (Cromsigt et al. 2013). Three elements broadly explain the severity and frequency of HWI:

(1) Humans are encroaching into wild habitats. Human population growth facilitates expansion into wild habitats, which sequentially creates an environment where HWI becomes a growing concern (Nyhus 2016). Top predators such as large carnivores characteristically use large home ranges, and consequently are more susceptible to urbanization and habitat fragmentation (Inskip and Zimmermann 2009, Morehouse et al. 2018).

(2) Opportunistic carnivores are thriving within fragmented habitats and have begun to expand and exploit (sub)urban areas, leading to increased HWI. In the U.S. for example, the growth of (sub)urban areas has allowed coyotes (*Canis latrans*) to take advantage of anthropogenic resources and extend their range into urban and suburban landscapes (Poessel et al. 2017).

(3) The interaction between land conversion (e.g., urbanization, agriculture) and climate change may further exacerbate the frequency and severity of HWI by driving species out of their typical habitat and into (sub)urban and agricultural areas. A large carnivore, the American black

bear (*Ursus americanus*; hereafter, black bear), has modified timing of emergence from winter denning in the spring due to warming temperatures in parts of North America (e.g., Johnson et al. 2017). As omnivores, black bears are opportunistic feeders that can move into human-dominated areas in search of anthropogenic resources, increasing the potential for human-black bear interactions (HBI), especially with bear denning length shortened by warming temperatures (Johnson et al. 2017). Hard and soft mast (e.g., acorns and berries, respectively), which the production and availability can vary year to year depending on climate conditions, are vital resources to black bears (Inman and Pelton 2002). Therefore, annual fluctuations in mast production can influence HBI (e.g., Baruch-Mordo et al. 2014).

Black bears are a species of key importance when examining HWI within anthropogenic landscapes, particularly because of the plasticity they display in both resource and habitat use. For example, black bears can shift to feeding on anthropogenic foods (e.g., garbage) within developed areas when natural resources are limited (e.g., mast failure), thus increasing the likelihood of interaction with humans; however, they return to foraging on natural resources when available (Baruch-Mordo et al. 2014, Johnson et al. 2017).

Beyond spatial considerations, annual life cycle stages – which guide the feeding behavior of black bears – should be tracked when attempting to understand how temporal shifts in resource availability can impact HWI (Oka 2003, Ryan et al. 2007). Black bear life cycle stages include: i) denning, when bears go through a period of extended torpor or pseudo-hibernation, ii) den emergence, iii) breeding season and summer activity, and iv) hyperphagia, a period where bears feed extensively to prepare for denning (Fig. 1.1).

The anthropogenic context experienced by black bears is another important concern when considering the spatiotemporal dynamics of HWI. Urbanization is expected to increase across black bears' range, which will likely result in an increased frequency of HBI and potential conflict with humans over time (Baruch-Mordo et al. 2014, Johnson et al. 2017) – another reason black bears are an ideal organism to study HWI. This increase in HBI has been particularly notable in the northeastern U.S. and other deciduous habitats in North America (Evans et al. 2014, Obbard et al. 2014).

In NJ, as in other states in the northeastern and eastern U.S., the dual increase in black bear population growth (Fig. 1.3) and urbanization have simultaneously caused an increase in HBI (Raithel 2017). The black bear management strategy recently in effect in NJ was defined by the Comprehensive Black Bear Management Policy (CBBMP, expired 21 June 2021), which compiled policy already in place and recommendations to enhance current mitigation techniques such as implementing the "Be Bear Aware" educational program in 2007, promoting the use of bear-proof containers, lethal and non-lethal control, harvest management, as well as research and monitoring activities (NJOAL 2015).

The CBBMP recognized the following as key contributions to successful mitigation of HBI: the euthanasia of Category I bears (bears that pose an immediate threat to public safety), the presence of an education program, the role of law enforcement in reporting interactions, and black bear harvest. The New Jersey Division of Fish and Wildlife (NJDFW) reinstated a black bear hunting season in 2003, 2005, and from 2010 to 2020 to reduce HBI, and to provide recreational opportunities on a recovered game species. However, the bear harvest season was closed in 2021 when the CBBMP expired. Thus, it is imperative to identify *when* (e.g., post-harvest, post-education campaign) and *where* (e.g., in relation to the location of garbage availability or other food subsidies such as crops) HBI tend to arise on the landscape, to help refine management strategies and further mitigate HBI in a state that carries the highest coupled densities of black bears, humans, and urbanization in the Continental U.S.

Our overarching objective was to quantify potential shifts in HBI over time (i.e., annually), and during time periods that reflect different portions of a black bear's life cycle (which we define as "bear life cycle stages") and space (land cover type) in NJ, where HBI information has been collected over a period of nearly two decades.

Temporal Dynamics of HBI

Throughout our study period and currently, NJ has remained the state with the highest human population density in the country. It is widely accepted that HBI will increase with increasing human and bear populations.

We predicted certain types of HBI would vary across the bears' life cycle (Fig. 1.1). For instance, we expected HBI frequency and severity to be less during denning, a period when bears are relying on stored reserves during caloric depravation and are quite lethargic and (Rogers 1987). We predicted garbage and birdfeeder complaints should increase at times of annual natural food paucity (den emergence). We also predicted sightings would coincide more with the breeding season when bears are moving across the landscape in search of mates. We expected the sharpest increase in HBI, specifically agricultural damage, to occur during hyperphagia when bears need to acquire sufficient resources to stockpile calories for winter denning. HBI severity should also increase during hyperphagia, because bears are likely taking more risks for a reliable food reward (e.g., breaking into houses, Category I).

Spatial Dynamics of HBI

Similarly, we predicted HBI should coincide with anthropogenic areas given the reliable food sources available to bears in those landscapes. Because NJ presents a habitat mosaic that includes mature deciduous forests, agricultural crops, and (sub)urban habitat, we expected there to be a high frequency of HBI throughout intermixed land cover types that includes both anthropogenic and natural habitats, but nothing that would rival HBI frequency in more anthropogenic areas within increasing levels of urbanization (e.g., developed-high intensity areas)). We expected HBI would increase with areas of increasing crop cover (e.g., cultivated crops).

We have the unique opportunity to quantify the impact that urbanization, the black bear hunting season, the incident management program, and the "Be Bear Aware" educational campaign has had on the frequency and dynamics of HBI. Because HBI have been divided into different management-relevant "behavioral" categories, we can further quantify the impacts of such activities on management-rated bear behaviors (e.g., destruction of bird feeder, feeding on garbage, threatening a human or pet). This more refined information is key in distinguishing between different levels of HBI, which will likely require different mitigation strategies based on HBI severity, as well as *where* and *when* HBI tend to arise.

STUDY AREA

The northeastern U.S. is a heavily forested landscape intermixed with anthropogenic pressure and development. The NJDFW has delineated seven "Bear Management Zones" (BMZs) throughout NJ (Fig. 1.2), each with unique land cover. The CBBMP defined optimal black bear habitat as areas where ≥ 51% of the land is forested, ≤ 33% of the land is urban, and ≤ 26% of the land is agricultural. The BMZs are classified as follows (NJOAL 2015): BMZs 1 and 3 each have >76% forested land cover and provide the best habitat for black bears; BMZs 2 and 4 are ~50% forested and provide moderately suitable habitat for black bears; BMZ 5 has an average forest cover >30% and includes a mixture of wetlands, urban land, and agricultural land, making up a less suitable habitat; BMZ 6 includes land cover that is mostly (~79%) unsuitable for black bears; BMZs 1– 6 all encompass the northern portion of the state, where the black bear population is more abundant; BMZ 7 is the largest area, making up the entire southern portion of NJ. Suitable habitat exists in BMZ 7, but the black bear population in this portion of the state is quite low and has not been studied as extensively.

MATERIALS AND METHODS

Black Bear Management in New Jersey

In the 1950s, the NJ black bear population reached a historical low point (<100 bears) after hundreds of years of habitat alteration and unregulated killing. Black bears were granted game animal status in 1953, which helped stabilize the population. Limited hunting was legal in 10 seasons from 1958 – 1970 and resulted in a harvest of 46 bears. Based on bear harvest rates, the bear population status was re-assessed, and the NJ Fish and Game Council closed the bear hunting season altogether in 1971 (Lund 1980), which lasted through 2002 (NJOAL 2015). This 32-year hunting moratorium has been identified as a key factor in the recovery of the population since its low point in the mid-1900s (Raithel 2017), up to 3,158 bears as of 2020 (*unpublished data,* NJDFW). However, multiple factors likely contributed to this population recovery including: i) the 32-year hunting moratorium, ii) bear immigration from concurrently increasing populations in the adjacent states of Pennsylvania and New York, and iii) improved habitat quality associated with the maturation and integrated management of mid-Atlantic deciduous forests (McConnell et al. 1997).

The black bear management strategy in NJ, led by the CBBMP, included several components (NJOAL 2015):

(1) An education program targeting people in both rural and urban areas, where the CBBMP aims to expand upon its success. The bear aware program mimics those adopted in other states, where implementation of the program has resulted in the decline in certain types of HBI. The program includes the distribution of brochures, public presentations, and TV and radio public service announcements. The educational campaign was first implemented in 2007 and continues to this day (NJDFW 2018).

(2) Feeding bans, which have been shown to reduce the likelihood of HBI, and the CBBMP has focused on strictly enforcing these bans. The current ban is effective in mitigating intentional feeding and further efforts are aimed at preventing unintentional feeding (e.g., garbage, birdfeeders).

(3) Research activities have been in place in the northern NJ due to increasing bear densities over the last three decades. This research will continue by using the latest state-of-the-art science to gain a better understanding of black bear population dynamics and to reduce HBI. Also, NJDFW will continue conducting research on black bear populations in the southern half of the state, where bear densities are lowest.

(4) The CBBMP also relies on a bear habitat suitability analysis through the designation of seven BMZs (Fig. 1.2), which has been effective in ensuring that a healthy black bear population in NJ can be sustained.

(5) Regarding lethal and non-lethal control, NJDFW implements a Black Bear Rating and Response Criteria (BBRRC), which ranks bears as Category I (most severe), Category II (moderate severity), or Category III (least severe). Category I bears are euthanized, whereas other nuisance bears are managed through the continuation of the hunting season, depredation permits, capture with aversive conditioning, and protocol followed by law enforcement.

(6) The CBBMP has acknowledged the Department of Environmental Protection's efforts in acquiring open space as an adequate practice in preserving black bear habitat.

(7) The CBBMP has further identified black bear population stabilizing goals while minimizing negative interactions by ensuring a stable population within suitable habitats, and by reducing the amount of emigration from suitable to unsuitable habitat via regulated harvest.

Data collection

HBI data were collected between 2001 and 2017, as interactions were reported by the public, which included: the reporter's name, date, address, county, municipality, and an incident description. These calls were either made to the NJDFW Bear Response Unit (via a 24-hour action line) or were reported via communication between the local authorities and the NJDFW. Since 2000, these reports have been categorized as Category I, II, or III. Each HBI category also determines the response from the NJDFW. Category I comprises the highest severity category, where a bear has either been deemed an immediate threat to public safety, has caused agricultural damage, or >$1,000 USD (previously >$500 USD) worth of property damage. Category I bears were euthanized by the NJDFW, by local law enforcement, or by the landowner if the opportunity to safely do so was presented. Category II bears were nuisance bears that caused property damage <$1,000 USD (previously <$500 USD) and did not pose an immediate threat to public safety; the

NJDFW and law enforcement officials used aversive conditioning (e.g., rubber buckshot, noise bangers) to ensure Category II bears associated humans with a negative experience. Category III included the lowest severity category, where a black bear was sighted and (or) exhibited normal, non- to slight nuisance and non-threatening behavior (e.g., traveling through yard, eating from birdfeeder). Category III bears were not captured, unless during urban removal, and the contacted authority or caller was given instructions on bear-proofing the caller's surroundings.

Data preparation

We used ArcGIS Pro (ESRI 2021) to synthesize the HBI data for the spatial portion of our analyses. We analyzed the total number of HBI reported between 2001 and 2017 to determine if there were any missing address fields and if so, removed those records because we would not be able to spatially locate those points further via geocoding (n = 1,668). Additionally, if any HBI records had information in their incident descriptions about where the conflict occurred but did not have a specific street address (e.g., ¼ MI. N. OF RT. 50 & RT. 557), points were manually located using Google Earth (n = 956) and were removed prior to geocoding so the point location was not overwritten. The remaining HBI records (n = 27,855) were geocoded in ArcGIS Pro based on location attribute information. HBI were geocoded using the ArcGIS World Geocode Service and were assigned coordinates based on matching the ArcGIS Pro criteria field to the appropriate column in the dataset. For example, the Address, City, County, State, and Zip Code fields were matched with the Address, Incident Municipality, Incident County, State, and Zip Code fields in ArcGIS Pro. In the geocoding options, we set Intersection Connectors to "& and" to help the geocoding process to find those locations we initially, manually designated as intersections in the NJDFW Address field. Once we conducted the geocoding on records with missing locations (n =

27,855), the points that were manually located (*n* = 956) were added back to the geocoded records. The final dataset for the spatial and temporal analyses contained 28,811 HBI records for 2001 – 2017.

We then projected the coordinates associated with each HBI location onto the ESRI basemap (USA States, Generalized; ESRI 2017) to define spatial bounds for the state of NJ. To display these points, we used the given latitude and longitude for all the records (*n* = 28,811), and the "display XY coordinates" tool. We then overlaid land cover classification from the NLCD onto the clipped map. This overlay allowed us to match each HBI data point to a particular land cover type in ArcGIS Pro by using the "extract values to points" tool, which let us analyze the HBI dataset by three broad land cover categories: (1) agricultural, (2) anthropogenic, and (3) natural, which are represented by 15 refined land cover types. For example, agricultural habitat consisted of hay/pasture and cultivated crop land covers. Anthropogenic habitat contained developed – open space, low intensity, medium intensity, and high intensity land covers. Natural habitat included open water, barren land, deciduous, evergreen, and mixed forest, shrub/scrub, herbaceous, woody wetlands, and emergent herbaceous wetlands.

We divided the HBI data collected by the NJDFW into three time-categories: (1) 2001 – 2006, (2) 2007 – 2010, and (3) 2011 – 2017 (Appendix 2 – Table A2.1, Fig. A2.1). This separation was tailored to fit data from the National Land Cover Database (NLCD), which provides 30-m pixel resolution datasets from 2006, 2011, 2016, and 2019 (MRLC 2019). We matched historical NLCD data to our long-term den dataset as follows: (1) 2006 NLCD and 2001 – 2006 HBI data (2) 2011 NLCD and 2007 – 2011 HBI data, (3) 2016 NLCD and 2012 – 2016 HBI data, and (4) 2019 NLCD and 2017 HBI data.

We categorized these HBI data further by refined HBI into 16 sub-categories: aggressive, agricultural damage, birdfeeder, campsite/tent, entry (e.g., home, vehicle), garbage, human attack, nuisance (e.g., bear looking in windows, lying on deck), property damage >$1,000 USD, property damage <$1,000 USD, protected livestock, provoked dog attack, sighting, unprotected livestock, unprovoked dog attack, and urban bear.

Data analyses

We assessed temporal trends in HBI by considering two general temporal categories: by year and bear life cycle stage. When defining time periods that would reflect different portions of a black bear's life cycle (i.e., life cycle stage, Fig. 1.1), we gave each period a distinct date range without overlap. For this component of the analysis to align with our study site, we derived these life cycle periods from previous studies focusing on black bears in the eastern U.S., when available. We defined denning as the period between 1 December – 31 March (Garshelis 1978, Quigley 1982, Fimbel 1990, Tri 2013), den emergence and spring maintenance as the period between 1 April – 31 May (Eagle 1979, Quigley 1982), breeding, which aligns with female estrous and summer activity as the period between 1 June – 31 August (Beeman 1975, Garshelis 1978, Eagle 1979, Villarrubia 1982), and hyperphagia, where bears feed extensively to prepare for denning, as the period between 1 September – 30 November (roughly when denning begins) (Villarrubia 1982, Nelson et al. 1983, Fimbel 1990, *unpublished data* NJDFW).

For both the temporal and spatial analyses, we tested for differences in the observed versus expected frequency of interactions between bear life cycle stages and land cover types utilizing Pearson's chi-square and contingency tests (White and Gehrt 2009, Poessel et al. 2013) using the R package 'MASS' (version 7.3 – 47).

To determine the risk and magnitude of HBI for both the temporal and spatial analyses, we calculated odds ratios (ORs) and their associated 95% confidence intervals (CIs), which represented the probability of HBI risk rather than actual HBI risk (Vaske 2008). ORs represent the chance that a specific exposure (bear life cycle stage or land cover type) would lead to a specific outcome (HBI) versus the chance of an absence of that exposure creating the outcome (Bland and Altman 2000). For example, when an OR = 1.0, the chance of HBI occurring is not affected by the bear life cycle stage or land cover type; when an OR < 1.0, the chance of HBI occurring is lower, and when an OR > 1.0, the chance of HBI occurring is more likely than due to chance alone (Lipsitz et al. 1991). ORs were considered significant if their 95% CIs did not overlap 1.0 (Szumilas 2010).

RESULTS

Of the 28,811 HBI records analyzed, we found HBI to vary both in time and space (Figs. 1.2, and 1.3 – 1.18; Appendix 2 – Tables A2.1 – A2.5, Figs. A2.1 – A2.3). Most HBI were Category II (n = 15,564), followed by Category III (n = 10,849) then Category I (n = 2,398). Although bears often exhibit sex-specific differences in behavior, the results presented below pertain to *both* sexes pooled together, because the HBI data were not delineated by sex or individual bear when the incident was reported.

Temporal trends of HBI

Annual analysis of HBI across the 2001 – 2017 study period revealed HBI declined in 8 of the 10 years following a black bear hunting season (Fig. 1.3). Conversely, HBI increased the subsequent year, following the black bear harvest of 2010 and 2013 (Fig. 1.3). From 2010 to 2011, however, HBI only slightly increased, whereas from 2013 to 2014, increases in HBI were more apparent (Fig. 1.3). Additionally, HBI declined two years post-reinstatement of black bear harvest, except for the second year following both the 2012 and 2013 black bear hunting seasons (e.g., in 2014 and 2015, Fig. 1.3). The trend in HBI complaints appears to track the trend in bear population size estimates (Fig. 1.4). After the NJ bear aware education program was implemented in 2007, overall HBI continually rose until harvest was reinstated again in 2010, with declines in HBI not apparent until 2012 (Fig. 1.4).

We also found the frequency of HBI was significantly different across bear life cycle stages ($\chi^2 = 79.29$, $df = 6$, p-value < 0.001). Explicitly, we found overall HBI to be highest during the breeding and summer activity period ($n = 13{,}188$), followed by den emergence ($n = 7{,}145$) (Fig 1.7, Appendix 2 – Table A2.2). When examining each conflict level separately among bear life cycle stage, we found Category I conflicts occurred more frequently than expected by chance during breeding and summer activity period and hyperphagia (Appendix 2 – Table A2.2). We also found Category II conflicts occurred more frequently than expected during denning, den emergence, and hyperphagia (Appendix 2 – Table A2.2). Additionally, we found Category III conflicts occurred more than expected during denning and the breeding and summer activity period (Appendix 2 – Table A2.2).

Our HBI analysis of refined categories revealed sightings ($n = 9{,}575$), followed by nuisance interactions ($n = 6{,}877$), then garbage conflicts ($n = 6{,}319$) occurred most frequently overall (Fig. 1.9, Appendix 2 – Table A2.4). Again, when examining each refined HBI level separately among bear life cycle stages, we found that during the denning period, birdfeeder damage, nuisance complaints, property damage <$1,000, attacks on protected livestock and unprotected livestock, and unprovoked dog attacks occurred more than expected by chance (Appendix 2 – Table A2.4).

During den emergence, we found bird feeder damage, garbage complaints, property damage <$1,000 and >$1,000, attacks on protected and unprotected livestock, and urban bear complaints occurred more than expected (Appendix 2 – Table A2.4). During the breeding and summer activity period, aggressive bear behavior, agricultural damage, campsite/tent entry, nuisance complaints, sightings, unprovoked dog attacks, and urban bear complaints occurred more than expected (Appendix 2 –Table A2.4). During hyperphagia, aggressive bear behavior, agricultural damage, garbage complaints, human attack, property damage $1,000, attacks on protected and unprotected livestock occurred more than expected (Appendix 2 – Table A2.4). Because overall sightings, nuisance and garbage complaints were the most frequent of the refined HBI categories, we chose to focus more on those three refined categories (Fig. 1.9, Appendix 2 – Table A2.4).

Odds ratios (Fig. 1.8) by life cycle stage and HBI category (I – III) indicated that during denning, there were significantly lower odds of Category I HBI (OR = 0.73, 95% CI: 0.60, 0.88) occurring, compared to the other HBI categories. During den emergence, we found there were significantly higher odds of Category II HBI (OR = 1.17, 95% CI: 1.10, 1.23) occurring, compared to the other HBI categories. During the breeding and summer activity period, we found significantly higher odds of both Category I (OR = 1.09, 95% CI: 1.01, 1.19) and Category III (OR = 1.15, 95% CI: 1.10, 1.21) occurring, compared to Category II. During hyperphagia, we found significantly higher odds of both Category I (OR = 1.18, 95% CI: 1.07, 1.30) and Category II (OR = 1.06, 95% CI: 1.00, 1.12) occurring, compared to Category III.

Odds ratios (Fig. 1.10) indicated that during the denning period, there were significantly lower odds of garbage complaints (OR = 0.82, 95% CI: 0.73, 0.92) occurring, compared to the other refined HBI types. During den emergence, there was significantly higher odds of garbage complaints (OR = 1.41, 95% CI: 1.32, 1.50) occurring, compared to the other refined HBI types.

During the breeding and summer activity period, there were significantly higher odds of both nuisance (OR = 1.16, 95% CI: 1.10, 1.22) and sightings (OR = 1.26, 95% CI: 1.20, 1.32) occurring, compared to garbage complaints. During hyperphagia, there were not any significantly higher or lower odds of garbage complaints, nuisance interactions, or sightings occurring.

Spatial dynamics of HBI

We observed significant spatial differences in the frequency of HBI across land cover types ($\chi^2 = 1144.90$, $df = 4$, $p < 0.001$). Most HBI occurred within anthropogenic land cover ($n = 25{,}934$), followed by natural ($n = 2{,}200$), then agricultural land covers ($n = 677$) (Fig. 1.11, Appendix 2 – Table A2.3,). When exploring each HBI level by land cover type, we found Category I HBI occurred more than expected by chance in natural land cover types (Appendix 2 – Table A2.3). We found Category II HBI occurred more than expected in anthropogenic and natural land covers (Appendix 2 – Table A2.3). We also found Category III HBI occurred more than expected in anthropogenic land cover (Appendix 2 – Table A2.3).

The analysis of refined HBI categories Indicated that sightings, followed by nuisance and garbage complaints, were the most frequent overall (Fig. 1.13, Appendix 2 – Table A2.5). Similarly, when exploring refined HBI categories independently among land cover types, we found that in natural landscapes, agricultural damage, campsite/tent, property damage <$1,000 and >$1,000, attacks on protected livestock, and provoked dog attacks occurred more than expected by chance (Appendix 2 – Table A2.5).

Odds ratios (Fig. 1.12) by land cover type and HBI category (I – III) showed Category I HBI were significantly more likely to occur within agricultural (OR = 9.31, 95% CI: 7.95, 10.91) and natural (OR = 1.47, 95% CI: 1.28, 1.69) land covers. We found Category II HBI were more likely to occur in anthropogenic landscapes (OR = 1.23, 95% CI: 1.14, 1.33), as well as Category III HBI (OR = 1.34, 95% CI: 1.23, 1.45). Again, there were higher frequency of sightings, nuisance interactions, and garbage complaints; however, we did not find higher odds of any of these three refined HBI categories occurring within agricultural or natural land covers (Fig. 1.18, Appendix 2 – Table A2.5). We found there were significantly higher odds of garbage complaints (OR = 1.49, 95% CI: 1.34, 1.65), nuisance HBI (OR = 1.34, 95% CI: 1.22, 1.47), and sightings (OR = 1.29, 95% CI: 1.18, 1.40), occurring in anthropogenic areas (Fig. 1.18).

DISCUSSION

HBI are quite complex, and our findings shed light on the relationships that exist between specific temporal and spatial dynamics, and the occurrence and severity of HBI.

Temporal dynamics of HBI

Conflict severity varied widely from year to year (Fig. 1.3, Appendix 2 – Figs. A2.2 – A2.3), but also by bear life cycle stage, and was important in explaining disparities in HBI frequency (Fig. 1.7, Appendix 2 – Table A2.2).

Overall, trends in HBI complaints appeared to track trends in bear population estimates (Fig. 1.4). HBI did decline each year following regulated bear harvest reinstatements, except in 2011 and 2014 (Fig. 1.4). Hunting itself could be generating a "landscape of fear" (Oriol-Cotterill et al. 2015), where non-habituated bears (Category III) avoid certain habitat types that may increase the likelihood of HBI the following year, which could explain the apparent increases in HBI in 2011 and 2014. Regulated bear harvest in NJ has been found to reduce nuisance HBI the subsequent year by removing black bears, more specifically nuisance black bears, from the landscape (Raithel et al. 2017). We also found HBI declined consistently two years post-reinstatement of the black bear harvest, except for the second year following 2012 and 2013 (i.e., in 2014 and 2015, Fig. 1.4), which indicates a lag effect of bear harvest on HBI following a reduction in population size and could simply be tracking a sows' typical two-year reproductive cycle. However, hunting related effects on HBI could be acting synergistically with a lack of natural resource availability, such as mast failure (Garshelis 1989; McDonald et al. 1994; Noyce and Garshelis 1997; Ryan et al. 2004, 2007; Howe et al. 2010), warranting future analyses of the links between harvest rates and natural resource fluctuations to gain better insights into variability in HBI over time (Obbard et al. 2014).

We found a dramatic increase in HBI from 2013 to 2014 was correlated with an increase in bear population size in 2014 [Lincoln-Petersen population estimate = 3,606 bears (95% CI: 2242, 4971), Fig. 1.4], the highest the bear population had ever been (*unpublished data*, NJDFW). However, increases in HBI from 2013 to 2014 may have also been attributed to a decrease in hard mast production from 2012 to 2013 (Fig. 1.5). Natural forage, such as hard mast, is a staple food source for bears (e.g., acorns, specifically from oaks species Pelton 1989), especially during hyperphagia to help them prepare for winter denning (Vaughan 2002). Poor hard masting years are driven in part by increased drought frequency (Sork et al. 1993, Howe et al. 2012). Given the ongoing and predicted temperature increase and drought frequency in NJ, particularly during the spring (NCDC 2019) when natural forage is fruiting (Inouye et al. 2000), natural foods could become limiting to bears, which could increase HBI. However, NJ has not conducted consistent surveys for hard and soft mast production, therefore we compared multiple states surrounding NJ, to determine what other mast data sources were available to use in post-hoc tests (Appendix 1). We found West Virginia (WV) to have comparable ecoregions, climate, and masting species as

NJ (Appendix 1). Therefore, we used hard mast data collected by the WV Division of Natural Resources, from indices calculated as [(abundant observations/total observations) + (common observations × 0.5)/total observations)] × 100, Barton, et al. 2018)], for all combined oak species, as a proxy for NJ hard mast production (e.g., Raithel 2017). For ease in post-hoc analyses, we converted WV mast indices each year to a categorical variable, which were derived from lower, middle, and upper quantiles and represented poor, average, and good hard mast production years. Post-hoc tests indicated significant differences in Category III HBI with respect to hard mast productivity (ANOVA, $F_{2, 14} = 3.78$, p-value = 0.04), specifically between average and good hard masting years, with lower Category III HBI following ($t + 1$) average hard masting years (t), and higher Category III HBI following ($t + 1$) good hard masting years (t). Bears are likely taking advantage of the abundant hard mast following a good hard mast year, thus increasing their likelihood of being sighted. Nonetheless, the NJDFW could benefit from conducting annual hard and soft mast surveys to identify if temporal fluctuations in nuisance and severe HBI is sensitive to year-to-year variation in mast production.

Overall HBI did not steadily decline after the implementation of education program in 2007 (Fig. 1.4). HBI did not decline again until 2010, but HBI levels still surpassed those of 2007 (Fig. 1.4). The bulk of the education material was produced in 2007, 2008 and 2010, with most personal contact programs occurring from 2007 to 2009 (NJDFW 2018), which could explain a lagged reduction in HBI. Although education material may not necessarily alter human behavior with respect to HBI (Gore et al. 2008, Baruch-Mordo et al. 2011, Campbell 2012, Dietsch et al. 2018), the effectiveness of education programs and materials have been tested elsewhere, with evidence of information retention and use in limiting attractants that can sequentially reduce HBI. For example, Marley et al. (2017) found educating people (e.g., in how to reduce garbage attractants, to aversively condition bears, and to effectively contact wildlife management) not only decreased the likelihood of HBI by 5% for every 1% of the human population educated, but this behavioral change by humans was also predicted to persist. However, one should interpret the findings by Marley et al. (2017) cautiously, given results were theoretical and were based on optimistic scenarios (e.g., humans uniformly implementing techniques to deter HBI) (Dietsch et al. 2018). Though, the education program itself may have negatively biased residents prompting significant dissension of black bears in local communities (Dietsch et al. 2018), thereby increasing the number of HBI reported after the education program was implemented. Nonetheless, the increase in HBI post-education program is likely an outcome of increasing bear and human populations (Fig. 1.3) in NJ over the past couple of decades, as well as an increase in the reporting of HBI following the "Be Bear Aware" educational campaign (Wilbur et al. 2018). HBI varied by bear life cycle stage (Fig. 1.7, Appendix 2 – Table A2.2). The frequency and severity of HBI was lowest during denning, and HBI increased during den emergence (Fig. 1.7, Appendix 2 – Table A2.2). The frequency of HBI ranked second highest during den emergence and encompassed more nuisance behavior (e.g., Category II, Fig. 1.7, Appendix 2 – Tables A2.2 and A2.4). Many of these Category II incidents included garbage complaints, but also calls about bears on porches looking into windows. Bears may be exhibiting bolder, nuisance behavior to exploit readily available, higher-quality anthropogenic resources after den emergence, particularly once their physiological state returns to normal (e.g., after 2 to 3 weeks post-den emergence, Nelson et al. 1983). This bolder behavior by bears seems plausible, because there were higher odds of more nuisance, Category II HBI occurring during den emergence, relative to the other main HBI categories (Fig. 1.10).

We found both garbage and birdfeeder complaints increased during den emergence, but garbage complaints (*n* = 6,319) were higher than birdfeeder complaints (*n* = 1,089) overall (Fig.

1.9, Appendix 2 – Table A2.4). Since the implementation of the bear aware program in 2007, the NJDFW has emphasized the removal of garbage, birdfeeders, and other attractants when bears are active and out of their dens (1 April – 30 November). The number of garbage complaints varied after 2007 and eventually declined (Fig. 1.14a), and birdfeeder complaints increased after 2007 but declined from 2008 to 2017 (Fig. 1.16a). A Pearson's correlation post-hoc analysis revealed birdfeeder complaints and bear population estimates have a weak, negative correlation ($r = -0.14$), which along with the Julian Date trend in birdfeeder complaints (Fig. 1.16b), indicate that emphasizing birdfeeder removal may be curtailing birdfeeder complaints overall.

HBI were most frequent during the breeding and summer activity period (Fig. 1.7, Appendix 2 – Table A2.2). This may stem from black bears encountering humans and anthropogenic resources as bears move throughout their home range, particularly in the intermixed landscape of NJ. Typical annual home ranges for black bears in NJ can span up to 70 mi^2 for males and up to 18.5 mi^2 for females (Fimbel et al. 1991, McConnell et al. 1997), with evidence of male home ranges more than doubling during the breeding season in this part of the U.S. (e.g., Alt et al. 1980), which may help to explain increased HBI during the summer.

During the breeding and summer activity period, increased dominance behavior among black bears is often observed (e.g., when sows kick out yearlings to raise future litters, Kilham and Spotila 2021; among breeding males, Kovach and Powell 2003), where dominant bears drive out subordinates, thus increasing the likelihood of HBI by displaced, less dominant bears. There is a propensity for most female black bears to come into estrus early in the breeding season (e.g., late June or early July, Fraker et al. 2006), where dominant males are very active and may reduce the amount of their own feeding (Rogers 1987, Coy and Garshelis 1992, Garshelis and Hellgren 1994), both of which may further explain the reduced garbage complaints between Julian Dates 152 – 179, as we observed (Fig. 1.15).

Sightings were the most frequent refined HBI category during the breeding and summer activity period (Fig. 1.8, Appendix 2 – Table A2.4), when more people are out on the landscape that time of year (e.g., recreating, working). The NJDFW education program has encouraged people to call in sightings, which could explain the higher frequency of sightings overall (Fig. 1.9, Appendix 2 – Table A2.4). Yet, because nuisance and garbage complaints were higher than the remaining refined categories during the summer (Fig. 1.9, Appendix 2 – Table A2.4), this suggests that when male bears are feeding during the breeding period, they may be taking risks for food to acquire continuously available trash with minimal foraging cost. These risks for food rewards were also apparent by higher odds of Category I complaints during the breeding and summer activity period (Fig. 1.8), which were frequently home, tent, or vehicle attempted or actual entries (Appendix 2 – Table A2.4). Given the increased odds of more severe HBI (Category I) during the breeding and summer period (Fig. 1.8), management should reinforce that the public continue to reduce attractants in and around their homes and vehicles, to ensure sightings do not become severe HBI, like home and vehicle entries.

Overall HBI did not coincide more with hyperphagia compared to the other life cycle stages as we had predicted (Fig. 1.7, Appendix 2 – Table A2.2). However, we observed more nuisance HBI (Category II) occurring during hyperphagia, when bears are highly active and more mobile on the landscape (Fig. 1.7, Appendix 2 – Table A2.2). Home ranges for black bears can also be quite extensive during hyperphagia, as they are trying to maximize their caloric intake (Noyce and Garshelis 2011). Thus, as bears extend their home ranges in search of food to prepare for winter denning, they are acquiring a diversity of resources along the way, which may explain why there were higher odds of Category I and II occurring during hyperphagia (Fig.1.8). Bears may be trying to access hard mast that may be more spatially clustered among homes within forested areas. Though, many of the Category I complaints consisted of attacks on protected livestock (e.g., chickens in a coop; Appendix A2 – Table A2.4). Given we cannot directly manage for natural resources in more forested areas, our results indicate management efforts should stress that residents continue to protect their livestock (e.g., through permanent electric fencing, livestock protection dogs, synchronized and (or) penned birthing of livestock, Taylor and Phillips 2020), to reduce the likelihood of more severe HBI during hyperphagia, especially following years of poor mast production.

We found garbage HBI complaints declined considerably after the breeding and summer activity period into and throughout hyperphagia, (Appendix 2 – Fig. A2.10). This downward trend in garbage complaints during hyperphagia, along with lower birdfeeder complaints, indicates bears are using natural resources more than anthropogenic ones during this period and implies there are likely an abundance of natural resources available to bears on the highly diverse and intermixed landscape of NJ. This trend in garbage complaints during hyperphagia also suggests residents may be more diligent during the fall in removing these specific bear attractants (e.g., trash and birdfeeders).

Spatial dynamics of HBI

HBI in NJ has been on the rise in anthropogenic landscapes, yet overall HBI has declined in recent years (e.g., 2014 – 2017, Fig. 1.4). Because there were higher odds of Category III HBI occurring in anthropogenic landscapes, compared to the other HBI categories (Fig. 1.12), this demonstrates that not all HBI that occur in anthropogenic areas are negative, because most of the

Category III HBI are sightings. However, when looking at the refined HBI categories, there were higher odds of garbage, followed by nuisance complaints in anthropogenic areas (Fig. 1.18). In NJ, urban growth and new development has been estimated at nearly 17,000 acres per year (Hasse and Lathrop 2001). As of 2020, urban lands in NJ constitute > 44% of the landscape – which is the highest in the country (NJDEP 2020), and is projected to increase to 62% by 2060 (Nowak and Greenfield 2018). Recent estimates of human population in NJ hovers around > 9 million, which equates to > 1,244 people per mi^2, and has increased by 2.4% between 2010 and 2017 (NJDLWD 2018). With human pressure comes an increase in the availability of anthropogenic attractants such as garbage, which has been recently estimated at >23 million tons produced annually throughout NJ, and growing annually at an average rate of ~2% of disposed waste and recycling products since 1995 (NJDEP 2019). Bears are highly opportunistic omnivores, and it seems intuitive that the increased frequency of HBI in anthropogenic landscapes is due to the increased human presence and assortment of anthropogenic attractants. Given bears are omnivorous, exhibit high behavioral plasticity, and have extensive home ranges (Fimbel et al. 1991, Mitchell and Powell 2007, Mayor et al. 2009), our results suggest that bears may be more prone to lower-severity (Category III) and nuisance (Category II) HBI when they use anthropogenic landscapes (Fig. 1.12). Although human populations have been growing over our study period (Fig. 1.3), the proportion of more severe HBI is quite small relative to other categories in these anthropogenic landscapes (Appendix 2 – Table A2.1). Higher odds of these more benign HBI (Category III) in anthropogenic landscapes could indicate potential coexistence among humans and bears in these habitats (Morehouse and Boyce 2017).

Although raw numbers of overall HBI rose disproportionately in habitats that were classified as anthropogenic (e.g., developed open space, low, medium, and high intensity, Fig.

1.11), there were significantly higher odds of Category I HBI occurring in agricultural land covers (e.g., pasture-hay and cultivated crops, Fig. 1.12). Agriculture and farmland in NJ comprises roughly 16% of the state and produces substantial food subsidies, such as corn (NJDA 2020). Corn (e.g., field and sweet corn) is a known important food source for bears (Dykstra 2015), likely contributing to the increased frequency of more severe HBI (Category I, McConnell et al. 1997). Further, higher odds of Category I HBI (Fig. 1.12) in agricultural landscapes could simply be a byproduct of HBI reporting bias and management vigilance (Baruch-Mordo et al. 2008), where agricultural landowners may be more willing to report conflict because of economic losses (Messmer 2000). HWIs are inherently multifaceted (Nyhus 2016), driven also by sociopolitical factors (e.g., stakeholder livelihood, history of conflict management, Zimmermann et al. 2020). Given this complexity in HWI, future research should be conducted to determine a level of education and tolerance necessary to minimize HBI in NJ.

Additionally, to determine the presence of reporting bias, future HBI research in NJ could benefit from categorizing HBI events under the three levels of human-wildlife conflict designated by Madden and McQuinn (2014). Currently, HBI events as they are categorized by the NJDFW, fall into the Level 1 (L1), defined as an initial dispute (Madden and McQuinn 2014). However, as descriptions of the event are recorded by the respondent, if a reporting individual is fearful of bears, or a prior history of conflict exists and the reporter provides information about their perception of how the prior conflict was previously controlled, the HBI category (I – III) could be delineated further as Level 2 (L2), with the reporting individual having underlying conflict. Finally, if HBI are left unregulated and the public perceives the event as life-threatening, either physically or to their livelihoods, the HBI category (I – III) could be classified further as Level 3 (deep-rooted conflict). This classification would essentially tailor management responses not only to the nature of the conflict, but it would account for the emotional state of the resident or landowner reporting the incident. This would help develop a spatial assessment of potential bias in the reporting and classification of HBI based on resident and landowner calls. We also suggest the refined levels of HBI (e.g., sightings, nuisance- and garbage-related) be used to build predictive models based on the spatio-temporal factors that lead to increased HBI, which will help managers prioritize, strategize, and implement appropriate HBI mitigation techniques.

The heterogeneous landscape throughout NJ, particularly in high-quality bear habitat in northwestern NJ (e.g., BMZs 1–4, and portions of BMZ 5, Fig. 1.2) is intermixed with various habitat types available to bears (Appendix 2 – Fig. A2.1). Previous research found the four dominant habitat types in order of usage by bears encompassed deciduous forest (>50% crown closure), deciduous wooded wetlands, cropland/pastureland, and single unit residential areas (Carr and MacKenzie 2003). The tendency of bears to favor single-unit residential areas as a dominant habitat type (Carr and MacKenzie 2003) aligns with our results, where ~61% of HBI occurred in developed, open space which constitutes mostly large-lot single-family homes (MRLC 2019). A study examining how recolonizing black bears distributed in response to housing density found bears favored exurban areas over areas of higher development (Evans et al. 2017). In our study, higher frequency of HBI in developed, low intensity areas (~22%), and in deciduous forests (~6%), may be explained by natural areas lying proximate to housing developments with lower housing density, but this would require further study.

There were significantly higher odds of Category I HBI in natural land cover types (Fig. 1.12), which may be explained by the landscape assemblage. This explanation seems plausible, particularly because high-quality bear habitat in NJ is comprised of >68% of the four dominant habitat types that bears use (e.g. deciduous forest with >50% crown closure, deciduous wooded wetlands, cropland/pastureland, and single unit residential areas, Carr and MacKenzie 2003). Our results may also be indicative of a risk-reward trade-off (e.g., Zeller et al. 2019), where bears are taking less severe risks in certain habitat types (e.g., anthropogenic), and only encounter humans by happenstance (e.g., Category III) when they are actively searching for forage in natural land covers (Fig. 1.12).

CONCLUSIONS

As landscape conversion encroaches more into bear habitat, understanding *when* and *where* HBI tend to arise is imperative to help define effective management actions that will help mitigate future HBI in NJ. Management strategies, beyond yearly application, should focus on specific life cycle events by limiting anthropogenic stimuli during these periods (e.g., access to garbage, birdfeeders, barbeque grills, pet food) to help reduce the likelihood of HBI escalating to a more severe category (i.e., Category I). During den emergence, management should work toward better securing garbage in bear-proof containers, which could be in the form of providing funding for or containers themselves, particularly in developed-open space, low intensity areas where the majority (83%) of overall HBI occurred. During the breeding period, management should reinforce that the public do more to reduce attractants to decrease home and vehicle entries, which could in turn decrease the likelihood of sightings turning into a nuisance (Category II) or severe (Category III) HBI. During hyperphagia, management should intensify awareness to the public for protection of domestic livestock and areas surrounding homes. Management efforts could consist of other measures beyond and in addition to electric fencing around domestic livestock (e.g., chicken coops, rabbit hutches), such as non-lethal taste aversion, which on its own has been successful in reducing black bear damage and deterring black bears from human foods [e.g., thiabendazole

(TBZ), Polson 1983, McCarthy and Seavoy 1994, Ternent and Garshelis 1999]. Management should mandate garbage and attractant control throughout the entire year but especially during den emergence and the breeding period, only if coupled with distributing fines to homeowners and business for violating ordinances (Taylor and Phillips 2020). Further, Garshelis et al. (2020) showed HBI could be reduced when HBI mitigation techniques were transferred to homeowners (e.g., homeowner responsible for reducing or securing attractants, allowing more residents to legally kill nuisance bears rather than wait for bear managers or law enforcement to respond, extended the hunting season for specific hunters to target crop depredating bears, Garshelis et al. 2020), where NJ may benefit from a similar policy shift in management. We also suggest regulated harvest continue to overlap with hyperphagia and early denning, given its effectiveness in reducing nuisance bear behavior (Raithel 2017). Further, we recommend the NJDFW increase their collaring efforts of both conflict and non-conflict bears, and among different age and sex classes, to identify how bears are using the landscape and resources, and if denning chronology may be a factor in explaining HBI during the denning months (Fig. 1.7, Appendix 2 – Table A2.2). With the projected trajectories of human population and development growth in NJ, anthropogenic food sources will inevitably increase, along with mirrored patterns in HBI. Thus, including aspects of reproduction (see Chapters 2 and 3) and life history events may help to further explain years of increased HBI in NJ (e.g., Shull 1994), and be able to inform better HBI management practices.

Despite the importance of spatiotemporal ecological factors in determining the frequency and levels of HBI, it is crucial to recognize that the complexity of HBI is also driven by a myriad of other factors that lay within social and cultural strata (Baruch-Mordo et al. 2009). Humans' perception of HBI can vary based on their own inherent individual characteristics (e.g., demographic characteristics, attitudes, prior conflict experience) but also as collective social units, whereby feedback of HBI can be disseminated among social groups (Lischka et al. 2018). Thus, social dimensions are to consider when attempting to mitigate HBI (Lischka et al. 2018). We stress the reinforcement of educational programs, including information about the temporal and spatial differences in HBI that are all generally driven by different levels of anthropogenic change (i.e., land conversion, urbanization, climate change), as well as involvement of local communities in discussing HBI with black bear managers. Our work demonstrates that the success of HBI mitigation measures requires an examination of HBI within *both* temporal and spatial constructs.

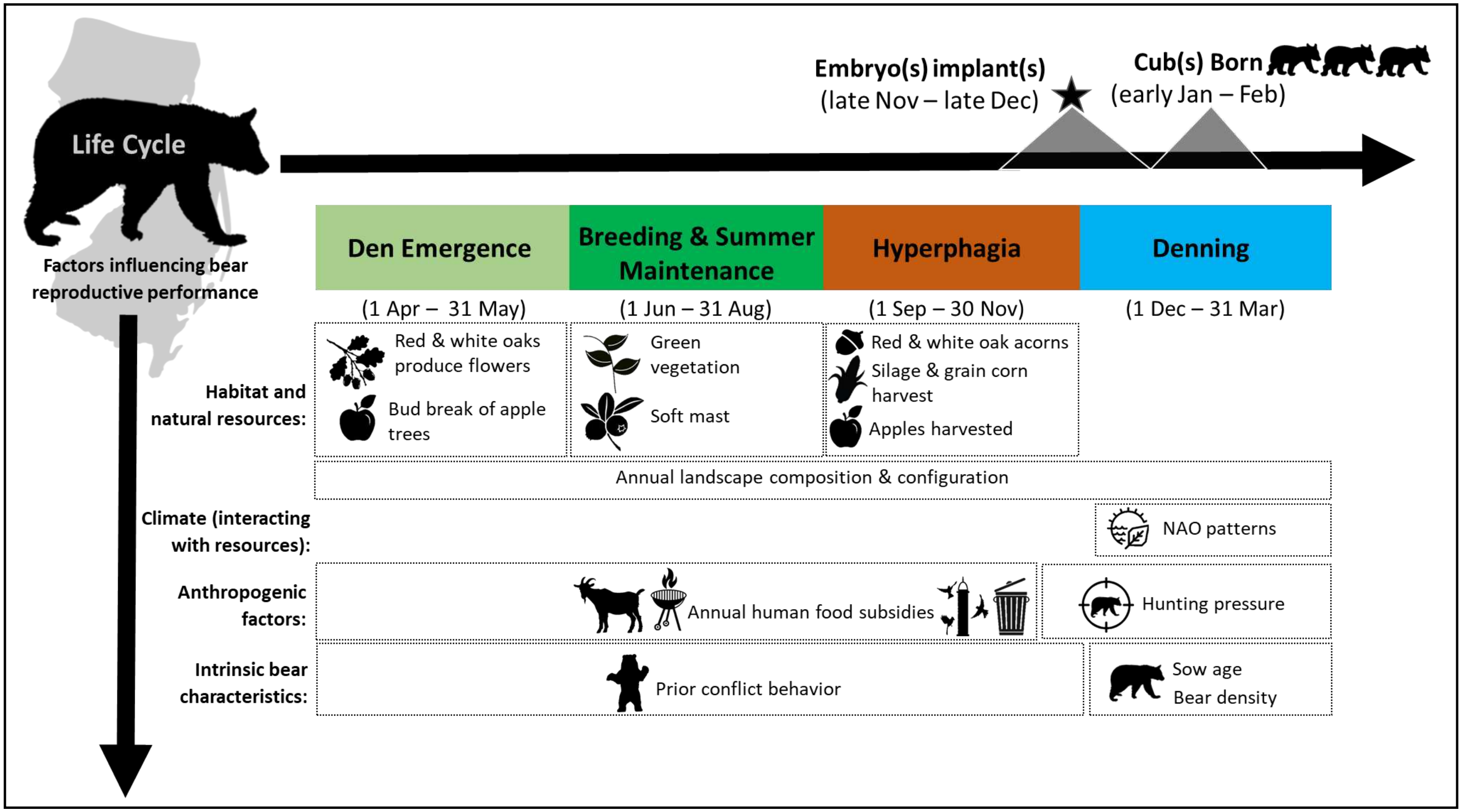


Figure 1.1. Annual life cycle of female (sow) American black bear (*Ursus americanus*) and the factors influencing sow reproductive performance in New Jersey and the northeastern U.S.

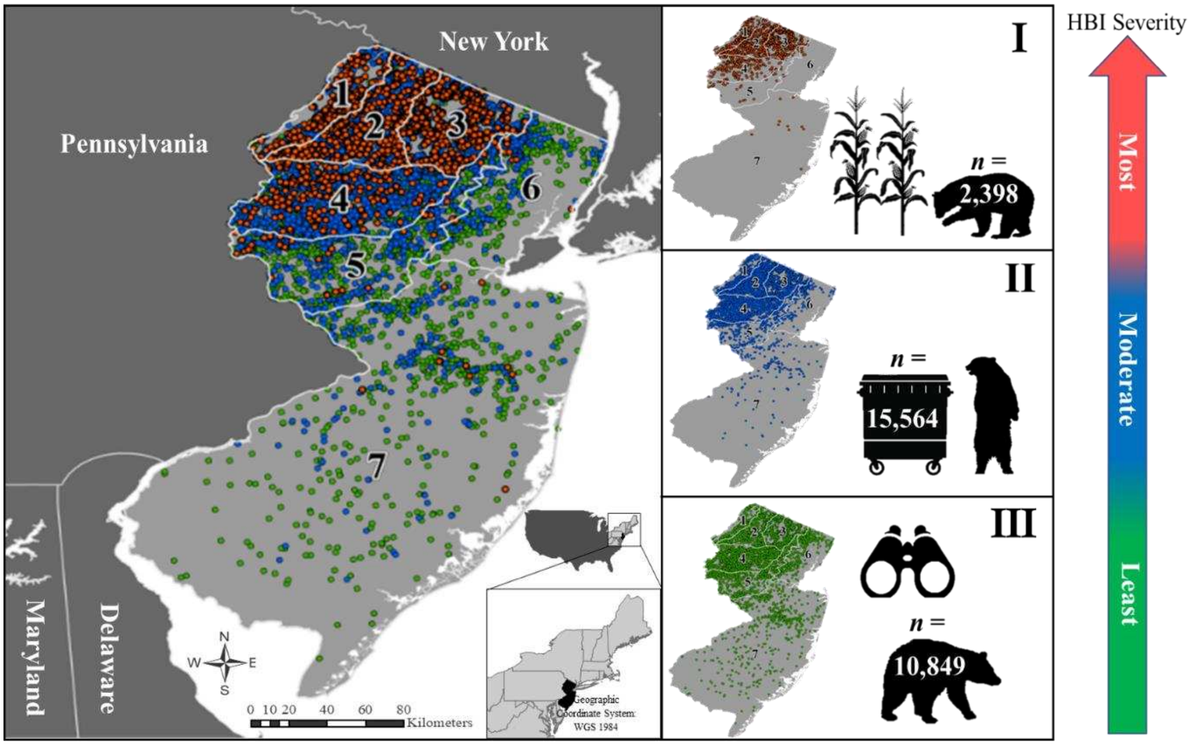


Figure 1.2. Spatial distribution of human bear interactions (HBI) (*n* = 28,811) among the seven current American black bear (*Ursus americanus)* management zones (BMZs) in New Jersey, 2001 – 2017. HBI points are colored by HBI category: I (most severe, e.g., aggressive bear), II (moderate severity, e.g., bear getting into garbage), and III (least severe, e.g., bear sighted walking through yard).

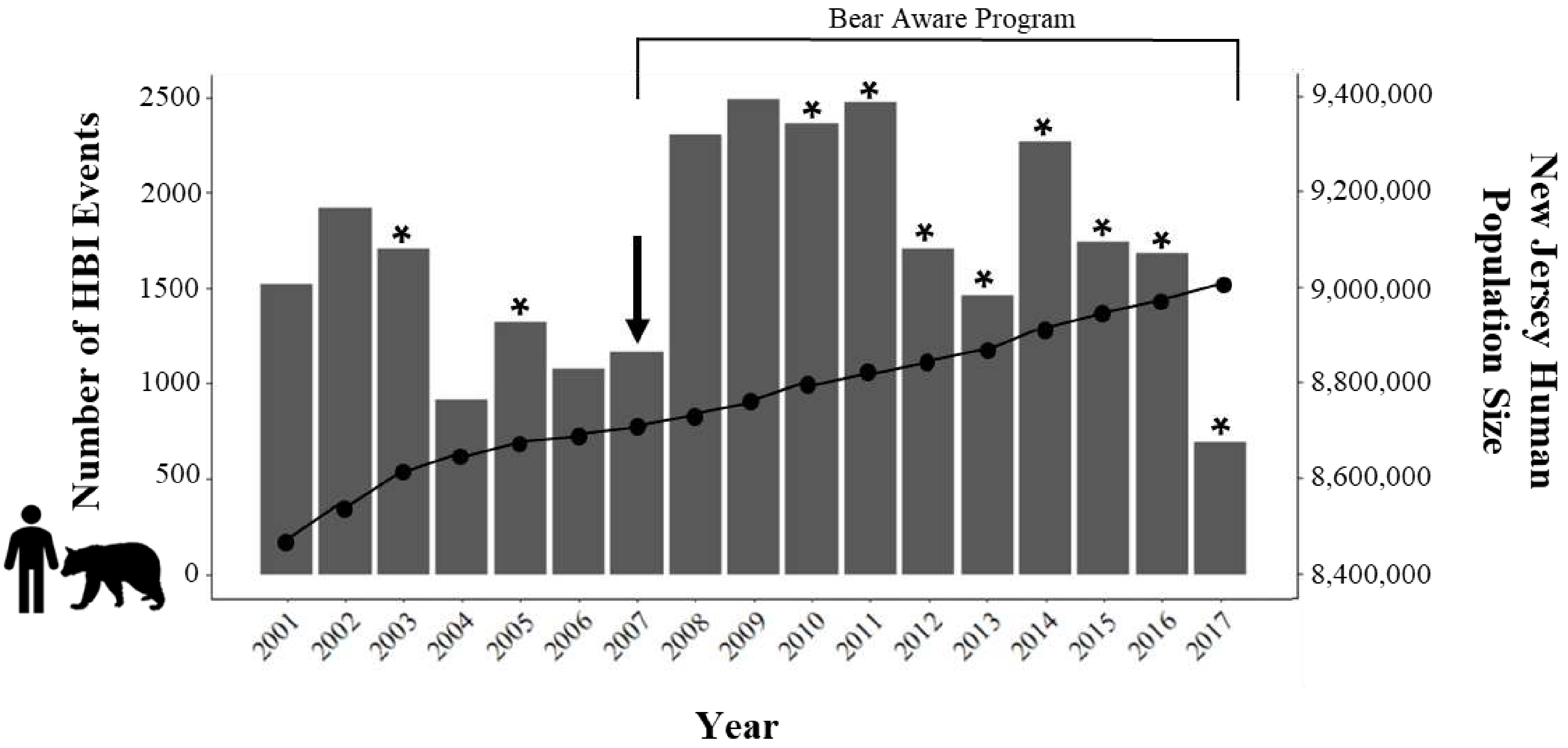


Figure 1.3. Annual trend in human-American black bear (*Ursus americanus*) interactions (HBI) data (*n* = 28,811) collected throughout the state of New Jersey, 2001 – 2017. An (*) denotes years (2003, 2005, 2010 – 2017) black bear harvest was allowed in New Jersey, and the arrow denotes when the New Jersey "Be Bear Aware" education program was implemented. Years where there is a black dot, is the annual New Jersey human population size.

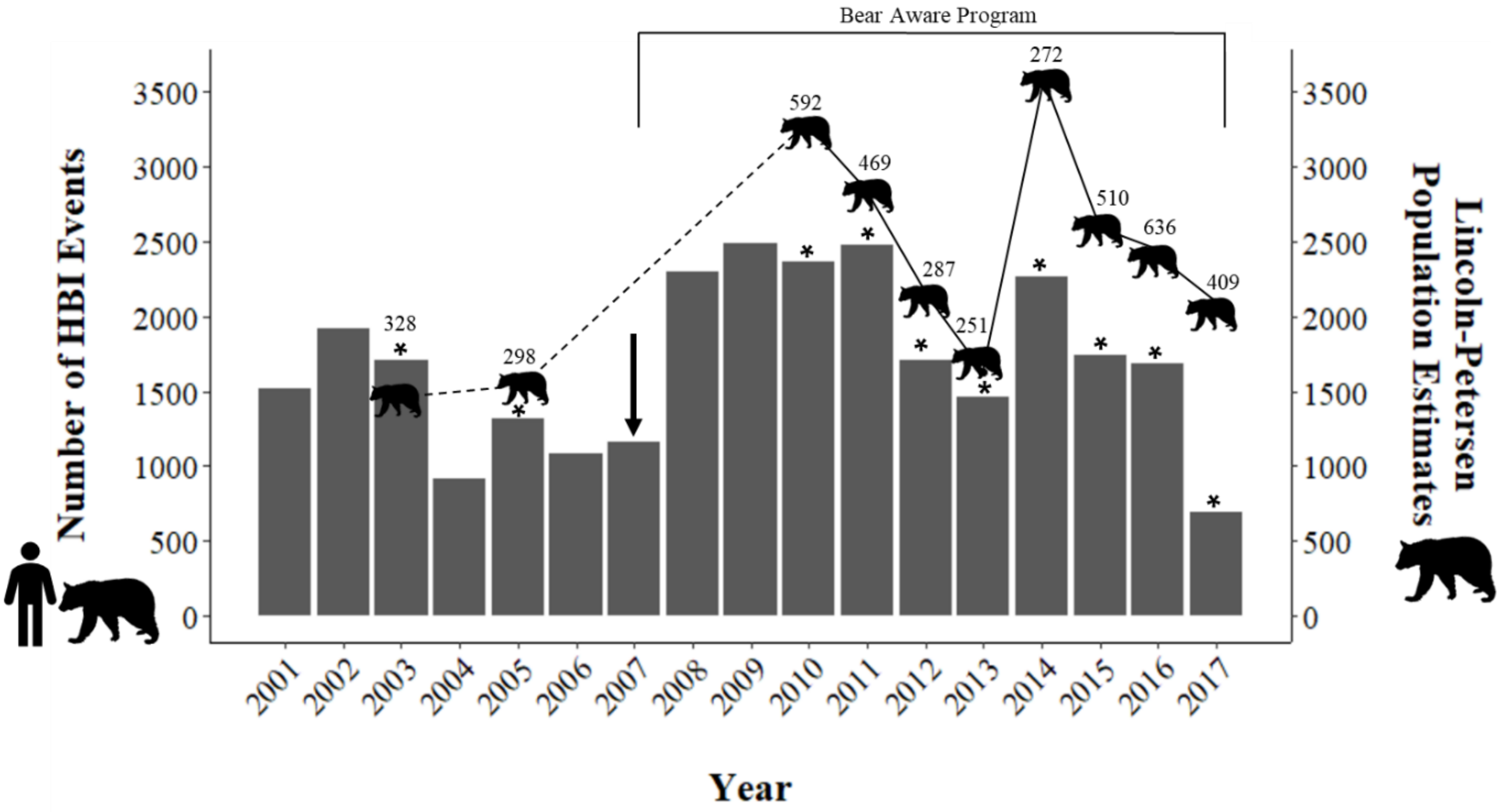


Figure 1.4. Annual trend in human-American black bear (*Ursus americanus*) interactions (HBI) data (*n* = 28,811) collected throughout the state of New Jersey, 2001 – 2017. An (*) denotes years (2003, 2005, 2010 – 2017) black bear harvest was allowed in New Jersey, and the arrow denotes when the New Jersey “Be Bear Aware” education program was implemented. Years where there is a black bear symbol, are the estimated population size of bears using the Lincoln-Petersen (L-P) estimator, where a dotted black line indicated years when L-P estimates are unavailable. The number above each of the bear symbols represent the total number of bears harvested that year.

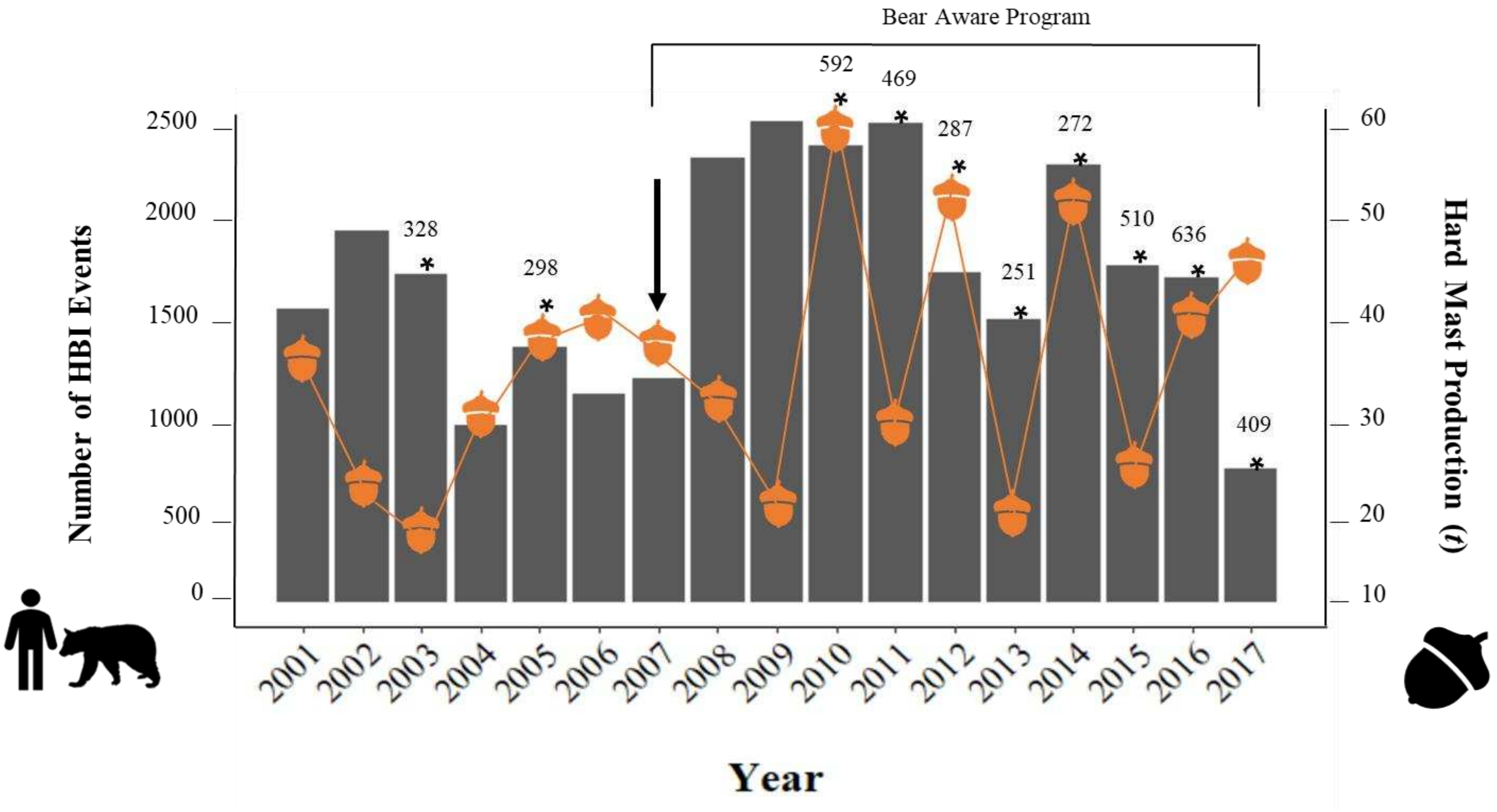


Figure 1.5. Annual trend in human-American black bear (*Ursus americanus*) (HBI) data collected throughout the state of New Jersey, 2001 – 2017 (*n* = 28,811). An (*) denotes years (2003, 2005, 2010 – 2017) black bear harvest was allowed in New Jersey, and the arrow denotes when the New Jersey "Be Bear Aware" education program was implemented. The orange acorn symbols represent the estimated hard mast production that year (*t*). The number above each of the grey bars represent the total number of bears harvested that year.

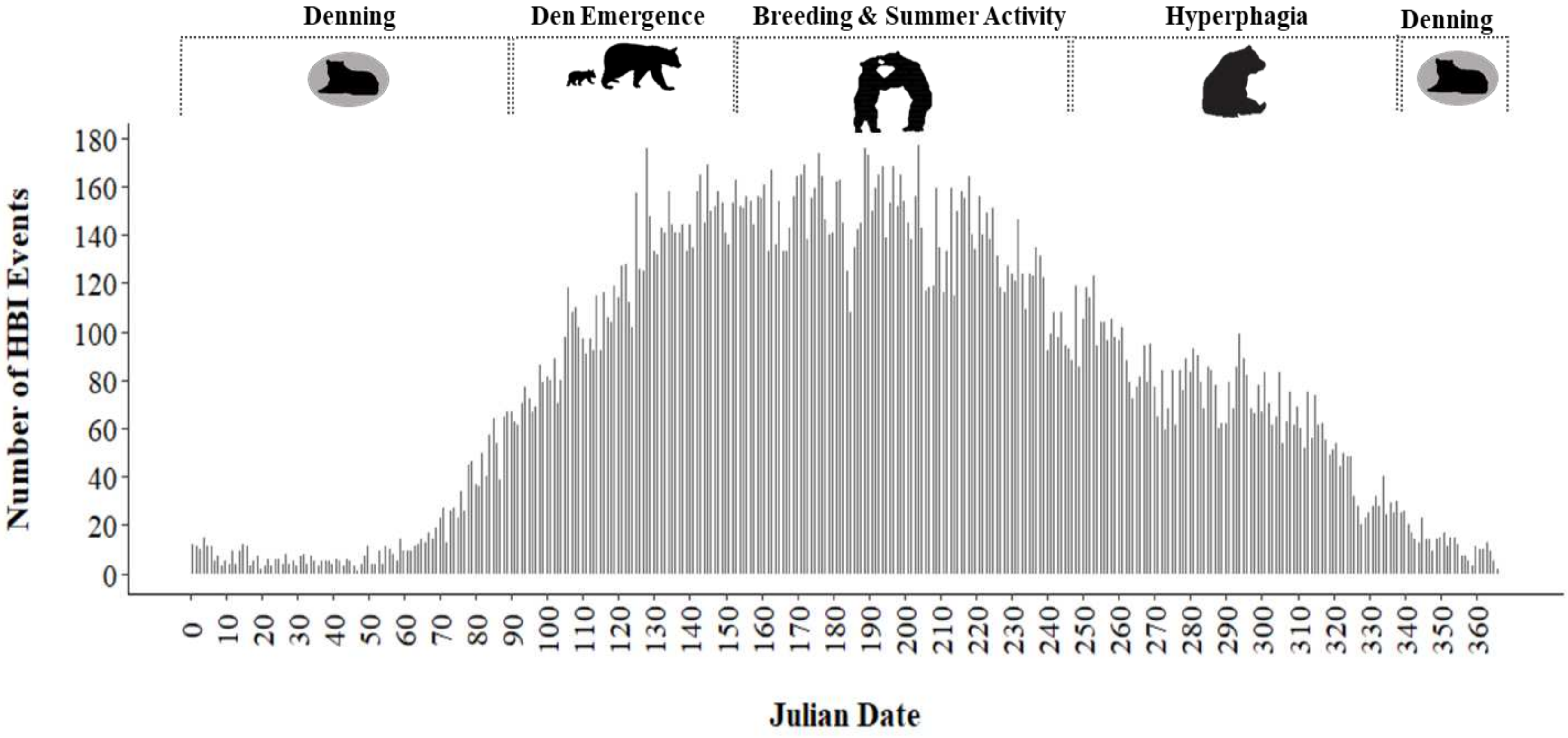


Figure 1.6. Julian Date variation of human-black bear interaction (HBI, *n* = 28,811) locations, presented over bear life cycle stages: Denning (1 December – 31 March; Julian Date = 001 – 090 and 335 – 365), Den Emergence (1 April – 31 May; Julian Date = 091 – 151), Breeding and Summer Activity (1 June – 31 August; Julian Date = 152 – 242), and Hyperphagia (1 September – 30 November; Julian Date = 244 – 334).

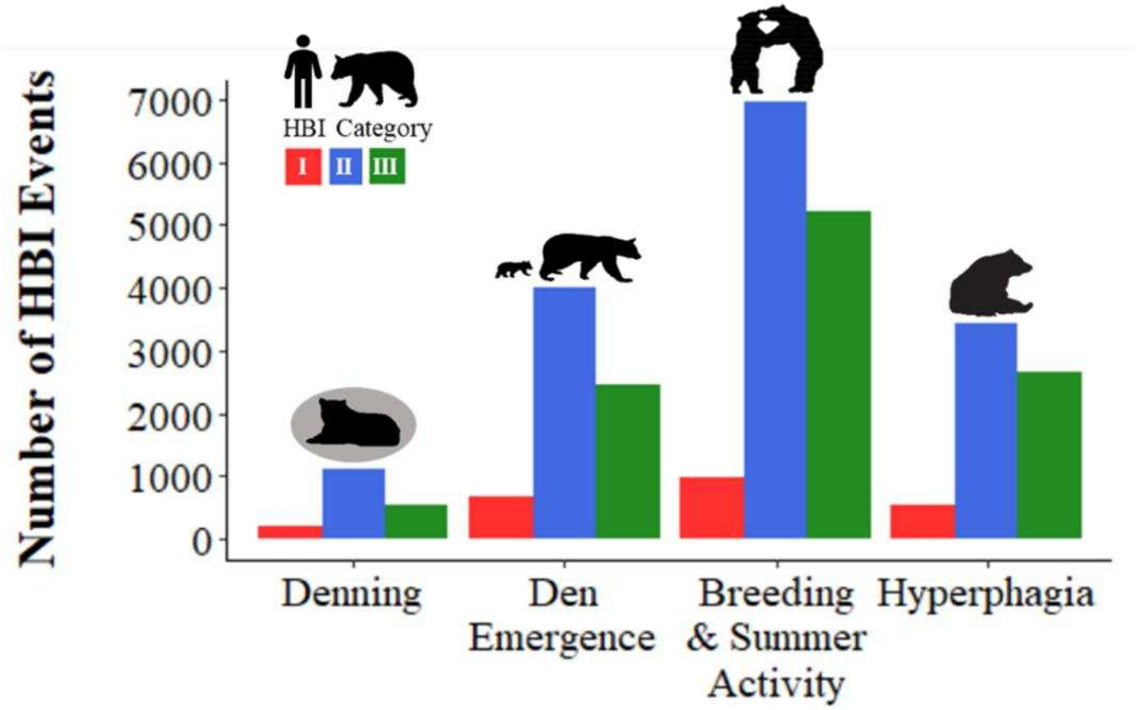


Figure 1.7. Seasonal trends in human-American black bear (*Ursus americanus*) interactions (HBI) data (*n* = 28,811) collected throughout the state of New Jersey, 2001 – 2017, by bear life cycle stage and HBI category. Bear life cycle stages: denning (1 December – 31 March), den emergence (1 April – 31 May), breeding and summer activity (1 June – 31 August), and hyperphagia (1 September – 30 November). HBI categories: I (most severe), II (moderate severity), and III (least severe).

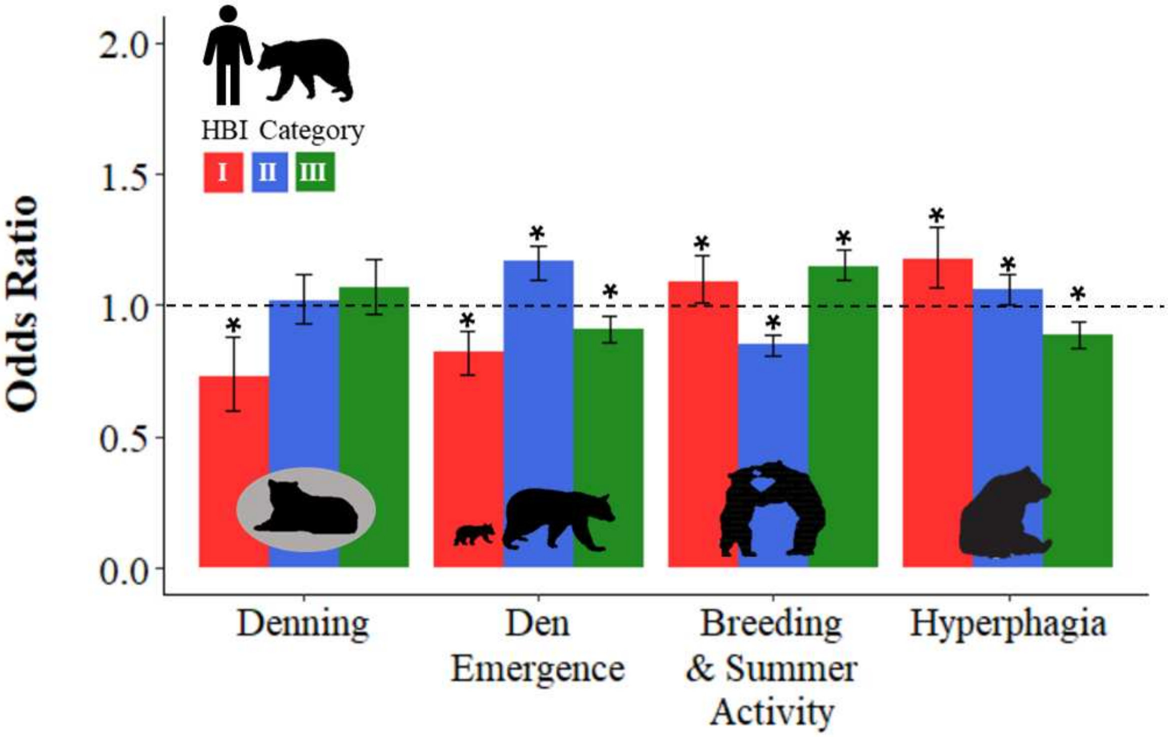


Figure 1.8. Calculated odds ratios (OR) and 95% confidence intervals representing the probability of risk of human-American black bear (*Ursus americanus*) interactions (HBI) by bear life cycle stage and HBI category (I – III, *n* = 28,811) collected throughout the state of New Jersey, 2001 – 2017. Bear life cycle stages: denning (1 December – 31 March), den emergence (1 April – 31 May), breeding and summer activity (1 June – 31 August), and hyperphagia (1 September – 30 November). OR = 1.0 (dashed line) indicates the bear life cycle stage does not affect the HBI, where OR > 1.0 denotes bear life cycle stage is associated with higher odds of HBI, and an OR < 1.0 means the bear life cycle stage is associated with lower odds of HBI. An (*) denotes the OR that are significant due to 95% upper and lower confidence intervals (black bars) not overlapping the null value (OR = 1.0).

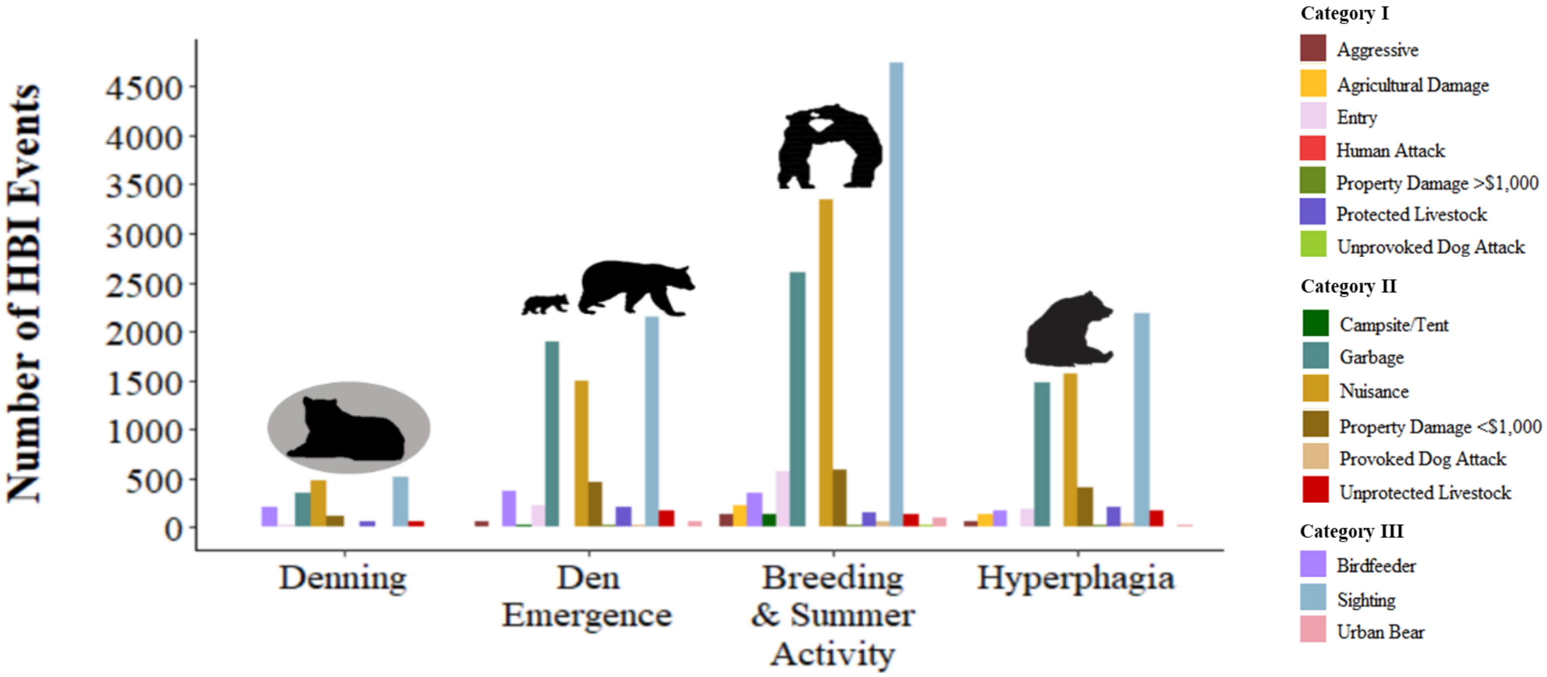


Figure 1.9. Temporal trend in refined human-American black bear (*Ursus americanus*) interactions (HBI) (n = 28,811) throughout the state of New Jersey, 2001 – 2017, by life cycle stages: Denning (1 December – 31 March), Den Emergence (1 April – 31 May), Breeding and Summer Activity (1 June – 31 August), and Hyperphagia (1 September – 30 November).

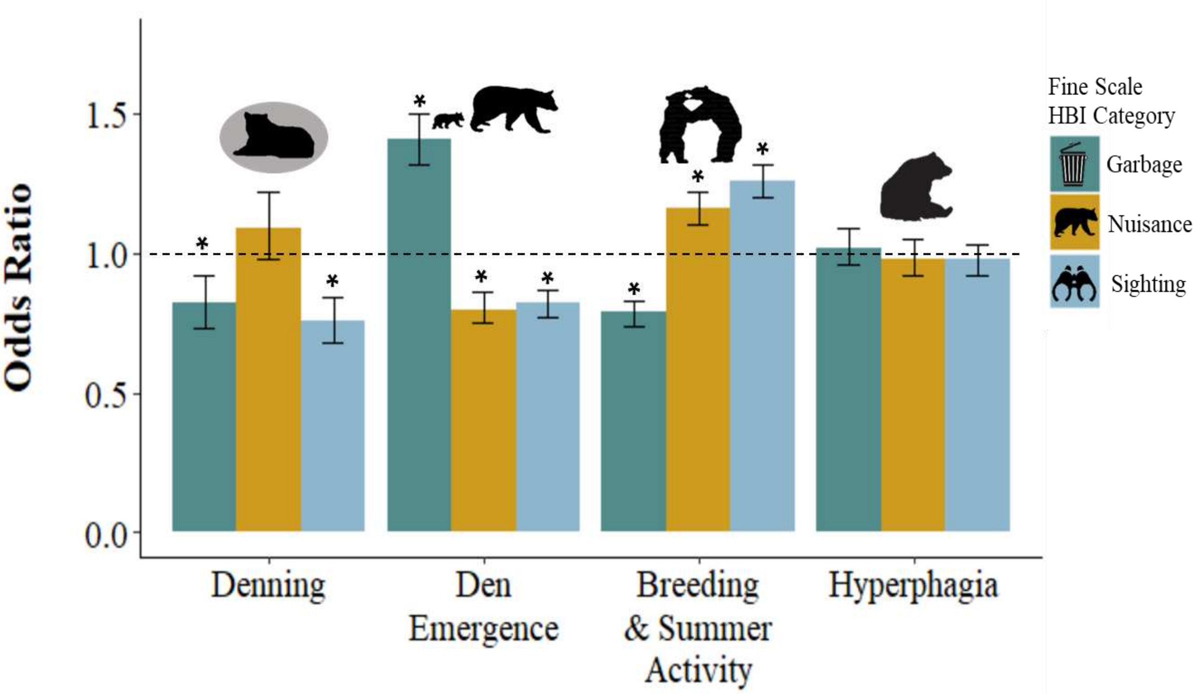


Figure 1.10. Calculated odds ratios (OR) and 95% confidence intervals representing the probability of risk of human-American black bear (*Ursus americanus*) interactions (HBI) by bear life cycle stage and refined HBI categories: garbage (*n* = 6,319), nuisance (*n* = 6,877) and sightings (*n* = 9,575), from HBI data collected throughout the state of New Jersey, 2001 – 2017 (*n* = 28,811). Bear life cycle stages: denning (1 December – 31 March), den emergence (1 April – 31 May), breeding and summer activity (1 June – 31 August), and hyperphagia (1 September – 30 November). OR = 1.0 (dashed line) indicates the bear life cycle stage does not affect the HBI, where OR > 1.0 denotes the bear life cycle stage is associated with higher odds of HBI, and an OR < 1.0 means the life cycle stage is associated with lower odds of HBI. An (*) denotes the OR that are significant due to 95% upper and lower confidence intervals (black bars) not overlapping the null value (OR = 1.0).

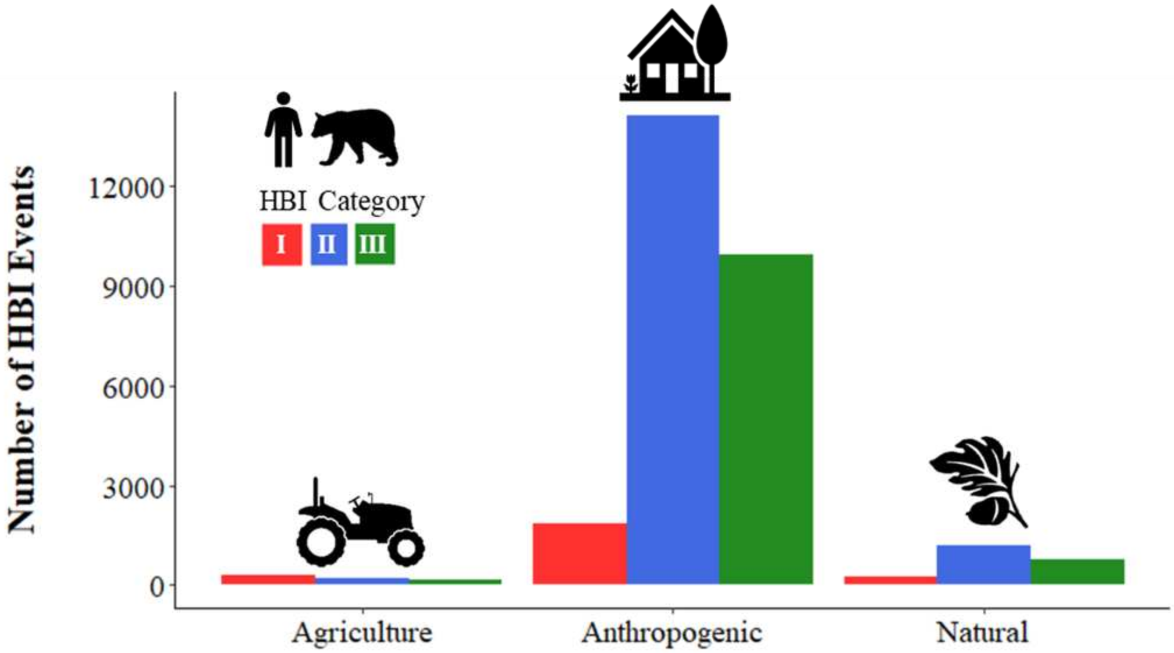


Figure 1.11. Spatial counts of HBI (n = 28,811) throughout the state of New Jersey, 2001 – 2017 by land cover distinctions (agriculture, anthropogenic, natural) and human-American black bear (*Ursus americanus*) interaction category: I (most severe), II (moderate severity), and III (least severe).

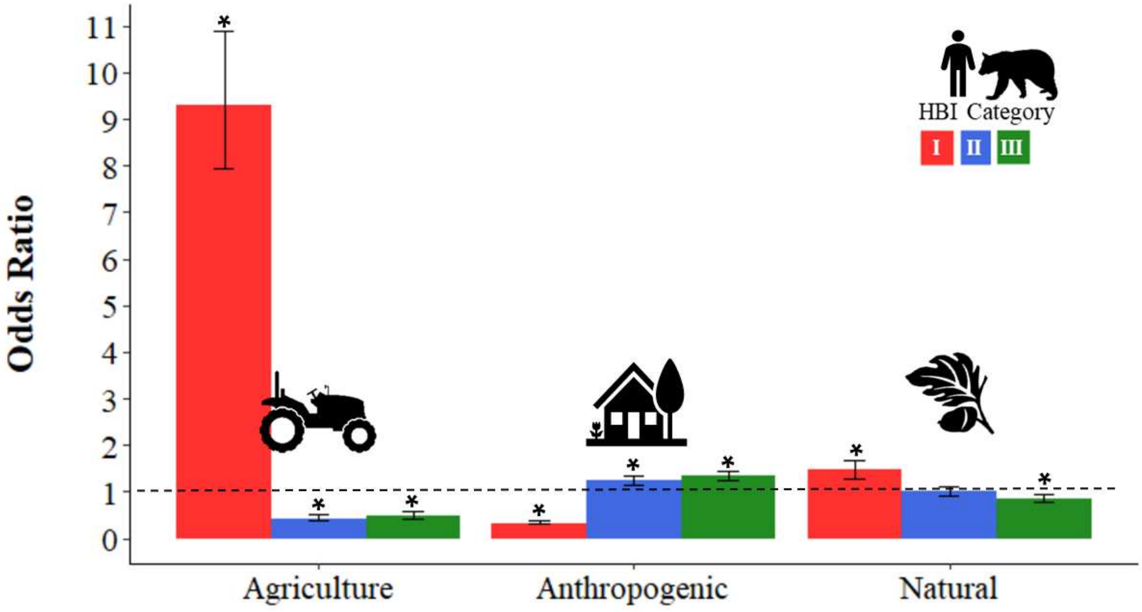


Figure 1.12. Calculated odds ratios (OR) and 95% confidence intervals representing the probability of risk of human-American black bear (*Ursus americanus*) interactions (HBI) (n = 28,811) by land cover type (agriculture, anthropogenic, natural) and HBI category (I – III) from data collected throughout the state of New Jersey, 2001– 2017. HBI categories: I (most severe), II (moderate severity), and III (least severe). OR = 1.0 (dashed line) indicates the land cover type does not affect the HBI, where OR > 1.0 denotes land cover type is associated with higher odds of HBI, and an OR < 1.0 means land cover type is associated with lower odds of HBI.

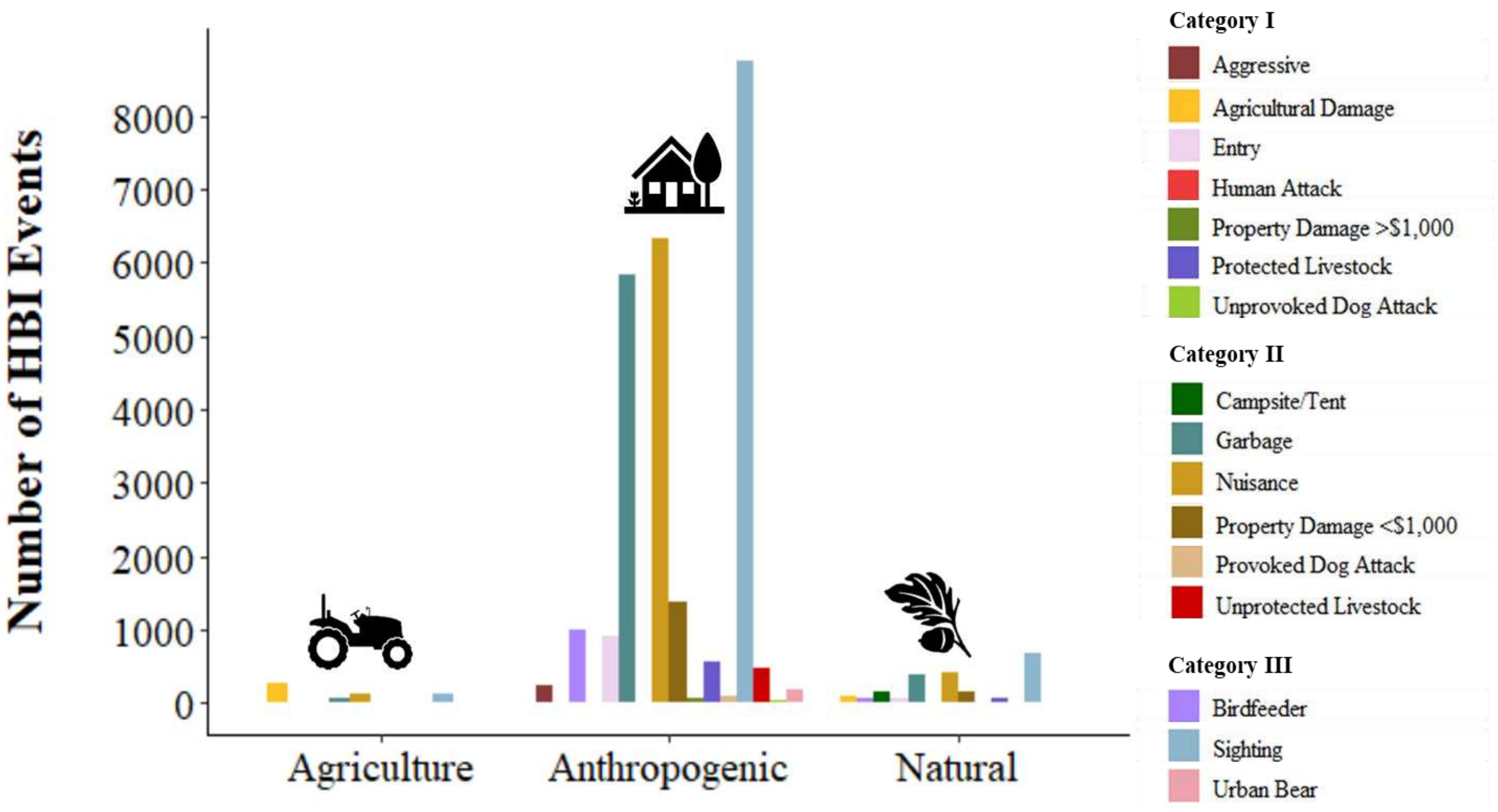


Figure 1.13. Spatial counts of refined human-American black bear (*Ursus americanus)* interactions (HBI) (n = 28,811) throughout the state of New Jersey, 2001 – 2017, by landcover distinctions (agriculture, anthropogenic, natural).

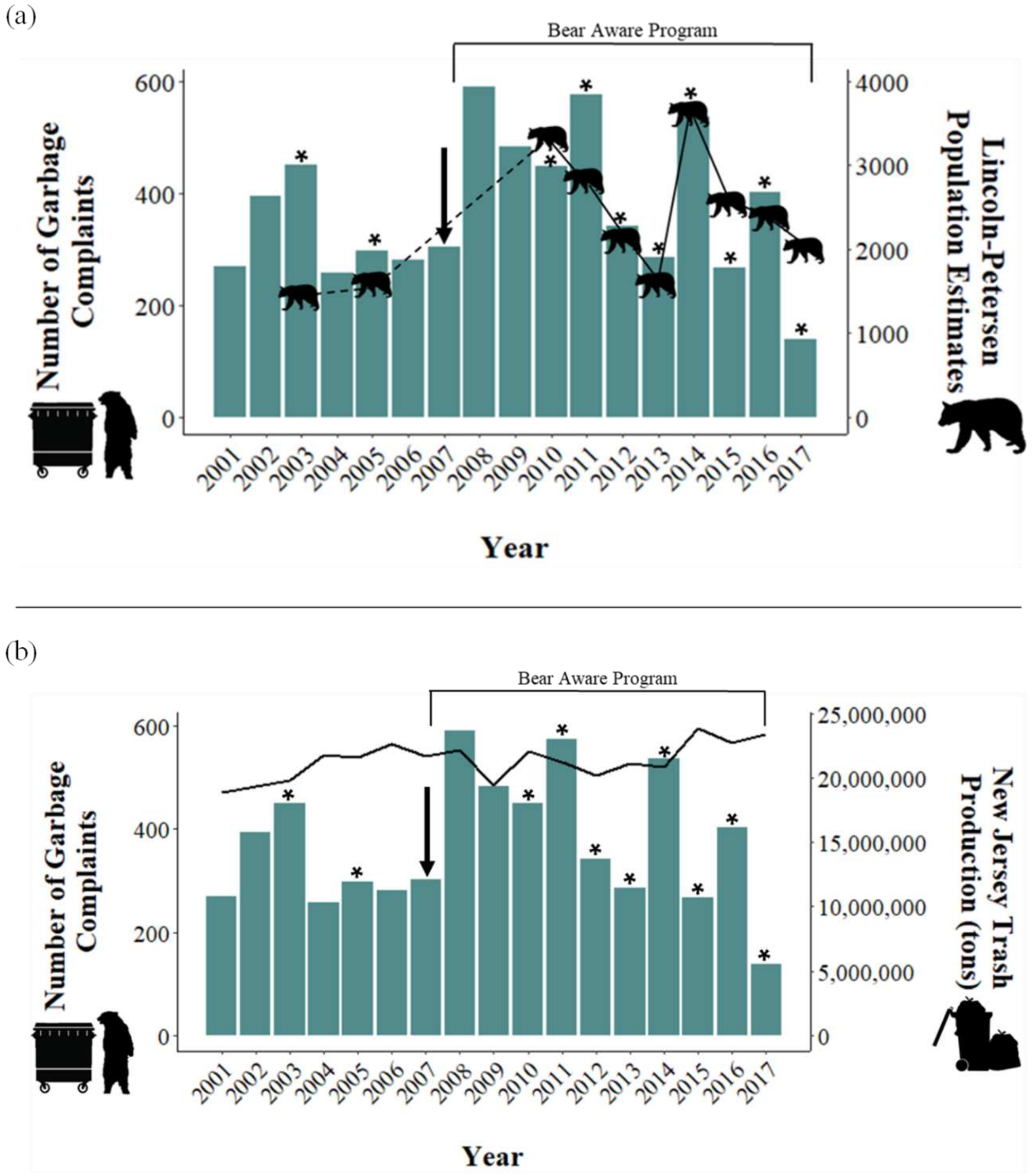


Figure 1.14. Annual trends in American black bear (*Ursus americanus)* garbage complaints from human-black bear interaction (HBI) data (n = 6,319) collected throughout the state of New Jersey, 2001 – 2017. An (*) denotes years (2003, 2005, 2010 – 2017) black bear harvest was allowed in New Jersey, and the arrow denotes when the New Jersey "Be Bear Aware" education program was implemented. Years where there is a black bear symbol in (a), are the estimated population size of bears using the Lincoln-Petersen (L-P) estimator, where a dotted black line indicated years where L-P estimates are unavailable. The number above each of the bear symbols in (a) are the total number of bears harvested that year. The black solid line in (b) indicates the state level annual trash production (tons) in New Jersey, 2001 – 2017. Trash production is the total disposal and recycling materials generated.

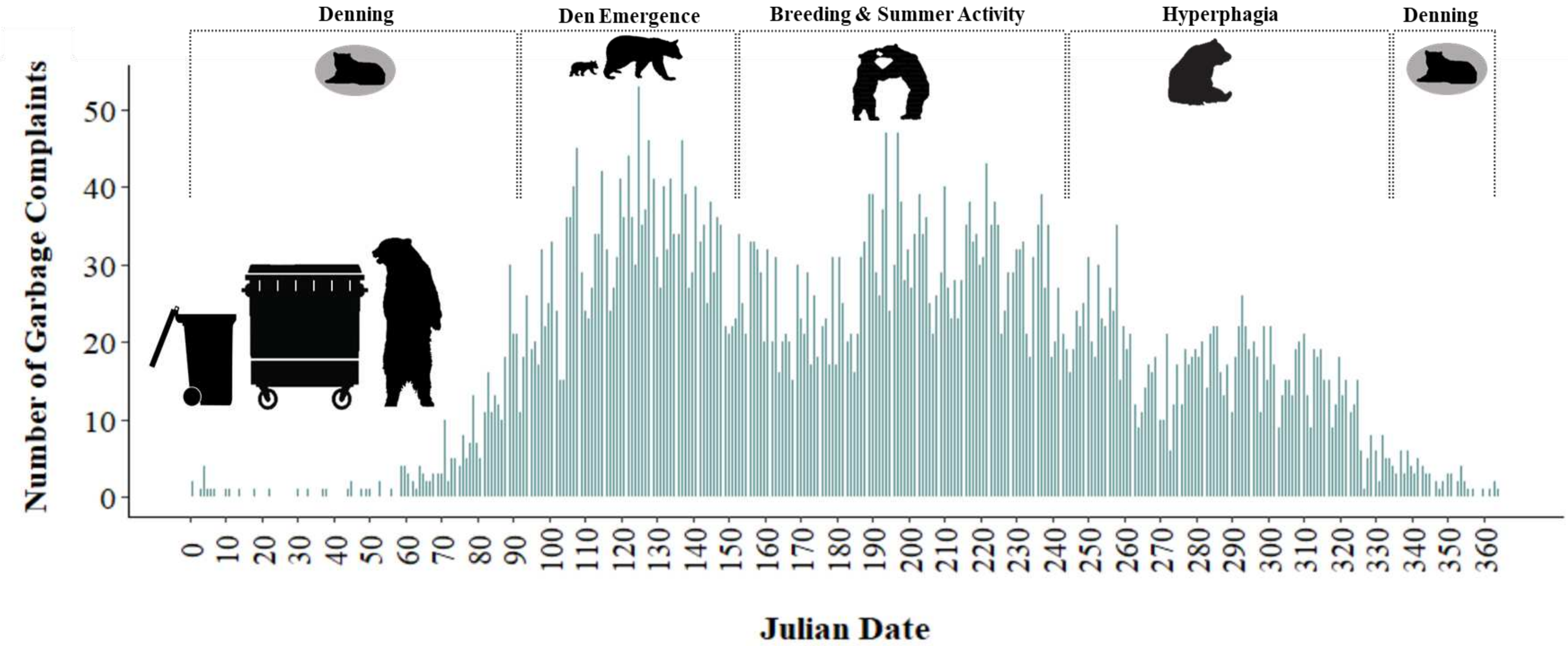
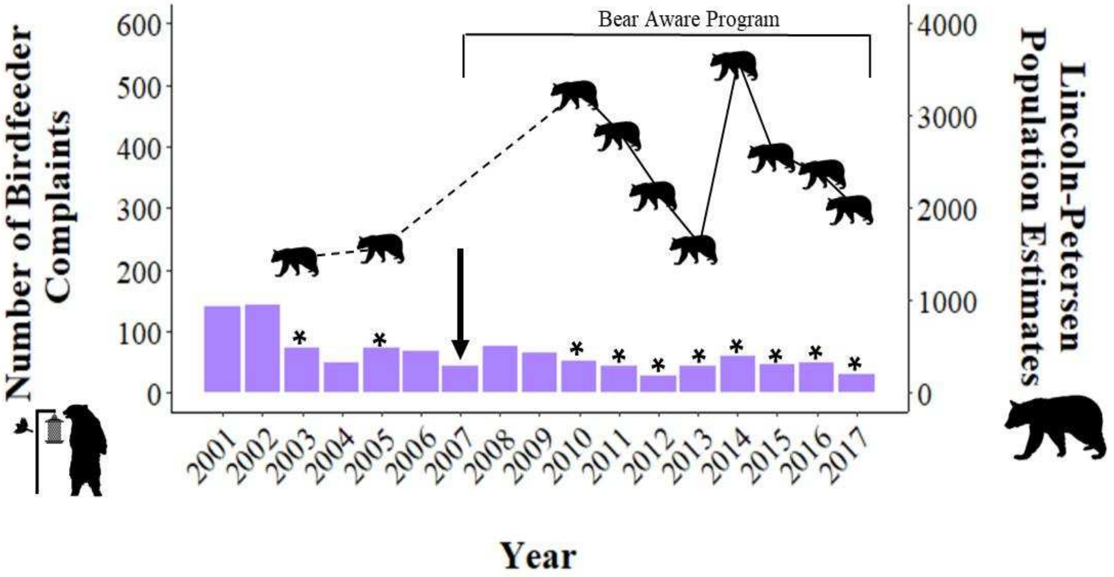


Figure 1.15. Julian Date variation of American black bear (*Ursus americanus*) garbage complaints (HBI; n = 6,319) from human-black bear interaction (HBI) data (n = 28,811) collected throughout the state of New Jersey, 2001 – 2017, presented over bear life cycle stages: Denning (1 December – 31 March; Julian Date = 001 – 090 and 335 – 365; n = 348), Den Emergence (1 April – 31 May; Julian Date = 091 – 151; n = 1,897), Breeding and Summer Activity (1 June – 31 August; Julian Date = 152 – 242; n = 2,600), and Hyperphagia (1 September – 30 November; Julian Date = 244 – 334; n = 1,474).

(a)



(b)

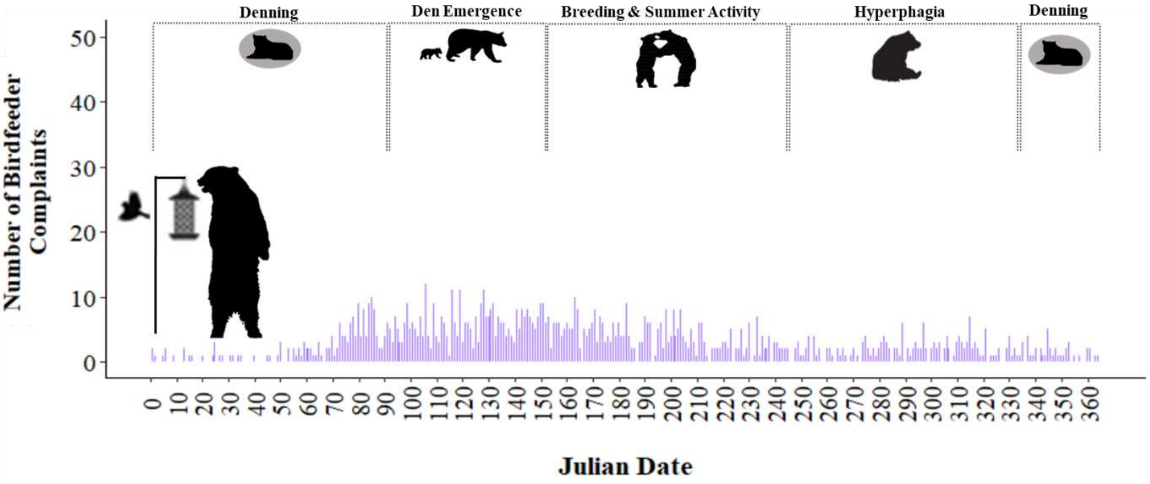


Figure 1.16. (a) Annual trend in American black bear (*Ursus americanus*) birdfeeder complaints (n = 1,089), from human-black bear interaction data collected throughout the state of New Jersey, 2001 – 2017 (n = 28,811). An (*) denotes years (2003, 2005, 2010 – 2017) black bear harvest was allowed in New Jersey, and the arrow denotes when the New Jersey “Be Bear Aware” education program was implemented. Years where there is a black bear symbol in (a), are the estimated population size of bears using the Lincoln-Petersen (L-P) estimator, where a dotted black line indicated years when L-P estimates are unavailable. The number above each of the bear symbols in (a) are the total number of bears harvested that year. (b) Julian Date variation of birdfeeder complaints presented over bear life cycle stages: Denning (1 December – 31 March; Julian Date = 001 – 090 and 335 – 365; n = 204), Den Emergence (1 April – 31 May; Julian Date = 091 – 151; n = 361), Breeding and Summer Activity (1 June – 31 August; Julian Date = 152 – 242; n = 357), and Hyperphagia (1 September – 30 November; Julian Date = 244 – 334; n = 167).

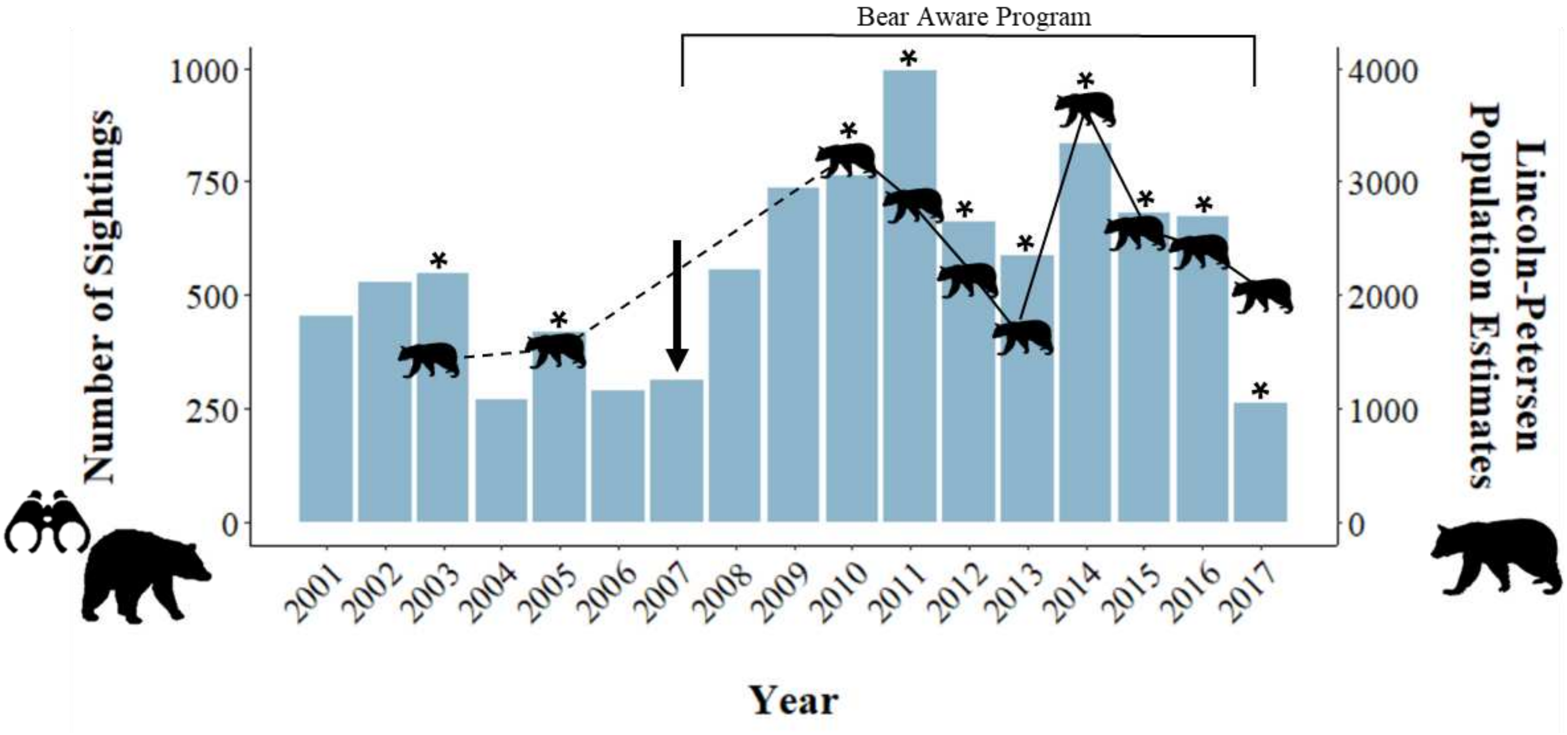


Figure 1.17. Annual trend in American black bear (*Ursus americanus*) sightings from human-black bear interaction (HBI) data (n = 9,575) collected throughout the state of New Jersey, 2001 – 2017. An (*) denotes years (2003, 2005, 2010 – 2017) black bear harvest was allowed in New Jersey, and the arrow denotes when the New Jersey "Be Bear Aware" education program was implemented. Years where there is a black bear symbol, are the estimated population size of bears using the Lincoln-Petersen estimator. The number above each of the bear symbols are the total number of bears harvested that year.

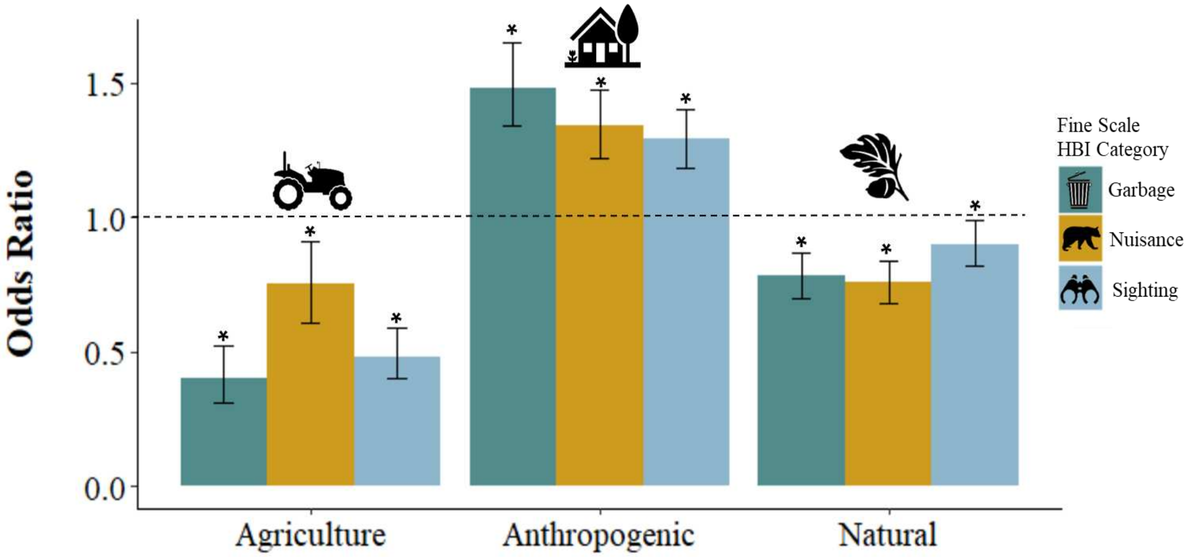


Figure 1.18. Calculated odds ratios (OR) and 95% confidence intervals representing the probability of risk of human-American black bear (*Ursus americanus*) interactions (HBI) (*n* = 28,811) by bear life cycle stage and refined HBI categories: sightings, garbage, and nuisance, from HBI data collected throughout the state of New Jersey, 2001 – 2017. Bear life cycle stages: denning (1 December – 31 March), den emergence (1 April – 31 May), breeding and summer activity (1 June – 31 August), and hyperphagia (1 September – 30 November). OR = 1.0 (dashed line) indicates the life cycle stage does not affect the HBI, where OR > 1.0 denotes the life cycle stage is associated with higher odds of HBI, and an OR < 1.0 means the life cycle stage is associated with lower odds of HBI.

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CHAPTER 2: GARDEN STATE BEARS – PREDICTORS OF FEMALE AMERICAN BLACK BEAR (*URSUS AMERICANUS*) BODY MASS IN AN ANTHROPOGENIC LANDSCAPE

SUMMARY

Anthropogenic pressure such as urbanization and habitat loss can wield many effects on wildlife that radiate through ecosystems. Large mammalian carnivores tend to experience these effects more severely than other species, diminishing their viability and altering ecosystem function by decreasing their role as an apex predator. Here, we quantified the effect of ecological and anthropogenic factors on female body mass of a large mammalian carnivore, the American black bear (*Ursus americanus*). We used data collected from dens ($n = 317$) in northern New Jersey (1984 – 2019) to examine the shared roles of climate change, anthropogenic pressure (e.g., human food subsidies, harvest), habitat composition and configuration, resource availability (e.g., hard mast production), and bear characteristics (e.g., age, history of human-black bear conflict) on female (sow) body mass. Sow body mass increased with increased availability of cultivated crop and within developed-low density land covers, suggesting that anthropogenic food subsidies are contributing to sows' overall body condition. Among key results, a prior history of nuisance conflict with humans explained heavier sow body mass, while a quadratic effect of age on body mass supported a senescent decline in sow body mass later in life. Monitoring changes in fitness components is fundamental to large carnivore conservation, and our results provide insight into the determinants of body mass – a key fitness component or female black bears, who must navigate an increasingly anthropogenic landscape in northern New Jersey.

INTRODUCTION

Anthropogenic pressure (e.g., urbanization, habitat fragmentation, deforestation, climate change) can wield many effects on wildlife that radiate through ecosystems. Large mammalian carnivores in particular experience these effects more severely than other species because of their demanding food requirements, larger home ranges, lower fecundity, and longer generation times (Ripple et al. 2014). Specifically, habitat fragmentation diminishes carnivore fitness and population viability, and alters ecosystem function by depressing carnivores' role as top-consumers (Estes 2010). This pivot in ecosystem structure can ultimately weaken ecosystem resilience through pathways such as secondary seed dispersal (Hämäläinen et al. 2017). Indeed, mammalian carnivores are ecologically pivotal species that are indicative of the integrity of entire ecosystems (Crooks 2002).

Anthropogenic pressure such as urbanization can directly affect carnivore fitness, but not always deleteriously (Gehrt et al. 2010). Increased anthropogenic pressure correlates with increased production of spatially and temporally reliable, and easily accessible food subsidies (e.g., food refuse, crop residuals, Oro et al. 2013) that can increase carnivore reproductive success (e.g., in coyotes, *Canis latrans*, Iossa et al., 2010), body mass, size (in red fox, *Vulpes vulpes*, Stepkovitch et al. 2019), maternal body condition and the number of fetuses carried (in banded mongoose, *Mungos mungo*, Otali & Gilchrist, 2004). However, habitat fragmentation and loss of natural corridors have also led to declines in carnivore reproduction because of their inability to connect to high-quality habitat patches and mates (Grilo et al. 2015), consequently reducing recruitment of young (e.g., in cheetahs, *Acinonyx jubatus*, Broekhuis, 2018). Further, anthropogenic areas and resources can induce human-habituation and conflict for carnivores that reduce maternal fitness (e.g., in brown bears, *Ursus arctos*, Shimozuru et al. 2020).

In carnivores, like in many species, larger body size denotes higher-quality individuals within more productive environments. For American black bears (*Ursus americanus*; hereafter, black bears), greater body mass often leads to increased reproductive success and recruitment (Samson and Huot 1995). Understanding spatiotemporal variability in the life history traits (e.g., female body mass) is essential to fully gauge carnivore population viability (Smith et al. 2017). While anthropogenic pressure on fitness may vary among carnivore species (Crooks 2002), these effects have the potential to shift fitness components via a reduction in natural resource availability, and (or) an increase in anthropogenic food subsidies.

Black bears are a relatively long-lived carnivore (e.g., up to 30 years in the wild), and are capital breeders that rely on the accrued capital of resources for body mass gains to fuel future reproduction (Chapter 1 – Fig. 1.1). Although black bears use a wide variety of habitats, prime habitat consists of escape cover (Lindzey and Meslow 1977), food and water availability (Rogers 1993), accessible den sites and daybeds for security and thermoregulation (Hayes and Pelton 1994), habitat diversity (Jonkel and Cowan 1971), and corridors (Noyce and Garshelis 2014). An abundance of natural resources throughout female black bears' home range can lead to body mass gains, which is a key determinant of earlier parturition (Hugie 1982), increased fecundity (Stringham 1990), and reduced breeding intervals (Costello et al. 2003). Sows (females) experience delayed implantation of blastocysts (i.e., developing embryo that remains dormant for 4 – 5 months after breeding, Wimsatt 1963) that is highly influenced by the availability of adequate food resources prior to implantation (Noyce and Garshelis 1994). Parturition takes place in the den between January and early February (Pelton 2003). Denning itself is an important life history adaptation for coping with harsh environmental conditions and limited resources (Johnson and Pelton 1980). Resources acquired prior to denning highly influence maternal weight, and are stored for sows to give birth, undergo lactation, and to sustain their own energy requirements during and after hibernation (Rogers 1976).

Black bears do not fit the traditional dichotomy of smaller, synanthropic carnivores that benefit from human development (e.g., coyotes, Newsome et al. 2015), and larger carnivores that suffer large fitness costs and population declines to habitat loss (Kuijper et al. 2016). The relationship that exists between fitness, body mass in particular, and anthropogenic resources may lead to increased variability in female reproductive output, which is more blurred in black bears than in any other carnivore species (Evans 2016). Previous work indicates that female black bears in urban settings should be at a fitness advantage (i.e., more fecund) when compared to females that depend on natural foods for reproduction (Raithel 2017). However, the apparent increase in body mass and fecundity from food subsidies may be less evident in habitat mosaics of mature deciduous forests, farmland, and (sub)urban areas.

Black bear fitness and reproduction are largely regulated by the availability of natural food resources (Powell et al. 1997), more specifically by hard (Costello et al. 2003) and soft mast (Jonkel and Cowan 1971). Seasonal hard mast production (e.g., acorns) is often unpredictable (Kelly and Sork 2002), whereas soft mast (e.g., huckleberry, *Gaylussacia* spp.) is often a more reliable food source for black bears (Inman and Pelton 2002). The availability of natural foods could be further regulated by extreme changes in climate (Grazer and Martin 2012). Specifically, spring frost and extremely low temperatures can be detrimental to plant tissues and disrupt plant growth (e.g., emerging buds, developing mast, Inouye et al. 2000). A disruption in natural food growth, could lead to a decline in sow reproductive output the following year (Marra et al. 2015), or it could prompt black bears to switch to anthropogenic food subsidies when natural food becomes limited or unavailable (Baruch-Mordo et al. 2014, Johnson et al. 2015), leaving body mass and reproductive output unchanged or improved.

Identifying the key determinants of spatiotemporal variability in body mass of reproductive female black bears is timely, particularly in the northeastern U.S. where black bear populations have steadily been on the rise, increasing more rapidly than populations in the rest of the nation (Southwick 2007), and have been intensifying their use of anthropogenic habitats. We used sow mass during den surveys, which is a reliable surrogate of sow nutritional condition and reproductive potential, because of the strong positive correlation that exists between weight and reproductive performance (Noyce and Garshelis 1994).

Variability in female body mass could be attributed to (i) *individual characteristics* such as sow age, experience, behavior (e.g., past interactions with humans), and (ii) the *environmental context* experienced by individuals such as resource abundance (Fuller and Sievert 2001), seasonality (Boyce 1979), climate (Boyce 1988), bear harvest dynamics (Raithel et al. 2017), and the interaction between (i) and (ii). We considered the respective impacts of (i) and (ii) on body mass of female black bears in New Jersey, using long-term (>30 years) den data collected by the New Jersey Division of Fish and Wildlife (NJDFW), a state the offers a mosaic of habitats including mature deciduous forests, agricultural crops, and (sub)urban habitat.

We predicted unchanged or less apparent changes in sow body mass when climatic conditions limited natural resource availability (H1, Fig. 2.1), with bears likely switching from feeding on hard and soft mast to human food subsidies. We also expected that a warmer and wetter winter a year or more prior to denning (t – 1, ~ 13 – 16 months prior), would allow for longer and better growing seasons the following year, which sows are likely capitalizing on throughout the year, thus reflecting in their increased body mass when they enter dens (H1, Fig. 2.1). We expected body mass to increase over time with increased anthropogenic exposure (e.g., increased trash production, H2, Fig. 2.1), with increased agricultural production (e.g., corn, apples, H2, Fig. 2.1), and with the periodic reinstatement of the black bear harvest in New Jersey in recent years, likely facilitating a release from intraspecific competition for resources (e.g., density-dependence, H2, Fig. 2.1). We also expected sow body mass would be tempered by individual characteristics such as age and should differ between sows that have a history of interacting with humans versus none, to capture the degree of past familiarity with anthropogenic food subsidizing exploitation (H3, Fig. 2.1). We predicted sows with a recurrent history of 'nuisance' and 'severe' human-bear interactions (see Methods for definition) would experience increased body mass (H3, Fig. 2.1). We further expected Bear Management Zones (BMZs, Fig. 2.2) to influence body mass disproportionately, due to differences in forest cover and bear densities among the BMZs (H4, Fig. 2.1). Finally, hard and soft mast availability should increase body mass, particularly when climatic conditions facilitate mast production (H1 × H4, Fig. 2.1).

MATERIALS AND METHODS

Study species and ecological context

Black bears were nearly extirpated from New Jersey post-European settlement (Regensburg 1978). In the 1950's after the black bear population reached an all-time low of <100 bears in the northwest region of New Jersey, due to combined effects of habitat loss (e.g., timber extraction), unregulated killing (Lund 1980), and a hunting moratorium that was initiated from 1971 to 2002, 2004, and again in 2006 to 2009, allowed bear populations to rebound and their spatial distribution to expand over the entire state (Carr and Burguess 2011). As of 2021, bear hunting closed again due to the expired current black bear management policy. In 2010, the population was estimated at approximately 3,300 bears in northern New Jersey, with densities approximately 0.83 bears per km^2 (Carr and Burguess 2011). The 2020 estimate places the population at approximately 3,158 bears in northern New Jersey (*unpublished data*, NJDFW). For additional details about the study area, see Appendix 1.

Data collection (den surveys)

During 1984 to 2019, NJDFW visited 317 black bear dens of 182 unique females (Fig. 2.2) and documented sow reproductive status, and number and sex of cubs. Den checks generally occurred between late January to early April (Julian date range = 25 – 104), with one outlier during the middle of January (Julian date = 13). The mean date of surveys was ~17 March (Julian date = 76 ± 7.9). Sows ranged in age from 3 to 21 years old ($\bar{x} = 7.1 \pm 3.4$ years old), their body mass at the time of the den survey ranged from 115 to 383 pounds ($\bar{x} = 214.81 \pm 47.40$ pounds), and collectively they produced 914 total cubs over the course of our study. All 182 sows were of breeding age (≥3 years old) and averaged 2.9 cubs per litter. Anecdotally, NJDFW has documented that three, two-year old females each produced one cub (1986, 1991, 2001), which is some of the first documentation of black bear yearlings both breeding and producing cubs in the northeastern U.S. (Raithel 2017). Yet, similar reports of black bears reproducing at two years of age have been documented in the southeastern U.S., specifically in Florida (Garrison et al. 2007) and in North Carolina (Gould et al. 2021).

Sows were chemically immobilized with ketamine hydrochloride and xylazine hydrochloride (Wildlife Pharmaceuticals, Inc., Fort Collins, CO, USA) via hand projector or dart rifle. Individuals of all ages were tagged in both ears with self-piercing, uniquely numbered, metal tags, style 56-L, size 36.5 x 9.5 mm (Hasco Tag, Co., Dayton, KY, USA). Individuals older than cubs were also tattooed on their inside lip with one of the unique ear tag numbers. To determine bear age, a premolar was extracted from all non-cub bears for cementum analysis (Matson's Lab, Manhattan, MT, USA). The den location (longitude and latitude), date, time, sex, weight, morphometric data (e.g., head circumference, paw width, full body length), and reproductive status (e.g., estrous, lactating) were recorded.

Covariates of interest

We selected covariates that represented intrinsic bear characteristics and the ecological context experienced by sows prior to denning (Chapter 1 – Fig. 1.1).

(i) Bear characteristics. Given age influences fitness and thus reproductive efficiency in sows (Alt 1989), we used confirmed age of each sow at the time of the den survey to test for the effects of age on sow body mass. We explored quadratic age effects, and similar to Eiler et al. (1989), we created and investigated sow age categories (e.g., young [3 – 4 years old], middle-aged [5 – 13 years old], and old [14+ years old]). We also tested for direct and indirect density-dependence effects on sow body mass. For direct effects, we used yearly, local bear abundance calculated from a Lincoln-Petersen (L-P) estimator applied to hunter harvest data. The L-P estimates were unadjusted for natural bear mortality rates (Kendall 1999), and environmental factors (e.g., natural food supply, weather, Lindzey et al. 1983, Schooley et al. 1994), and were the only systematic annual estimates of abundance available in the study area. Because black bear sows have a two-year reproductive cycle, we also assessed the total number and relative proportion of bears, sows, and prime reproductive-age sows (e.g., 4 – 13 years old, Raithel 2017) harvested two bear hunting seasons prior ($t - 2$), to detect an indirect release of density-dependence.

To determine if a history of interaction(s) with humans could affect sow body mass, we created "management behavior" indices for each female based off current human-bear conflict categories designated by NJDFW. Category I bears are a threat to public safety and property damage and are primarily euthanized (e.g., bear killed livestock). Category II are nuisance bears which are not a threat to public safety or property damage, and are often aversively conditioned (e.g., bear raided garbage). Category III bears exhibit normal behavior and are not a nuisance or threat to public safety (e.g., bear sighted walking through yard). For each sow we created the following covariates as our behavioral index: (1) the sum of conflict occurrences for each individual category (I, II or III, separately) up to the focal den survey to isolate the effects of previous severe (I), nuisance (II), and/or benign (III) bear behavior on future sow body mass; and (2) the sum of conflict categories combined (I + II +III; I + II, and II + III) up to the focal den survey to identify the cumulative effects of bear behavior on sow body mass regardless of individual incident type. We also included a legacy category (I – III) for each sow, which represented the collective behavioral category continuously assigned to the bear based on prior conflict behavior.

(ii) Ecological covariates. We considered the previous winter North Atlantic Oscillation (NAO) index as a proxy for annual climate variability (Ottersen et al. 2001) and natural food availability (Yom-Tov and Geffen 2011), to investigate how broader climatic phenomena could potentially impact sow body mass via changes in resource availability. We explored other climate covariates (e.g., monthly, seasonal, and annual mean temperature precipitation, drought, as well as specific and localized indices) by bear life cycle stage (e.g., denning, den emergence, breeding and summer activity, and hyperphagia – see Chapter 1, Fig. 1.1 for details) and by season only with interactions with hard mast production, but none of the interactive models demonstrated significant effects (e.g., 95% confidence bounds did not overlap zero; interaction model results not presented here for the sake of conciseness). Therefore, we chose previous winter NAO, because climate variability can produce a lag effect on vegetation and fruit production (Koenig and Knops 2000), which can in turn impact sow body mass the following year. Further, we focused on winter NAO, because atmospheric variability is more dominant during winter months (Rogers 1990). We calculated the previous winter NAO as the monthly mean NAO from December two winters prior to denning, and January and February of the previous winter. For example, if a den was surveyed during March 1984, then the corresponding previous winter NAO ($t-1$) covariate was the average NAO from December 1982, and January and February of 1983.

To test the effects of local anthropogenic change on sow body mass, we included anthropogenic covariates such as a historical, county-level annual total disposed plus recycling records in New Jersey for 1995 – 2018 (NJDEP 2019). Information prior to 1995 was not available due to that being the first year the solid waste program began generating these numbers.

Habitat diversity is one of the most important features to black bears (Jonkel and Cowan 1971, Kemp 1979, Lawrence 1979). Landscapes are spatially heterogeneous areas distinguished by both habitat composition and configuration (Turner 2005), and to capture this we quantified anthropogenic influence, specifically agricultural crops, and quantified agricultural land cover heterogeneity. We considered agricultural production, because crops in general offer a substantial food source for black bears in New Jersey, with corn and apple crops used extensively by bears in our study area (McConnell et al. 1997). Given sows' spatial patterns are influenced by the availability and distribution of resources, particularly at multiple scales (Lindzey and Meslow 1977, Smith and Pelton 1990), we used historical Cropscape – Cropland Data Layers (CDL, USDA 2021) from 2002, and 2008 – 2019 to compare variability in sow body mass by crop type, across various spatial scales. We created shapefiles for each annual CDL, then overlaid them with the den site locations. Home ranges of female bears in New Jersey range from 0.36 km^2 (unpublished data, J.D. Raithel) to 26.52 km^2 (McConnell et al. 1997). Thus, for landscape composition we extracted the relative proportion of crop types from rasterized CDL layers within a den buffer around each den point location of 2, 4, and 6 km, based on the 25th, 50th, and 75th quantiles of sow home ranges (i.e., 3.14, 12.56, and 28.26 km^2) in New Jersey and the northeastern U.S., using class-level metrics (e.g., PLAND) in Fragstats©v4.2 (McGarigal et al. 2012). Sow home range buffers fell slightly outside of New Jersey, therefore we merged CDL rasters for New Jersey, New York, and Pennsylvania. For landscape heterogeneity, we extracted the class-level standardized coefficient of variation (CV) from rasterized CDL layers for each crop land cover type within the three den home range buffers (2, 4, 6 km). Landscapes with smaller relative proportion of crop cover and higher CVs (which indicates more dispersion of land cover) denote a more heterogeneous landscape. Initially, we found only corn production data were available spatially within our three buffers for the entire time range (2002, and 2008 – 2019), while other crops were only available for a limited period (e.g., one year).

We compared variability in sow body mass across the four BMZs, because each zone consists of unique landcover and varied anthropogenic pressure. To capture habitat composition and configuration, we used 30-m pixel land cover data (again merged from New Jersey, New York, and Pennsylvania), from the National Land Cover Database (NLCD) for years 1992, 2001, 2006, 2011, 2016, and 2019 (MRLC 2019). We matched historical NLCD data to our long-term den dataset as follows: (1) 1992 NLCD and 1984 – 1992 den data, (2) 2001 NLCD and 1993 – 2001 den data, (3) 2006 NLCD and 2002 – 2006 den data, (4) 2011 NLCD and 2007 – 2011 den data, (5) 2016 NLCD and 2012 – 216 den data, and (6) 2019 NLCD and 2017 – 2019 den data. We created shapefiles for each of the six NLCD datasets, then overlaid them with den locations within nine and cover types (e.g., cultivated crops, deciduous forest; developed – low, medium, and high intensity; evergreen forest; mixed forest, open water, sedge/herbaceous). Like crop data, we extracted the composition (e.g., relative proportion) and configuration (e.g., calculated CV) for each of the nine land covers within the three den buffers (e.g., 2, 4, 6 km).

Finally, natural resource availability included hard mast data from West Virginia, which is a state that shares a similar ecoregion, climate characteristics, and masting species to New Jersey (for which consistent masting data was not available – see Appendix 1 for further information). We used hard mast data collected and calculated by the West Virginia Division of Natural Resources, which are indices calculated for all combined oak (Quercus) species as: [(abundant observations/total observations) + (common observations × 0.5)/total observations)] × 100 (Barton et al. 2018)].

Modeling framework

We estimated the relationship between sow body mass and the covariates presented above using generalized linear mixed-effects models (GLMMs). We used mixed models to account for correlations induced by the repeated body mass observations for females over time (Bolker et al. 2009). We used sow body mass as our response variable with the rationale that sow body mass mediates the relationship between resource availability and reproductive output. Sow body mass is a reliable surrogate of sow nutritional condition and reproductive potential, because of the strong positive correlation that exists between weight and reproductive performance (Noyce and Garshelis 1994). Prior to fitting GLMMs, we conducted a simple linear regression to confirm that the linear relationship between sow body mass and litter size held true in our study system. We were unable to use body condition (e.g., residuals from linear regression of straight body length and total body mass, Cattet et al. 2002) as our response variable and index of sow condition due to incomplete morphometric data. Because surveys were conducted during denning, in which bear body condition declines throughout the denning period, we back-calculated and standardized sow body mass during denning to estimate sows' den entry weight [early weight = 9.41 + (2.16 × litter weight) + (0.96 × later winter weight), Samson and Huot 1995], as our response variable.

We first developed models that included covariates treated as fixed effects, except for female identifier, which we fit as random effect. We used sow age (either quadratic or age category) as a fixed effect in all null model contenders to control for the effects of sow age on sow body mass. We compared null models with sow age treated as a quadratic effect versus sow age treated as a category effect (i.e., young: 3 – 4 years old; middle-aged: 5 – 13 years old; and old: 14+ years old) to determine our underlying model structure.

Once the baseline model set, we evaluated univariate models, which better captured some of our initial hypotheses. Covariates had to exhibit a strong effect on our response variable (95% confidence bounds did not overlap zero) before we allowed them in further analyses. We considered interactions between covariates only when they were biologically relevant (e.g., NAO × hard mast) and displayed strong effects on our response. We created a global multivariate model with all the strong covariates of univariate and interactive models, and then tested it against other models consisting of relevant covariate combinations from the global model. Prior to fitting multivariate models, we tested for multicollinearity among all covariates by calculating variance inflation factors (VIF > 10.0, Montgomery and Peck 1992). We considered both linear and quadratic relationships when they made biological sense (e.g., effect of sow age on sow body mass to capture biological senescence). We ranked our models at each modeling stage, using Bayesian

Information Criterion (BIC) and designated candidate models based on ΔBIC ≤ 2.0 (Burnham and Anderson 2002). All analyses were performed using package lme4 in Program R version 3.6.2 (Bates et al. 2015). Trends, estimates, and their 95% confidence intervals were depicted using the *ggplot2* package in Program R 3.6.2.

RESULTS

We used records of sow body mass from 182 sows in 317 dens from 1984 to 2019. After accounting for differences across sows, there was a strong, positive relationship between sow mass and litter size [$\beta = 0.007$, 95% CI: (0.005, 0.009), $R^2 = 0.21$, Appendix 3 – Fig. A3.1].

Our null model structure included sow 'ID' as a random effect and sow age quadratic as a fixed effect (BIC = 3077.20, $k = 5$), which outcompeted a similar model (BIC = 3140.31, ΔBIC = 63.11, $k = 4$), where sow age was binned into the 3 age categories (e.g., young, middle-aged, and old). Among candidate multivariate models, the top model supports the hypotheses that bear characteristics, habitat type, and composition were all good predictors of sow body mass, while climate was not (Tables 2.1 and 2.2).

A quadratic effect of sow age was a strong predictor of sow body mass, which peaked at 15 – 17 years old, following a senescent decline in body mass past 17 years of age [sow age: β = 68.65 (54.05, 82.93); sow age^2: β = –42.95 (–57.05, –28.56), Table 2.2, Fig. 2.3]. Behavior was also key in explaining variability in sow body mass. Specifically, we found sow body mass in year $t + 1$ was greater for those females that had a history of Category II human-bear interactions [β = 7.86 (1.16, 14.57), Table 2.2, Fig. 2.4], when compared to other interactions (e.g., Category I and III).

We found sow body mass was significantly different across BMZs (Table 2.2, Fig. 2.5). Average sow body mass was higher in BMZ 2 (262.36 ± 38.51 pounds) and BMZ 4 (262.74 ±

48.79 pounds), than in BMZ 1 (241.80 ± 52.41 pounds) and BMZ 3 (242.50 ± 51.60 pounds). Post-hoc analyses revealed that there were significant differences in sow body mass between BMZs (ANOVA, $F_{3,\ 305} = 2.91$, *p*-value = 0.02), specifically in BMZs 1 and 4 (*p*-value = 0.03, LMER, Tukey post-hoc). However, there were no clear differences in sow body mass between BMZs 1 and 2 (*p*-value = 0.07, LMER, Tukey post-hoc), BMZs 1 and 3 (*p*-value = 0.94, LMER, Tukey post-hoc), BMZs 2 and 3 (*p*-value = 0.22, LMER, Tukey post-hoc), BMZs 2 and 4 (*p*-value = 0.81, LMER, Tukey post-hoc), BMZs 3 and 4 (*p*-value = 0.08, LMER, Tukey post-hoc).

Habitat composition was also an important, positive predictor of sow body mass, but only within two of the three home range extents (Tables 2.1 and 2.2). Sow body mass improved with increased relative percentage of cultivated crop land cover within the 4km buffer around dens [β = 8.49 (2.59, 14.40), Fig. 2.6]. Similarly, sow body mass increased with increased relative percentage of developed – low intensity land cover within the 6km buffer around dens [β = 11.79 (6.45, 17.15), Fig. 2.7]. However, two competing models slightly challenged the top model, indicating the relative percentage of deciduous forest cover within the 6km buffer around dens and cultivated crop land cover configuration within the 4km buffer around dens were also good predictors of sow body mass (Table 2.1). Given the BIC model weight of our top model ($w_i = 0.57$, Table 2.1), we focused on our top model for results.

DISCUSSION

Our results provide strong support that both individual bear characteristics and the environmental context experienced by sows play an important role in explaining variability in their body mass over 35 years in the highly fragmented landscape of northern New Jersey.

As expected, sows that had a prior history of nuisance (problematic) interactions with humans (Category II), were heavier at the onset of denning when compared to sows that never experienced negative interactions with humans previously (Table 2.2; H3, Figs. 2.1 and 2.4). Category II interactions often reflect bears getting into garbage, but also into barbeque grills, bird feeders, and campsites. Our results demonstrate sows that took risks and perhaps exhibited more frequent, bolder behavior to acquire anthropogenic resources also experienced a fitness reward, which has been reported in a variety of taxa (Smith and Blumstein 2008). Between 2001 and 2017, ~54% (*n* = 15,564) of the total human-bear interactions (*n* = 28,811) were Category II complaints, and ~41% (*n* = 6,319) of the total Category II complaints were garbage-related and ~44% (*n* = 6,877) were considered more of a nuisance (see Chapter 1). Sows in New Jersey could be experiencing simultaneous and opposing population-level effects from using more developed areas and resources (e.g., improved body condition and reproductive success with higher mortality rates, Johnson et al. 2020), especially since adult sows are two times more likely to be harvested than males (Raithel 2017). Nonetheless, adverse bear behaviors to humans may be minimized further by management efforts, for example with the reduction of anthropogenic attractants (Baruch-Mordo et al. 2013), as there are currently no municipal trash ordinances to help limit negative human-black bear interactions in New Jersey.

Environmental quality and resource saturation have been linked to delayed biological aging in many long-lived taxa (e.g., chamois, *Rupicapra rupicapra*, Bleu et al. 2015). The baseline structure of our top model indicated sow body mass was mediated by age (Tables 2.1 and 2.2; H3, Fig. 2.1). Specifically, we found sow body mass plateaued in older females (e.g., 15 – 17 years old, Fig. 2.3), followed by a senescent decline in older individuals, although our sample size past that threshold was limited. Sow body mass is an important proxy of reproductive potential in black bears (Noyce and Garshelis 1994), and this potential typically peaks in sows that are 8 – 9 years old in the western U.S. (Beckmann and Lackey 2008) and 4 – 13 years old in New Jersey (Raithel 2017). Our results indicate sows' reproductive senescence in eastern bears, particularly in New Jersey, could be delayed further than what was previously recognized there, and delayed even further than western black bear populations. This delay could represent a 15 – 31% extension beyond the typical peak reproductive age of sows (e.g., 13 years old) in New Jersey. Our results provide an interesting comparison with sows in the western U.S., where Johnson et al. (2020) found a 90% probability of sows being barren by 20 years of age in Colorado. However, biological aging (e.g., as captured by shortened telomeres) in Colorado bears was influenced more by environmental (e.g., latitude, vegetative productivity) than individual bear characteristics (e.g., age, sex, body size, Kirby 2016). These findings on biological aging in black bears along with our results, reinforce the need to evaluate the environmental factors driving not only reproductive success, but also reproductive senescence of sows in New Jersey (Chapter 3).

As expected, sow body mass varied across BMZs, likely capturing differences in forest cover and bear density (Table 2.2; H4, Figs. 2.1 and 2.5). Higher densities can conceivably impact body mass and in turn influence important vital rates (e.g., reproduction, Ronget 2018) in bears (Garshelis 1994). Density-dependent life history responses in large-bodied, long-lived animals are assumed to occur in populations at or above carrying capacity (Fowler 1981). We found possible signals of a density-dependent response, as average sow body mass at the onset of denning was higher in BMZs 2 and 4 but was reduced in BMZs 1 and 3. BMZs 1 and 3 are considered excellent bear habitat and have an average 76% of forest cover and the highest bear densities of any other BMZ (NJOAL 2015). BMZs 2 and 4 are marginal habitat containing 50% forest cover with lower bear densities than BMZs 1 and 3 (NJOAL 2015). Since sow body mass was not strongly affected by the periodic reinstatement of black bear harvest in New Jersey as we had anticipated (Table 2.2; H2, Fig. 2.1), our results suggest more bears in excellent bear habitats (BMZs 1 and 3) could be competing for resources, thus slightly reducing sow body mass there. However, we are aware that buffers around each den site conceivably overlapped multiple BMZs for a handful of females, whereby sows could access resources from multiple BMZs.

Landscape heterogeneity is a key determinant of habitat diversity (Tews et al. 2004) and is defined as the number and proportions of different land cover types (compositional heterogeneity) and their complex spatial arrangement of habitats (configurational heterogeneity) (Fahrig and Nuttle 2005). Increased landscape heterogeneity implies more opportunities for resources for bears (Costello and Sage, Jr. 1994). Yet, fragmented habitats and resources can diminish fitness in bears (Rogers 1976). Contrary to our predictions, our results indicate landscape composition, more than configuration, strongly affected sow body mass (H4, Fig. 2.1), particularly within middle to larger sow home ranges (e.g., 4 and 6km buffers, Table 3.2). Increased agricultural configuration may denote more opportunities for sows to acquire resources, consequently increasing the likelihood for bears to have negative interactions with more farmers across the landscape who are defending crops (Jonker et al. 1998), which may explain why agricultural composition rather than configuration strongly increased sow body mass.

Our top model suggests that specific anthropogenic food sources (e.g., garbage, crop type) may not be as important for sows (Table 2.2; H2, Fig. 2.1). Rather having increased percentages of anthropogenic stimuli available, particularly in cultivated crop and developed-low density land covers (e.g., birdfeeders, barbeque grills, garbage, gardens, domestic livestock such as chickens, pet food), are better predictors of sow body mass. Anthropogenic resources and habitats, particularly crops (Garshelis and Hellgren 1994, Howe et al. 2012, Ditmer et al. 2016), are "caloric jackpots” for bears, helping stabilize food availability during poor natural forage years (Hatler 1967, Rogers 1976, Mattson 1990, Jonker et al. 1998, Baruch-Mordo et al. 2014, Johnson et al. 2015) and can ultimately reduce a bear’s home range while simultaneously improving and sustaining body mass (Beckmann and Berger 2003).

Our results were also scale-dependent and contingent upon the resource type. For example, sow body mass increased with the relative percentage of crop land cover within the middle home range extent (4 km buffer) and the relative percentage of developed-low intensity land cover within the larger home range extent (6 km buffer) (Table 2.2, Figs. 2.6 and 2.7). Perhaps the differences in sow body mass relative to different spatial scales indicate that an average home range (4 km) allows sows a large enough area to acquire resources while concurrently limiting competition from conspecifics (Garshelis 1994) and risk of using the agricultural landscape (e.g., infanticide, LeCount 1987, Garrison et al. 2007; human presence, Ditmer et al. 2015; lethal control, Hristienko and McDonald 2007). Yet, natural food resources for bears are spatially and temporally erratic (Eagle and Pelton 1983, Inman and Pelton 2002) and may require larger home ranges when human food subsidies are not available.

Developed-low intensity areas consist mainly of areas including large-lot single family homes within more vegetated areas in the form of lawns and recreational settings (MRLC 2019). Cultivated crop land cover is comprised of annual crops (e.g., corn, vegetables) and perennial crops (e.g., orchards, vineyards; MRLC 2019). Given sow body mass was greater in areas with lower percentages of both cultivated crop and developed-low intensity land covers (Figs. 2.6 and 2.7, respectively), this suggests that anthropogenic resources that are adjacent to, and intermixed with these more vegetated and natural areas, could be providing both foraging opportunities and refugia for sows, especially those with cubs (McConnell et al. 1997). Additionally, sows are highly philopatric to natal areas, where they establish home ranges close to their birthplace, which often overlaps their mother's (Rogers 1977, 1987, Smith and Pelton 1990, Moyer et al. 2007), and even grandmother's home ranges (Waser and Jones 1983, Kilham and Spotila 2021). Therefore, our results at these two spatial scales, could be indicative of sows having a large enough area of adequate food resources to help them not only maintain their own body mass and fitness, but also ensure the success of their daughter(s) and potentially granddaughter(s).

Sow body mass did not change when climatic conditions constrained natural resource availability the previous year (Table 2.2; H1 × H4, Fig. 2.1). Contrary to our predictions, warmer and wetter winters (+ NAO) a year or more ($t - 1$, ~13 – 16 months) prior to denning did not lead to an increase sow body mass a year or more later ($t + 1$; H1, Fig. 2.1). Instead, the top model suggested that with mild, wet winters with reduced severity (+ NAO), sow body mass the subsequent year decreased, although the effect on sow body mass was noticeably weak and not significant (Table 2.2). Broad-scale climate indices, such as the NAO, simplify complex weather patterns both spatially and temporally. Thus, the winter NAO index could be too broad to isolate climatic effects on sow body mass yet outcompeted more fine-scale climatic variables.

Our results shed light on three decades of sow fitness over a progressive, yet significant land conversion of the New Jersey landscape. Female black bear fitness in New Jersey reflects the environmental context they experience, which can vary considrably with sow age, history of conflict with humans, anthropogenic resources (e.g., from cultivated crop and developed-low intensity landcovers), landscape context (i.e., composition), and spatial scales. New Jersey was branded as the "Garden State" in the mid-1800's, to advertise its agricultural production and farmland to other state and has been compared to "…an immense barrel, filled with good things to eat and open at both ends…" (Heston 1926). Thus, black bears in New Jersey appear to be the poster child for the “Garden State” where they have certainly earned their nickname of “Garden State Bears”. Our findings provide important implications for large carnivore management in New Jersey, particularly since an increase in sow body mass is dependent upon anthropogenic food availability. Our results suggest that more emphasis should be placed on reducing anthropogenic attractants, particularly trash during den emergence and the breeding and summer activity period (see Chapter 1) especially within the context of climate change, as current increasing temperature trends in New Jersey could limit denning length and extend the time sows forage on the landscape, thus increasing HBI (see Chapter 1)

Table 2.1. Generalized linear mixed-effects model selection results evaluating how environmental context (e.g., climate, anthropogenic, habitat and natural resources) and intrinsic characteristics (maternal age and condition, behavior) influence body mass (lbs) of female (sow) American black bears (*Ursus americanus*, n = 182 individuals) in New Jersey between 1984 – 2019 (n = 317 den surveys). Prior to model-fitting, continuous covariates were standardized. Models are sorted by ascending Bayesian Information Criteria (BIC) and results include number of parameters (k), log-likelihood (LL), change in BIC from top model (ΔBIC), and BIC model weight (w_i).

Model Rank	**Candidate Model**	k	**LL**	**BIC**	**ΔBIC**	w_i
1	Sow Age – Sow Age^2 – Previous Winter NAO + Cat II HBI + BMZ + Cultivated Crop % (4km) + Developed-Low Intensity % (6km)	12	–1440.77	2949.98	0.00	0.57
2	Sow Age – Sow Age^2 – Previous Winter NAO + Cat II HBI + BMZ + Cultivated Crop % (4km) + Developed-Low Intensity % (6km) + Deciduous Forest % (6km)	13	–1438.61	2951.36	1.38	0.29
3	Sow Age – Sow Age^2 – Previous Winter NAO + Cat II HBI + BMZ + Cultivated Crop % (4km) + Developed-Low Intensity % (6km) + Deciduous Forest % (6km) + Developed-Low Intensity Configuration (CV) (2km)	14	–1436.52	2952.90	2.92	0.13
4	Sow Age – Sow Age^2 – Previous Winter NAO + Cat II HBI + BMZ + Cultivated Crop % (4km) + Developed-Low Intensity % (6km) + Deciduous Forest % (6km) + Developed-Low Intensity Configuration (CV) (2km) + Cultivated Crop Configuration (CV) (4km)	15	–1437.03	2959.62	9.64	0.00
5	Sow Age – Sow Age^2 – Previous Winter NAO + Cat II HBI + BMZ + Cultivated Crop % (4km) + Developed-Low Intensity % (6km) + Deciduous Forest % (6km) + Developed-Low Intensity Configuration (CV) (2km) + Cultivated Crop Configuration (CV) (4km) + Deciduous Forest Configuration (CV) (6km)	16	–1434.68	2960.61	10.63	0.00
6	Sow Age – Sow Age^2 – Previous Winter NAO + Cat II HBI + BMZ + Cultivated Crop % (4km)	11	–1451.48	2965.69	15.71	0.00
7	Sow Age – Sow Age^2 – Previous Winter NAO + Cat II HBI + BMZ	10	–1459.36	2975.75	25.77	0.00
8	Sow Age – Sow Age^2 – Previous Winter NAO + Cat II HBI	7	–1473.63	2987.18	37.20	0.00

Table 2 2. Results of top ranking generalized linear mixed-effects model (BIC = 2949.98) testing for multivariate effects of covariates within four hypothesized predictor categories (climate, anthropogenic, bear characteristics, habitat and natural resources) on the body mass (lbs) of female (sow) American black bears (*Ursus americanus*, n = 182 individuals) in New Jersey between 1984 – 2019 (n =

317 den surveys). Results presented are from standardized data and include regression coefficient estimates (β), standard errors (SE), 95% upper and lower confidence intervals (CI). Covariates presented in bold show a strong effect (confidence bounds did not overlap zero) on female body mass.

Covariate Category	**Covariate**	β	**SE**	**95% CI**
	Intercept (BMZ 1)	250.91	4.69	(241.82, 259.97)
Climate	Previous Winter NAO	–2.46	1.55	(–5.47, 0.54)
Bear Characteristics	**Sow Age**	68.65	7.31	(54.05, 82.93)
	Sow Age^2	–42.95	7.26	(–57.05, –28.56)
	Frequency of Prior Cat II Human-Bear Interactions	7.86	3.45	(1.16, 14.57)
Habitat and Natural Resources	**BMZ 2**	253.57	7.08	(239.86, 267.32)
	BMZ 3	244.37	5.06	(234.54, 254.29)
	BMZ 4	261.15	9.08	(243.60, 278.77)
	Relative % of Cultivated Crop Land Cover (4km)	8.49	3.05	(2.59, 14.40)
	Relative % of Developed-Low Intensity Land Cover (6km)	11.79	2.68	(6.45, 17.15)

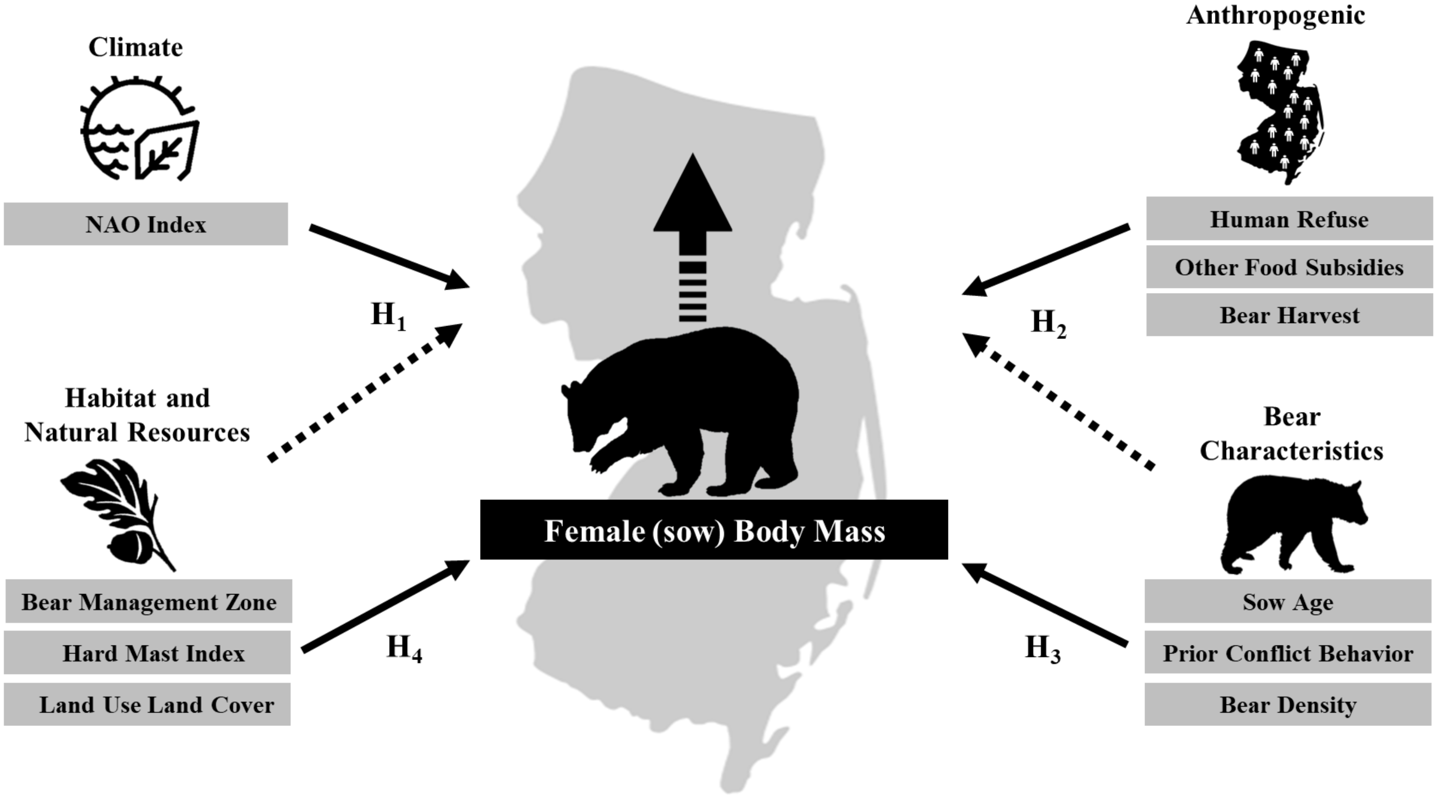

Figure 2.1. Predicted relationships between key categories of interest (climate, anthropogenic, bear characteristics, habitat and natural resources) and their effect(s) on female (sow) body mass (lbs) in American black bears (*Ursus americanus*) in New Jersey.

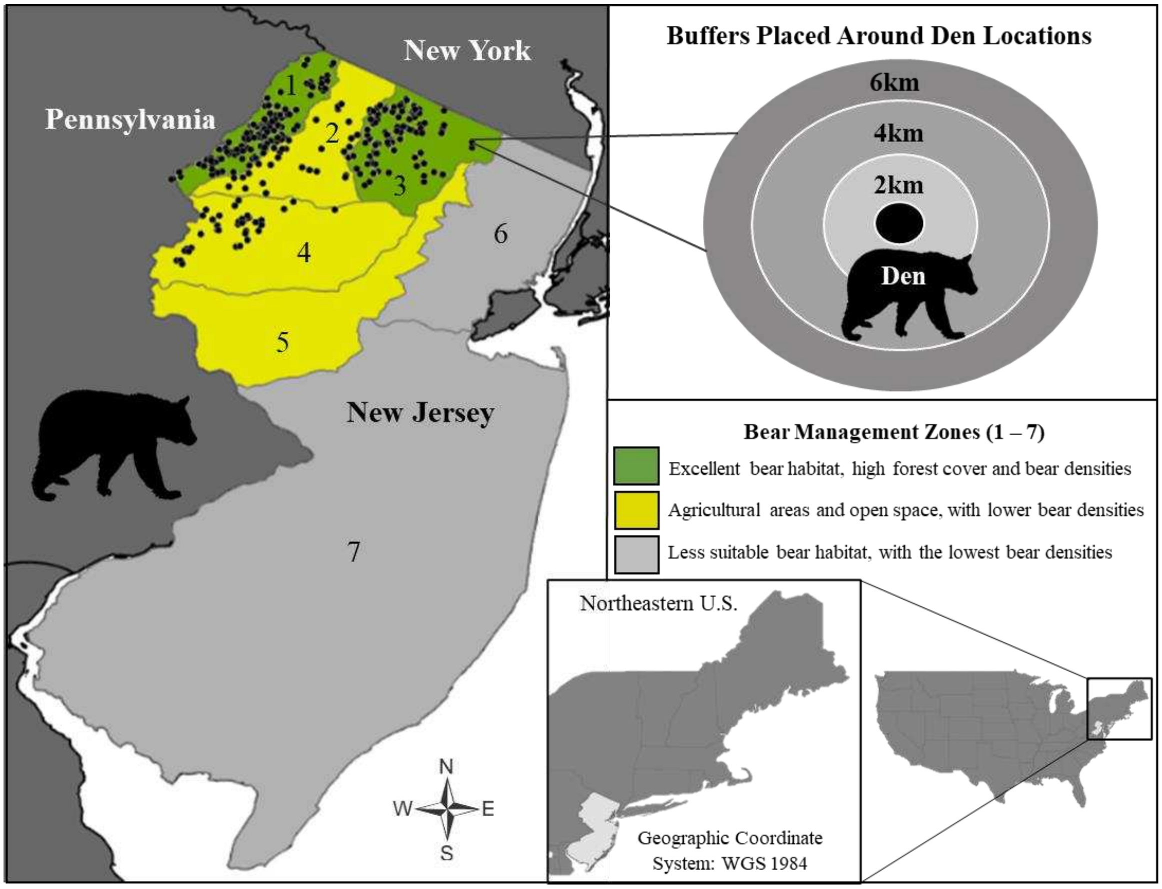

Figure 2.2. Current American black bear (*Ursus americanus*) management zones (BMZs) and spatial distribution of female bear den site locations (black dots, *n* = 317) surveyed by the New Jersey Division of Fish and Wildlife in northern New Jersey between 1984 and 2019. BMZs are designated by the Comprehensive Black Bear Management Policy in New Jersey (NFDFW 2015). BMZs 1 and 3 constitute excellent bear habitat with high forest cover and bear densities. BMZs 2, 4, and 5 comprise agricultural areas and open space with lower bear densities. BMZs 6 and 7 are designated as less suitable bear habitat with lower bear densities than BMZs 2 and 4.

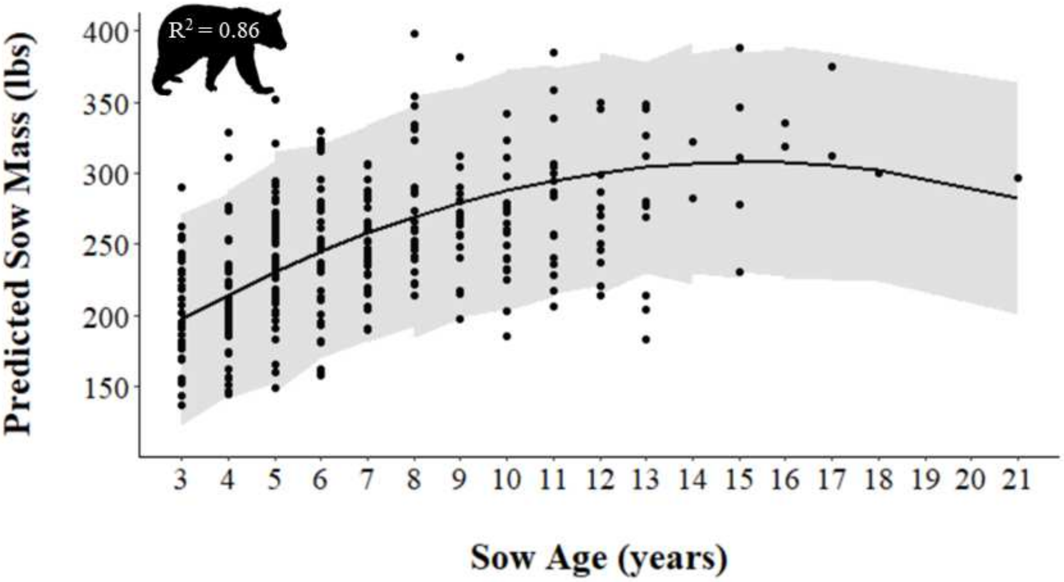

Figure 2.3. Predicted female (sow) American black bear (*Ursus americanus*) body mass (lbs) relative to strong effects of sow age (years), in the top generalized linear mixed-effects model (GLMM). Sow mass measured at den site locations ($n = 317$) between late January – early April, surveyed by the New Jersey Division of Fish and Wildlife in northern New Jersey between 1984 – 2019.

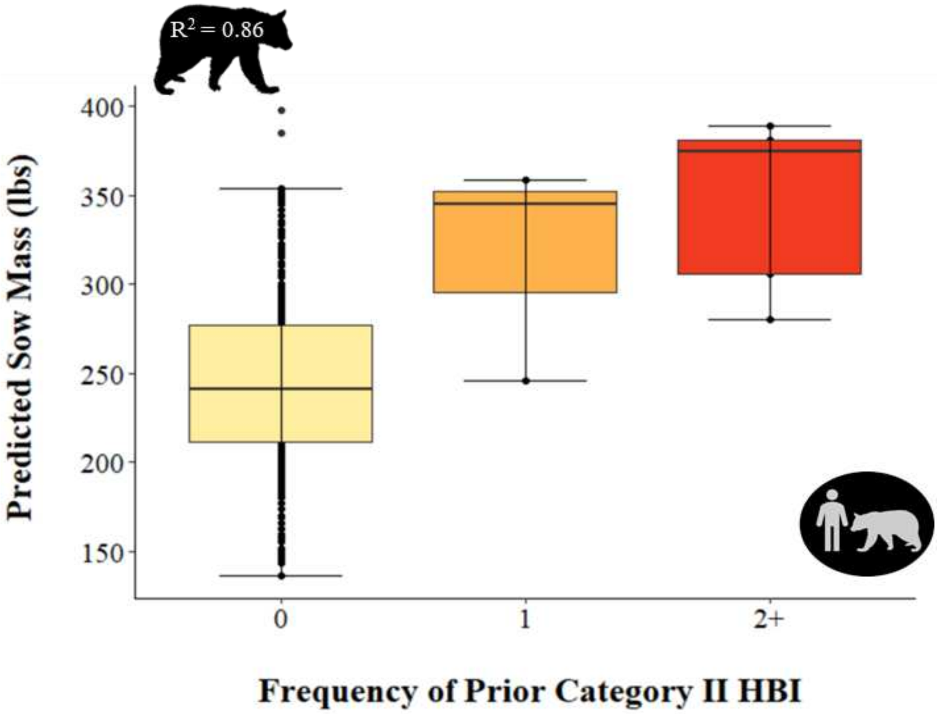

Figure 2.4. Predicted female (sow) American black bear (*Ursus americanus*) body mass (lbs) relative to strong effects of the frequency of prior Category II human-bear interactions, in the top generalized linear mixed-effects model (GLMM). Sow mass measured at den site locations (n = 317) between late January – early April, surveyed by the New Jersey Division of Fish and Wildlife in northern New Jersey between 1984 – 2019.

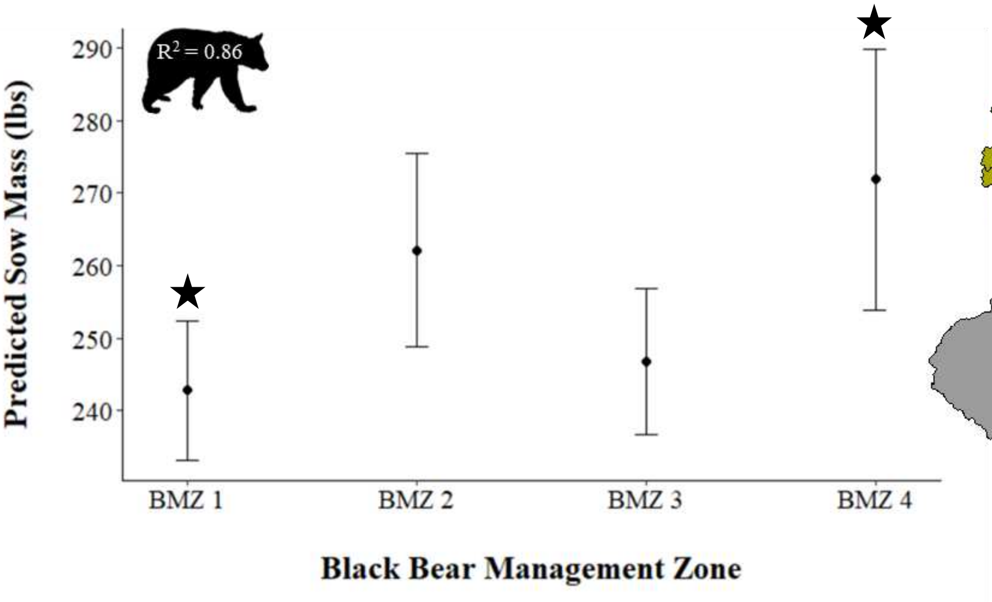

Figure 2.5. Predicted female (sow) American black bear (*Ursus americanus*) body mass (lbs) relative to strong effects of Black Bear Management Zones (BMZs), in the top generalized linear mixed-effects model (GLMM). Sow mass measured at den site locations (n = 317) between late January – early April, surveyed by the New Jersey Division of Fish and Wildlife in northern New Jersey between 1984 – 2019. BMZs with stars indicate significant differences among them (i.e., p-value < 0.05).

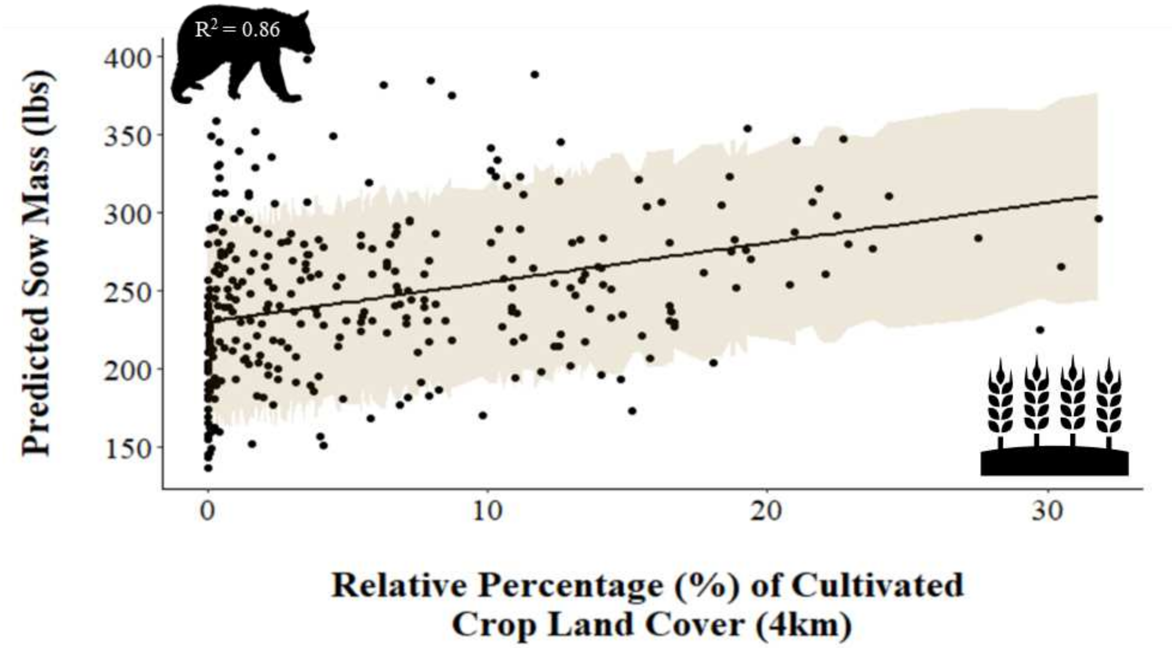

Figure 2.6. Predicted female (sow) American black bear (*Ursus americanus*) body mass (lbs) relative to strong effects of the relative percentage (%) of cultivated crop land cover within a 4km buffer around dens, in the top generalized linear mixed-effects model (GLMM). Sow mass measured at den site locations (*n* = 317) between late January – early April, surveyed by the New Jersey Division of Fish and Wildlife in northwestern New Jersey between 1984 – 2019.

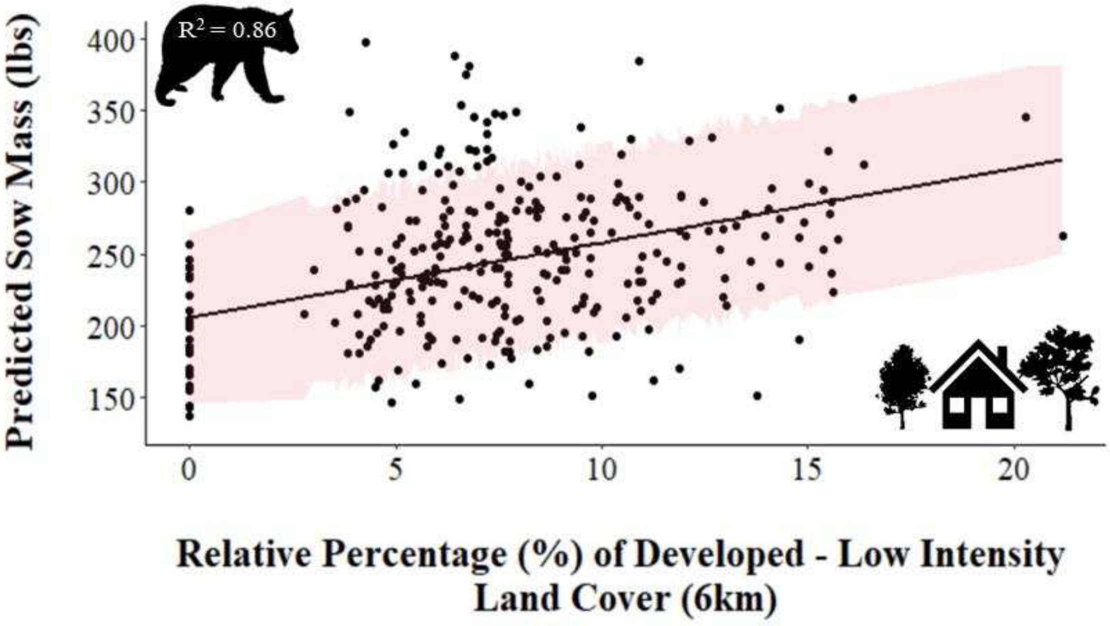

Figure 2.7. Predicted female (sow) American black bear (*Ursus americanus*) body mass (lbs) relative to strong effects of the relative percentage (%) of developed – low intensity land cover within a 6km buffer around dens, in the top generalized linear mixed-effects model (GLMM). Sow mass measured at den site locations (n = 317) between late January – early April, surveyed by the New Jersey Division of Fish and Wildlife in northwestern New Jersey between 1984 – 2019.

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CHAPTER 3: AMERICAN BLACK BEAR (*URSUS AMERICANUS*) LITTER SIZE, CONDITION, AND COMPOSITION IN A HUMAN-DOMINATED LANDSCAPE

SUMMARY

American black bear (*Ursus americanus*) populations have rebounded across the U.S., particularly in the eastern U.S. in New Jersey, where both human and bear populations have expanded spatially, resulting in an increase in human-bear interactions and conflicts. Therefore, investigating the factors contributing to the high abundance and success of black bears in New Jersey is imperative to effectively manage black bear populations. Here, we used data collected over three decades (1984 – 2019) from a population of female (sow) black bears in northern New Jersey, where bear populations are highest in the state. We tested the effects of maternal factors (e.g., age, body mass, den type selection, legacy of human-bear conflict), litter features (e.g., sex ratio, mass, composition), environmental context (e.g., trash generated, hard mast or acorn production, bear management zone, county), and population characteristics (e.g., bear population size and hunting pressure) on the litter size of sows using generalized linear mixed effects models (GLMMs). Our results demonstrated maternal condition, experience, and litter composition (e.g., same sex-female, same sex-male, or mixed sex) influenced litter size. Contrary to prior studies, we found no apparent trade-off between litter size and mass. Collectively, our results suggest the success of female black bears in northern New Jersey is partially attributable to the environmental context experienced by sows, as well as maternal characteristics.

INTRODUCTION

Anthropogenic pressures, such as climate change, habitat fragmentation and urbanization, are intensifying across the globe, encroaching into natural habitats at unprecedented rates (Watson et al. 2016). Large carnivores in particular are some of the most threatened species worldwide and have experienced substantial population declines as a result of anthropogenic impacts (Ripple et al. 2014). Anthropogenic pressure can (in)directly alter many life history traits, especially reproductive processes, which are vital to the long-term persistence of wildlife populations (Stearns 1992, Mills 2007). For example, hunting – beyond direct impact to harvested adults, can reduce offspring recruitment in wolves (*Canis lupus*, Ausband et al. 2015). Climate-associated impacts (e.g., higher temperatures during denning) have lengthened interbirth intervals and reduced pup survival in African wild dogs (*Lycaon pictus*, Woodroffe et al. 2017). Reproductive behaviors (e.g., denning, communication through scent marking and scrapes, Wilmers et al. 2013; selection of nursery sites, Yovovich et al. 2020) of pumas (*Puma concolor*) are extremely sensitive to human development as well. Despite variable and deleterious large carnivore reproductive responses to anthropogenic pressures, one such large carnivore, the American black bear (*Ursus americanus*; hereafter, black bear), has made a remarkable comeback within human-modified landscapes. Recent estimates show resident black bear populations have increased in 60% (*n* = 24 out 40 states) of the U.S. (FFWC 2019). In the eastern U.S., 73 % (*n* = 11 out of 15) of the states had increasing resident bear populations (FFWC 2019), and also exhibited some of the highest reproductive rates in the country compared to central and western regions (Hristienko and McDonald 2007).

Female (sow) reproduction is among the key life history processes regulating population growth in black bears (Powell et al. 1996, Clark and Eastridge 2006). Reproduction is an energetically costly process, shaped by both intrinsic and ecological factors (Stearns 2000). Ursids have some of the lowest reproductive rates of any North American terrestrial mammal (Jonkel and Cowan 1971, Bunnell and Tait 1981), where their reproductive performance is a function of age of primiparity, litter frequency and size (Lindzey and Meslow 1980, Bunnell and Tait 1981). Maternal age has been directly linked to reproduction in black bears, with younger, less experienced sows producing smaller litters (Alt 1982, McLaughlin et al. 1994, Miller 1994, Noyce and Garshelis 1994, Godfrey 1996, Ternent and Sittler 2011). As sows age, however, there is a decline in reproductive performance and output (e.g., reproductive senescence, Nussey et al. 2013, Lemaître and Gaillard 2017). Reproductive senescence has been observed primarily in brown bears (*Ursus arctos*, Schwartz et al. 2003), but was recently documented in western black bears (e.g., in Durango, Colorado, Johnson et al. 2020). Raithel (2017) demonstrated reproductive senescence was evident in sows >18 years of age that denned within anthropogenic habitats in New Jersey, but his work did not investigate the specific intrinsic and extrinsic factors that may be contributing to sow reproductive dynamics and senescence in this population.

As capital breeders, sows rely on resources previously acquired and accumulated for future reproductive investment. Sows in good body condition (e.g., elevated body size) with access to abundant natural resources (e.g., hard mast) experience earlier parturition (Hugie 1982), increased fecundity (Kolenosky 1990, Stringham 1990), and reduced breeding intervals (Jonkel and Cowan 1971, McMillin et al. 1976, Rogers 1987a, Elowe and Dodge 1989, Costello et al. 2003, Clark 2004). Thus, the environmental context, and specifically access to both natural and anthropogenic resources, are key drivers of variation in reproduction. Although classified as a carnivore, black bears are true omnivores which opportunistically feed on a broad assemblage of food items. The coupled hyperabundance of anthropogenic and natural foods has long been considered an important factor in improving black bear reproductive rates in Pennsylvania (Alt 1981), a neighboring state that shares populations with New Jersey. Anthropogenic subsidies, namely access to garbage, improves reproductive performance in black bears by lowering the age of primiparity compared to wildland conspecifics, for example (Beckmann and Berger 2003, Beckmann and Lackey 2008). Increased reproductive success and litter size of younger (e.g., two-year old) black bear sows have also been tied to the access and use of urbanized areas (Gould et al. 2021). There is also strong evidence that highly productive natural food years and environments increase reproductive success in black bears (Jonkel and Cowan 1971, Rogers 1987a, Eiler et al. 1989, Elowe and Dodge 1989, Schwartz and Franzmann 1991, McLaughlin et al. 1994, Miller 1994). Much attention has been brought to how increases in hard mast (e.g., acorns), particularly from oak (*Quercus*) species, improve reproductive success in black bears (e.g., Eiler et al. 1989, Elowe and Dodge 1989, Pelton 1989, Costello et al. 2003, Clark 2004).

Sows in good condition tend to invest into larger litters, and may also invest preferentially into sons, while females in poor condition may bias the sex composition of their litter towards daughters (i.e., the Trivers-Willard hypothesis, Trivers and Willard 1973, Veller et al. 2016). Specifically, sows in good condition will tend to invest more into sons if they perceive sons would confer them with a greater fitness advantage than daughters. Because black bears have male-biased dispersal (Rogers 1987b), it may be beneficial to invest more into sons when bear harvest pressure is high or when density-dependence creates a landscape of female intraspecific competition with negative fitness repercussions for the sow and her female progeny. Litter sex ratios in eastern black bear populations are typically balanced (Alt 1989, Elowe and Dodge 1989, Kolenosky 1990), but with a tendency towards a male skew (Alt 1981, 1982). Since larger male black bears are typically at a reproductive advantage compared to smaller males, it seems intuitive that sows in better maternal condition would maximize their reproductive payoff by producing more males. However, life history theory predicts a compromise between offspring number and size (Smith and Fretwell 1974). While maternal mass and litter size are strongly and positively correlated in black bears (Noyce and Garshelis 1994), and maternal costs often increase with litter size (e.g., through lactation, Farley and Robbins 1995), the compromise between offspring number and size (e.g., trade-off, Smith and Fretwell 1974) may be undetected if maternal characteristics are not considered.

Sow maternal behavior can affect reproductive output in a myriad of other ways, with den site selection being an additional path by which a sow's choice may affect littler size, cub condition, and survival (Hellgren 1998). Den sites are particularly important for parturition and early cub growth development in black bears (Clark et al. 1998). Optimal den sites are highly insulated for thermoregulation (Oli et al. 1997), are protected from spring flooding (Hellgren and Vaughan 1989, Oli et al. 1997, Clark et al. 1998, White et al. 2001), disturbance by humans (Tietje and Ruff 1980, Rogers 1987a, Goodrich and Berger 1994, Oli et al. 1997a, Linnell et al. 2000, Gaines 2003, Reynolds-Hogland et al. 2007) and (or) predators (Davis et al. 2011), and are near adequate resources (e.g., food, water, shelter) upon den emergence (LeCount 1983). Indeed, den site type has been found to influence cub of the year survival in black bears (Alt 1984, McDonald and Fuller 1998).

Like many species, black bears exhibit seasonal variation in behavior, with an increase in resource acquisition in the fall to increase fat reserves for denning (e.g., during hyperphagia, Nelson et al. 1983), which in turn can influence reproductive output. Bears may take more risk(s) to acquire resources, especially when natural forage production is low (e.g., Noyce and Garshelis 1994, Baruch-Mordo et al. 2014), resulting in increased conflict with humans. Thus, a constant risk for food reward over the lifetime of an animal could increase lifetime reproductive success, particularly as sows gain mass through experience (e.g., improved hunting skills, Derocher and Stirling 1994; greater knowledge of local food sources, Rogers 1987a).

The provisioning of easily accessible anthropogenic resources does come at a cost for sows. For example, lethal management is on often employed when black bears exploit anthropogenic resources and have a negative interaction with humans. In addition, and though highly controversial, bear harvest is typically used to reduce black bear population size to below carrying capacity, especially in the eastern U.S. (NBBTC 2012, Raithel 2017). Indeed, black bear populations are often characterized by low rates of natural mortality in adult age classes, but with high rates of anthropogenic mortalities (e.g., through vehicle strikes). Nonetheless, reductions in black bear population size through increased bear harvest can boost black bear sow reproduction (e.g., via a release from density-dependence and compensatory mortality, Sinclair et al. 2006), particularly in young sows that experience lower densities (e.g., Czetwertynski et al. 2007, Obbard and Howe 2008). Whether bear harvest mortality is compensatory or additive to natural mortality is up for debate in certain U.S. states, but increased reproduction due to increased bear harvest could result from less intense intraspecific competition for resources and (or) infanticide (e.g., the "increased reproduction hypothesis", Stringham 1980, 1983, McCullough 1981).

Given the success of the American black bear in the U.S., it is critical to understand if higher reproductive rates in the eastern U.S., particularly in New Jersey – the state with highest coupled density of humans and black bears in the country – is attributed to anthropogenic change and (i) the *environmental context* experienced by sows, and (or) to (ii) *maternal condition and behavior,* (iii) *litter characteristics, and* (iv) *black bear population dynamics*. We hypothesized that sow age, condition, and experience explain substantial variability in black bear litter size as well as litter sex ratio, while the environmental context experienced, a history of conflict with humans, and bear harvest can further influence those individual-based investments into litter size, condition, and composition.

METHODS

Focal species

Sow black bears exhibit delayed sexual maturity (≥3 years old, Pelton 2003), lower reproductive rates (Bunnell and Tait 1981), and prolonged period of parental care and investment (e.g., sows care for their young for 16 – 17 months, Powell et al. 1997). Sows produce litters of two to three cubs on average (McDonald and Fuller 2001, Hristienko et al. 2004), and are reproductively successful well into their mid-twenties (Alt 1989, McLaughlin 1998, Hristienko and McDonald 2007). Sows mate during the summer (in New Jersey typically 1 June – 31 August, but peaking in June and July, *unpublished data*, NJDFW), after which they experience delayed implantation of blastocysts (i.e., developing embryo) that is highly influenced by the availability of adequate food resources prior to implantation (Noyce and Garshelis 1994). After approximately 4 – 5 months blastocysts implant (Wimsatt 1963) in late November to early December, generally after den entry, followed by a ~55-day gestation period (Fraker et al. 2006). Sows then give birth to altricial cubs in the den in mid-January to early February (*unpublished data*, NJDFW; Pelton 2003). Sows breed and produce litters every two years, but can reproduce annually if a litter is lost (Alt 1989).

Study area and data collection

A long-term study area was established by the New Jersey Division of Fish and Wildlife (NJDFW) in northern New Jersey, located primarily north of I–78 and west of I–287, spanning four designated Bear Management Zones (BMZs 1 – 4) and portions of seven counties (e.g., Bergen, Hunterdon, Morris, Passaic, Somerset, Sussex, and Warren, NJOAL 2015). BMZs 1 and 3 contain the best bear habitat with high forest cover (e.g., >76%) and bear densities (NJOAL 2015). BMZs 2 and 4 contain less suitable habitat consisting of more agricultural areas and open space and lower bear densities.

Northern New Jersey is characterized by elevated highlands (e.g., up to 1800 feet in elevation, Russell 1981) and valleys, with continental climate that is colder and has higher precipitation than the other regions of the state (Runkle et al. 2022). Habitat in northern New Jersey consists of forests dominated by mixed oak (*Quercus*) and hickory (*Carya*) species, accompanied by pockets of northern hardwoods [e.g., maple (*Acer* spp.), birch (*Betula* spp.)], white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), and some isolated stands of red spruce (*Picea rubens*) (NJDEP 2020). There are currently ~9.3 million people living in New Jersey, with estimates of ~1,260 people per mi^2 (NJDLWD 2021), making it the most densely populated state in the U.S, with human populations projected to increase by 9% between 2010 and 2030 (NJDLWD 2013). Historically, black bear populations in New Jersey were nearly extirpated due to unregulated killing, habitat loss, ultimately plummeting to <100 bears in the 1950's (Lund 1980). However, after a 32-year and intermittent hunting moratoriums (1971 – 2002, 2004, 2006 – 2009, 2021 – present) bear populations in northern New Jersey have rebounded to recent estimates of ~3,100 bears in 2020, a ~41% increase in bears since 2019 (*n* = 2,200, *unpublished data*, NJDFW).

The NJDFW visited 419 dens of 214 individual, radio-collared sows from January to April (Julian date range = 13 – 104) between 1984 and 2019 to determine the reproductive status (e.g., with cubs of the year or yearlings, barren), age, and body mass of each sow, and to sex, mark, and count cubs. Radio-collared sows were tracked and chemically recaptured (e.g., with ketamine hydrochloride and xylazine hydrochloride, Wildlife Pharmaceuticals, Inc., Fort Collins, CO, USA) at winter den sites. The first primary premolar was sectioned for sow aging (Matson's Lab, Manhattan, MT, USA). Age at first reproduction of sows in our study population was three years old. However, earlier age at first reproduction (e.g., two years old) was documented in our study area by three sows that each produced one cub (1986, 1991, 2001). Reports of this earlier primiparity at two years of age in black bears have been documented in a recovering black bear population in Florida (Garrison et al. 2007), as well as in urban areas in North Carolina (Gould et al. 2021). Yet, we did not include two-year-old sows in our analyses, given they contribute very little to the overall population productivity in New Jersey (*unpublished data*, NJDFW).

Covariates of interest and hypothesized relationships with fecundity

Maternal Characteristics

The long-term den dataset (n = 419) was used to assemble maternal covariates important to litter size. ***Sow age*** was collected each year of the study for 205 individual sows. Because sow age is an important maternal factor influencing reproduction, we included this covariate in our baseline model structure. For ease in interpreting results, we classified sow age into three different categories (e.g., young [3 – 4 years old], middle-aged [5 – 13 years old], and old [14+ years old]), similar to suggestions by Eiler et al. (1989).

Sow body mass was also collected each year for 182 individual sows, and was back-calculated and standardized to early winter sow body mass, to accommodate variability in overwinter body mass declines (Samson and Huot 1995). We expected maternal condition (*both* sow body mass and age, H_1, Fig. 3.1) will have a pronounced, additive effect on litter size. We predicted litter size will increase with sow age but will decline in older sows, while we expect a strong positive relationship between sow body mass and litter size. We expected heavier sows in good maternal condition will bias the litter sex ratio toward males. We also predicted an interactive effect between sow age and litter mass, along with sow body mass and litter mass, on litter size.

Den selection: the ***den type*** was recorded for all 214 individual sows. There were 12 den types identified by the NJDFW, which we reduced into four den site categories (to simplify statistical analyses and allow model convergence), that consisted of ground dens (e.g., brush pile, open nest, excavation), manmade dens, rock dens (e.g., rock cavity), and tree dens (e.g., root ball, blowdown, hollow tree/stump/log). We hypothesized the type of den selected by mothers, particularly when coupled with sow age (interactive effect), will influence litter size ($H_1 \times H_2$, Fig. 3.1). We predicted litter size should increase, especially in sows that are middle-aged and have more experience than younger sows and have chosen dens that improve thermoregulation and protection from disturbance (e.g., rock and tree dens) compared to dens that are more open and potentially more vulnerable to disturbance (e.g., ground and manmade dens) (H_1, Fig. 3.1).

We also expected sows that have a ***legacy of conflict*** throughout their lifetime will have more cubs, likely because they are taking more risk(s) to gain access to anthropogenic resources (H_1, Fig. 3.1). A legacy of conflict category was assigned to individual sows by the NJDFW through research trapping and (or) other den surveys, depending upon behavior of sow and damage severity and type. For example, sows were categorized as either Category I (most severe) that posed immediate threat to public safety and caused >$1,000 USD in damages or categorized as Category II (nuisance) that were not an immediate threat to public safety and caused <$1,000 USD in damages.

Litter Characteristics

Litter size was obtained from 205 individual females from counting the number of cubs per sow during each den survey. We indexed litter size (e.g., 0, 1, 2, 3, ≥4 cubs) because higher litter sizes (e.g., of five and six cubs per litter) had lower frequencies (Appendix 4 – Fig. A4.1) that would not allow model convergence. Additionally, den surveys with zero cubs or with yearlings produced the previous year were censored from our analysis. We hypothesized a negative relationship (i.e., trade-off) between litter size and ***litter mass***. We also expected litter size may partially depend on ***litter sex ratio*** (e.g., female-dominated, male-dominated, or same sex), and ***litter composition*** (e.g., same sex – female, same sex – males, mixed sexes) (H_2, Fig. 3.1). We predicted the litter sex ratio of male to female cubs would statistically differ from equality (e.g., 50:50). We expected litter size would be lower with male-dominated litter sex ratios and litters composed of only males, because sows may invest more resources into fewer, more robust males, whereas lighter sows should produce more daughters, particularly those of lower fitness (e.g., lower cub mass) (H_2, Fig. 3.1; Fig. 3.2).

Environmental Context

We obtained historical (1995 – 2018) ***trash production*** data (NJDEP 2019), which were standardized by county area, that consisted of annual total trash and recycling disposed. Upon initial examination of the trash production data, we found a non-normal distribution. Therefore, we categorized the trash data into low and high production, based on falling below and above the mean, respectively. We hypothesized that sows will be at a reproductive advantage (i.e., have larger litter sizes) in dens (*t*) following years of high trash production (*t* – 1) (H_3, Fig. 3.1). For natural forage, we acquired historical (1983 – 2018) ***hard mast production*** data for all combined oak species from West Virginia (Barton et al. 2018), a state with comparable ecoregions and hard masting species to New Jersey, where consistent hard mast survey data were not available (see Appendix 1 for further information). We categorized hard mast as poor, average, and good production years, based on lower, middle, and upper quantiles. We hypothesized the abundance of hard mast will not influence litter size, because of the abundance of both natural and anthropogenic resources available to bears on the landscape (*unpublished data*, NJDFW) (H_3, Fig. 3.1). Specifically, we expected the effect of hard masting years (*t* – 1, *t* – 2) on sows producing more cubs the winter(s) following poor, average, and good hard masting years (*t*) would be negligible (H_3, Fig. 3.1). We also predicted that annual masting production would not affect litter size, and that this relationship would not be tempered by sow condition (no interactive effect). We hypothesized litter size would vary by BMZ and county, because each differ in habitat characteristics and bear densities (H_3, Fig. 3.1). We expected litter size will be lower in BMZs 2 and 4 because they have < 51% forested land (≥ 51% forested land is considered optimal bear habitat, NJOAL 2015), compared to BMZs 1 and 3 which are considered excellent bear habitat (~76% of forest cover, NJOAL 2015). We also predicted litter size would be lower in Sussex and Passaic counties, because they have the highest and densest bear populations (e.g., density-dependent depression in litter size), compared to Morris and Warren counties (McConnell et al. 1997).

Population Characteristics

We used yearly (2003, 2005, 2010 – 2018), local ***bear population size*** derived from a mark-recapture population estimator (e.g., Lincoln-Petersen Index) from the fraction of marked bears recovered during annual bear harvest (i.e., ***bear harvest pressure***) in New Jersey. We predicted litter size (*t*) should decrease following increases in bear population size the previous year (*t* – 1) and the previous two years (*t* – 2). We predicted litter size (*t*) should increase following increases in the number of bears and especially male bears harvested the previous hunting season (*t* – 1, ~1 – 5 months) and two hunting seasons prior (*t* – 2, ~16 – 17 months), because a decrease in bear population size will inherently reduce competition for resources (H_4, Fig. 3.1).

Data analysis

Because our response of litter size are count data, we used generalized linear mixed models (GLMMs), which included a random effect of female identifier to account for correlations due to repeated observations from the same sow (Bolker 2015). We fit Poisson GLMMs given there was lack of overdispersion (e.g., variance exceeds the mean) in our count data (litter size), using the *glmmTMB* package (Brooks et al. 2017). We used the *emmeans* function from the R package *EMMEANS* to quantify the impact of a specific covariates on litter size, while maintaining all other covariates in the model at their mean value, and to conduct post-hoc Tukey tests to make pairwise comparisons between covariate levels of interest *a posteriori* (Lenth 2020).

We used a one-proportion *z*-test to determine if the litter sex ratios between the number of male and female cubs were statistically different from a balanced sex-ratio (50:50), and if the number of male cubs were statistically greater than female cubs. We also fit one-way ANOVAs to determine if litter mass differed among litter sex ratio (e.g., female-dominated, male-dominated, same sex), as well as among litter composition (e.g., same sex – female, same sex – male, mixed sexes).

All statistical analyses were performed in RStudio (2020). While we had a large dataset spanning 35 years and 214 individuals, complex multivariate models did not always provide reliable estimates. We fit models that tested for a pre-determined set of hypotheses of interest and discuss both the biological and statistical significance of the effects below. We specifically report results [back-transformed estimated margin means (emmean) to the original scale of our response (litter size) and associated 95% confidence intervals] from less complex models that exhibited strong effects on litter size, as related to maternal and litter characteristics, the environmental context, and black bear population dynamics.

RESULTS

Maternal Characteristics

Variability in litter size was best explained by an additive effect of sow age and body mass (BIC = 1003.97), rather than an interactive effect (BIC = 1013.20), thus becoming the baseline structure of the null model (i.e., we kept this parameterization moving forward in all models). We found sow age and body mass were good predictors of litter size in the baseline model with sows ranging in age from 3 to 28 years old and in body mass from 137 to 398 pounds (Appendix 4 – Table A4.1). Average litter size increased up to 6 and 7 years of sow age, fluctuated and ultimately increasing at 17 years of age, and then peaked at 18 years of age (Appendix 4 – Fig. A4.2). Our baseline GLMM revealed litter size was highest in middle-aged sows (emmean: 2.94, 95% CI: 2.72, 3.18, Fig. 3.3a) compared to older sows (emmean: 2.78, 95% CI: 2.01, 3.84, Fig. 3.3a) and younger sows (emmean: 2.56, 95% CI: 2.19, 2.99, Fig. 3.3a), and litter size increased with increasing sow body mass (Appendix 4 – Table A4.1, Fig. 3.3b).

The type of den site selected by the sow did not predict significant differences in litter size (post-hoc Tukey test for all six contrasts, p-value > 0.05, Appendix 4 – Table A4.2). We found litter size was similar in ground (emmean: 2.78, 95% CI: 2.43, 3.19), tree (emmean: 2.78, 95% CI: 2.24, 3.46), manmade (emmean: 2.31, 95% CI: 1.72, 3.11) and rock dens (emmean: 2.75, 95% CI: 2.36, 3.20).

Litter Characteristics

Out of the 419 dens surveyed from 1984 to 2019, there was a total of 1,109 cubs produced, with an average litter size of ~2.7 cubs per litter. Total litter sizes ranged from zero to six cubs per litter (Appendix 4 – Fig. A4.1). Sex of the cubs was identified for litters in 414 out of the 419 dens surveyed. We found there was no significant departure from sex ratio expectation (50:50) between the number of male ($n = 561$) and female ($n = 533$) cubs ($\chi^2 = 0.72$, p-value = 0.41), and the number of male cubs were not statistically greater than female cubs ($\chi^2 = 0.67$, p-value = 0.21). Most ($n = 244$) of the litters where sex had been identified and had ≥ two cubs present ($n = 349$ litters) were predominantly mixed sex. In mixed litters of twins ($n = 42$), we found the litter sex ratio was always 50:50.

We found no significant differences in litter mass among litter sex ratio (e.g., female-dominated, male-dominated, same sex, ANOVA, $F_{2,373} = 0.15$, p-value = 0.86). We did find, however, significant differences in litter mass among litter composition type (e.g., same sex – female, same sex – male, mixed sex, ANOVA, $F_{2,373} = 29.60$, p-value < 0.001). In litters of twins, average litter mass was slightly heavier in same sex – female litters (11.70 ± 4.40 pounds, $n = 21$), compared to same sex – male litters (11.0 ± 3.40 pounds, *n* = 28) and mixed sex litters (11.10 ± 2.80 pounds, *n* = 42). In litters of triplets, same sex – male litters (16.20 ± 3.90 pounds, *n* = 23) on average weighed more than mixed sex (15.30 ± 3.50 pounds, *n* = 113) and same sex – female litters (15.20 ± 3.10 pounds, *n* = 24). In mixed triplet litters that were male dominant, average litter mass was slightly heavier (15.60 ± 3.50 pounds, *n* = 58) than mixed triplet litters that were female dominant (15.10 ± 3.40 pounds, *n* = 53), and considerably heavier than triplet litters with the same sex ratio (10.90 ± 0.14 pounds), with this later instance being extremely rare (*n* = 2). In litters with ≥4 cubs, average litter mass of mixed sex litters (19.50 ± 4.80 pounds, *n* = 89) was relatively higher than same sex – male (18.20 ± 3.90 pounds, *n* = 6) and same sex – female litters (16.20 ± 1.60 pounds, *n* = 3). Though, in mixed sex litters with ≥4 cubs, average litter mass of female-dominant (19.50 ± 5.10 pounds, *n* = 30), male-dominant (19.50 ± 4.80 pounds, *n* = 31) and same sex (19.60 ± 4.80 pounds, *n* = 28) litters were all relatively similar.

We did not find evidence of a trade-off between litter size and litter mass (Fig. 3.4), where litter size was highest in litters with above average mass (emmean: 3.29, 95% CI: 2.84, 3.80) compared to litters with below average mass (emmean: 2.39, 95% CI: 2.07, 2.75). A post-hoc test revealed litter size was significantly different between above average and below average litter mass (post-hoc Tukey test, *p*-value = 0.0001). But we did find that litter size and mass were more constrained in older sows (Fig. 3.4a) compared to younger and middle-aged sows (Fig. 3.4b). Contrary to our predictions, we did not find a significant interactive effect of sow age and litter mass, and sow body mass and litter mass on litter size (Appendix 4 – Table A4.3). We also found that litter size was not significantly different among different litter sex ratios (post-hoc Tukey test for all three contrasts, *p*-value > 0.05, Appendix 4 – Table A4.2).

We found litter composition predicted differences in litter size (Appendix 4 – Table A4.2). Litter size was considerably higher in mixed sex litters (emmean: 3.10, 95% CI: 2.73, 3.52, Fig. 3.5), compared to litters only consisting of male (emmean: 2.25, 95% CI: 1.87, 2.72, Fig. 3.5) and female cubs (emmean: 2.21, 95% CI: 1.78, 2.74, Fig. 3.5). A post-hoc test confirmed significant differences in litter size only among mixed and same sex female litters (post-hoc Tukey test, *p*-value = 0.002).

Environmental Context

Trash production did not predict significant differences in litter size (post-hoc Tukey test, *p*-value = 0.67, Appendix 4 – Table A4.2). Litter size was not significantly influenced by the type of hard masting year, both one year after ($t + 1$) and two years ($t + 2$) after hard mast production (post-hoc Tukey test for all 3 contrasts for each of the two time periods, p-value$_{(t+1)} > 0.05$ and p-value$_{(t+2)} > 0.05$, Appendix 4 – Table A4.2). Although, we noted litter size was slightly higher following a good hard mast year ($t + 1$, emmean: 2.85, 95% CI: 2.41, 3.36) compared to a poor ($t + 1$, emmean: 2.71, 95% CI: 2.35, 3.13) and an average hard mast year ($t + 1$, emmean: 2.73, 95% CI: 2.34, 3.19). While litter size was slightly higher two years after an average hard mast year ($t + 2$, emmean: 2.83, 95% CI: 2.42, 3.31) compared to two years after a poor ($t + 2$, emmean: 2.68, 95% CI: 2.32, 3.09) and good hard mast year ($t + 2$, emmean: 2.79, 95% CI: 2.38, 3.28), but confidence intervals largely overlapped. As predicted, we did not find an interactive effect of maternal condition (e.g., body mass) and type of hard masting year on litter size (Appendix 4 – Table A4.3).

We found BMZ did not significantly predict differences in litter size (post-hoc Tukey test for all six contrasts, *p*-value > 0.05, Appendix 4 – Table A4.2). Similarly, county was a not a good predictor of litter size (post-hoc Tukey test for all six contrasts, *p*-value > 0.05, Appendix 4 – Table A4.2), with minimal differences in litter size between Warren (emmeans: 2.85, 95% CI: 2.42, 3.36), Passaic (emmean: 2.75, 95% CI: 2.11, 3.57), Sussex (emmean: 2.73, 95% CI: 2.39, 3.11), and Morris (emmean: 2.68, 95% CI: 2.06, 3.47) counties.

Population Characteristics

Litter size was highest slightly higher the year after (t + 1) an estimated above average bear population size (emmean: 3.11, 95% CI: 2.41, 4.01) compared to a below average population size (emmeans: 2.96, 95% CI: 2.36, 3.71). Yet, litter size was slightly higher two years after (t + 2) an estimated below average population size (emmean: 3.15, 95% CI: 2.41, 4.12) compared to an above average population size (emmean: 3.06, 95% CI: 2.17, 4.31). However, confidence intervals systematically overlapped, and bear population size was found not to be a strong predictor of differences in litter size (post-hoc Tukey test, $p\text{-value}_{(t+1)} = 0.70$ and $\text{p-value}_{(t+2)} = 0.85$, Appendix 4 – Table A4.2). Similarly, we found that bear harvest was a not a strong predictor of variability in litter size (post-hoc Tukey test for all 3 contrasts for each of the two time periods, $p\text{-value}_{(t+1)} > 0.05$ and $\text{p-value}_{(t+2)} > 0.05$, Appendix 4 – Table A4.2).

DISCUSSION

Our study highlights the contribution of maternal features, litter characteristics, environmental context, and bear population dynamics to black bear littler size, condition, and composition in a human-dominated landscape.

Maternal Characteristics

Our results are supported by several other studies that detected a positive relationship between sow body mass and reproduction (Rogers 1976, Kolenosky 1990, Stringham 1990, Noyce and Garshelis 1994). While a positive relationship among sow age and litter size has already been documented (e.g., Kordek and Lindzey 1980, Elowe and Dodge 1989, Kolenosky 1990, McLaughlin et al. 1994, Noyce and Garshelis 1994), reports of reproductive senescence in black bears are limited, particularly in eastern black bears. Johnson et al. (2020) found *both* bear body fat and reproduction peaked in prime-aged (8 – 11-year-old) sows in Colorado. Previous research indicated reproductive potential of sows in our study area typically peaks in sows that are 4 – 13 years old (*unpublished data*, NJDFW; Raithel 2017), which align with our results seen in middle-aged (5 – 13-year-old) sows (Fig. 3.3a). However, our results show sow body mass peaked in older bears in our study (15 – 17 years old, Chapter 2). Because older sows (14+ years old) are on average producing litter sizes (Fig. 3.3a) equivalent to the overall average litter size of our study period (e.g., ~2.7 cubs per litter), along with the high influx of cubs produced by middle-aged sows (Fig. 3.3a), may help counterbalance the increased mortality of cubs and yearlings (e.g., from vehicle strikes, Raithel 2017) and the relative proportion of young (3 – 4 years old: 0.76) and middle-aged (0.21) females harvested that may otherwise reduce the population size in northern New Jersey. Thus, our results demonstrate sow fitness, *both* body mass (Chapter 2) and reproduction, are maintained longer than previously expected, and are likely a key contributing factor to sustained higher bear populations in northern New Jersey.

Litter Characteristics

Evidence of a trade-off between litter size and offspring mass has been identified in ursids (e.g., brown bear, Gonzalez et al. 2012, Van de Walle et al. 2020; polar bear, *Ursus martimus*, Derocher and Stirling 1998; black bear, Miller 1963, Alt et al. 1980, Alt 1981). We were surprised by the lack of trade-off among litter size and mass in black bears in our study area (Fig. 3.5). However, a positive correlation among competing life history traits such as litter size and mass indicates high heterogeneity in resource availability available to sows (van Noordwijk and de Jong 1986). Yet, the constraints we found in the range of litter size and mass among sow age and body mass (Fig. 3.5) are likely due to individual variability in resource acquisition (e.g., intake and digestion) and allocation (e.g., portioning among physiological functions) among sows (van Noordwijk and de Jong 1986, Reznick et al. 2000). However, we did not assess the relationship between litter size and yearling body mass, so we are unsure if a trade-off is masked until later in life for cubs because of sibling competition for maternal resources (e.g., Gonzalez et al. 2012).

Our results do not support the Trivers-Willard hypothesis (Trivers and Willard 1973), and are more generally supported by Fisher's fundamental sex ratio theorem (Fisher 1930) of equal sex ratio, and align with earlier findings of balanced litter sex ratios in black bears (Reynolds and Beecham 1980, Alt 1989, Elowe and Dodge 1989, Kolenosky 1990, Beck 1991). At first glance, sows do not appear to bias their energy expenditure on sons and daughters because litter sizes were comparable regardless of litter sex ratio, and litter size was highest in mixed sex litters and was similar among same sex – female and same sex – male litters (Fig. 3.6). One sex does not seem more costly for sows to produce (Fisher 1930), which aligns with earlier findings in other mammals (e.g., roe deer, *Capreolus capreolus*, Hewison et al. 1999) and other bears (e.g., polar bear, Atkinson et al. 1996). However, sows could be investing more into sons *only* in triplet litters that are male-biased, because their litter mass (x̄ = 15.6 ± 3.5 pounds, *n* = 58) exceeded female-biased (x̄ = 15.1 ± 3.4 pounds, *n* = 53). Though, higher averager litter mass in mixed triplet litters that were male-biased may be more indicative of male cubs outcompeting female cubs for maternal resources such as milk (Derocher and Stirling 1998), rather than sows investing more heavily into sons. Factors predicting biased offspring sex ratios are quite complex and are often driven by the combined effects of maternal age, reproductive history, environmental conditions, and population density (Kruuk et al. 1999, Martin and Festa-Bianchet 2011, Froy et al. 2016), which we were only able to partially explore. Including prior reproductive history of sows would be an important consideration for future research to provide insights into the consequences of litter sex ratio changes on long-term population dynamics of black bears in northern New Jersey.

Environmental Context

Black bears cover a very broad trophic niche, and bears in this portion of the eastern U.S. have access to a hyperabundance of both anthropogenic and natural resources (Alt 1981). As such, we were not surprised by the lack of relationships between trash and natural resource production (e.g., hard mast) and litter size. Yet, given garbage complaints constitute ~41% of more nuisance (Category II) complaints (Chapter 1), and a prior history of nuisance conflict by sows significantly increases sow body mass (Chapter 2), these results indicate our levels of trash and mast production were likely not at the appropriate scale to discern precise differences (e.g., township-level trash generated, hard mast produced in northern New Jersey).

Litter sizes were not lower in BMZs 2 and 4, as we expected, and did not align with sow body mass differences among BMZs (Chapter 2). There are likely a variety of other factors contributing to the apparent differences in litter sizes among BMZs (e.g., land use practices, human population density and urbanization pressure, localized bear carrying capacities) that we were unable to capture at the BMZ level. Additionally, we did not detect any trends between sow body mass, litter mass, and litter size among the four counties in our study area, likely disguised by differences in habitat across the study area (Garshelis 1994).

Population Characteristics

Given population dynamics involve density-dependent changes in population growth, a variety of life history traits are generally shaped by density-dependence. Effects of population density on litter size have amassed throughout the literature, with many studies demonstrating a negative relationship between population density and litter size (e.g., Morris 1998, Wielgus and Bunnell 2000, Forchhammer et al. 2001, Czetwertynski et al. 2007, Flajšman et al. 2018). Thus, our finding of no effect of bear population size on litter size was telling. Yet, density-dependent effects to litter size may have been ultimately confounded by interannual demographic and environmental stochasticity, as well as proximity to carrying capacity (Fowler 1981, McLaughlin 1999, Miller et al. 2003, Zedrosser et al. 2006).

It is hypothesized that more cubs will be produced in areas with higher quality food resources irrespective of the removal of bears, and more specifically male bears (e.g., "no effect" hypothesis, Bunnell and Tait 1981, Knight and Eberhardt 1985, Rogers 1987a). The lack of effect of bear harvest on litter size supports this hypothesis and other work not detecting hunting-related density-dependent responses in bear populations (Miller 1990, Derocher and Taylor 1994, Garshelis 1994, McLellan 1994). Nevertheless, we did not assess litter size versus population density, where density incorporates an element of space and is an important consideration for reproduction and population structure (Christian 1971, Myers et al. 1971). Thus, future work should incorporate population density relative to individual sows (e.g., Zedrosser et al. 2013) to determine if there are elevated concentrations of bears in certain areas that could contribute to variability in reproductive effects that were not captured here.

CONCLUSION

Black bear litter size in northern New Jersey is ultimately mediated by maternal condition, experience, and litter composition, with sow age and body mass being the best predictors of litter size. Given the lack of trade-off between litter size and litter mass in our study area, along with extended maternal condition (Chapter 2) and reproductive ability of sows well into older ages, our result support the “superflea” theory by Reznick et al. 2000. As such, female bears in northern New Jersey are perhaps “superbears” and can circumvent trade-offs by acquiring a variety of resources ultimately improving their body condition (e.g., body mass, Chapter 2) allowing them to have *both* “big houses and cars” (Reznick et al. 2000), or in this case larger body mass, litter size and litter mass. Yet, the observed variability in litter size and mass suggests differences in resource acquisition and allocation, mostly explained by age, but also perhaps by other constraints not captured here (e.g., genetic, Arnold 1992; developmental, Kauffman et al. 1985; (bio)chemical, Sterns 1992; functional, Arnold 1992, Reznick and Travis 1996).

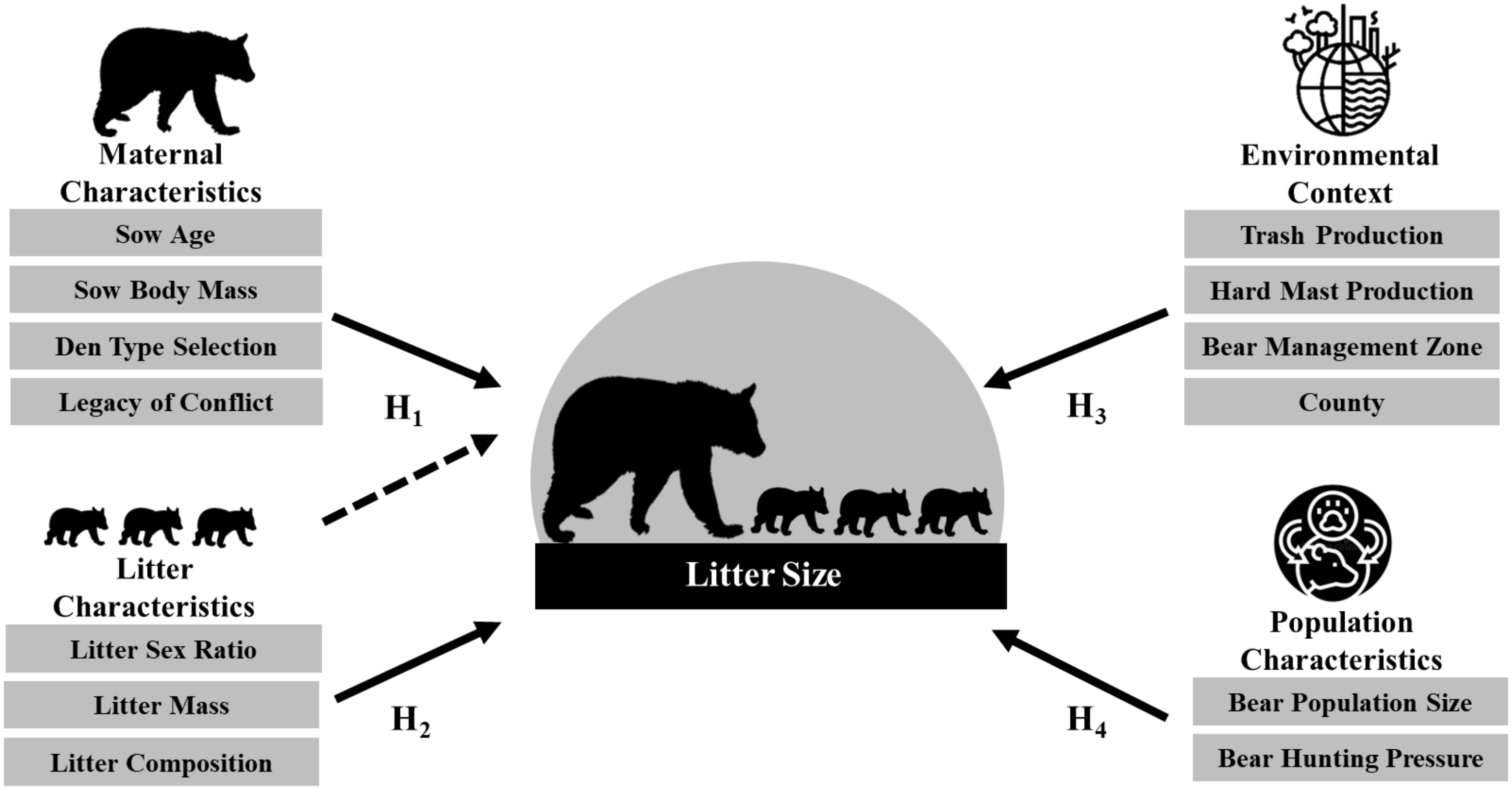

Figure 3.1. Predicted relationships between key categories of interest (climate, anthropogenic, bear characteristics, habitat, and natural resources) and their effect(s) on litter size (number of cubs) in female (sow) American black bears (*Ursus americanus*) in northern New Jersey.

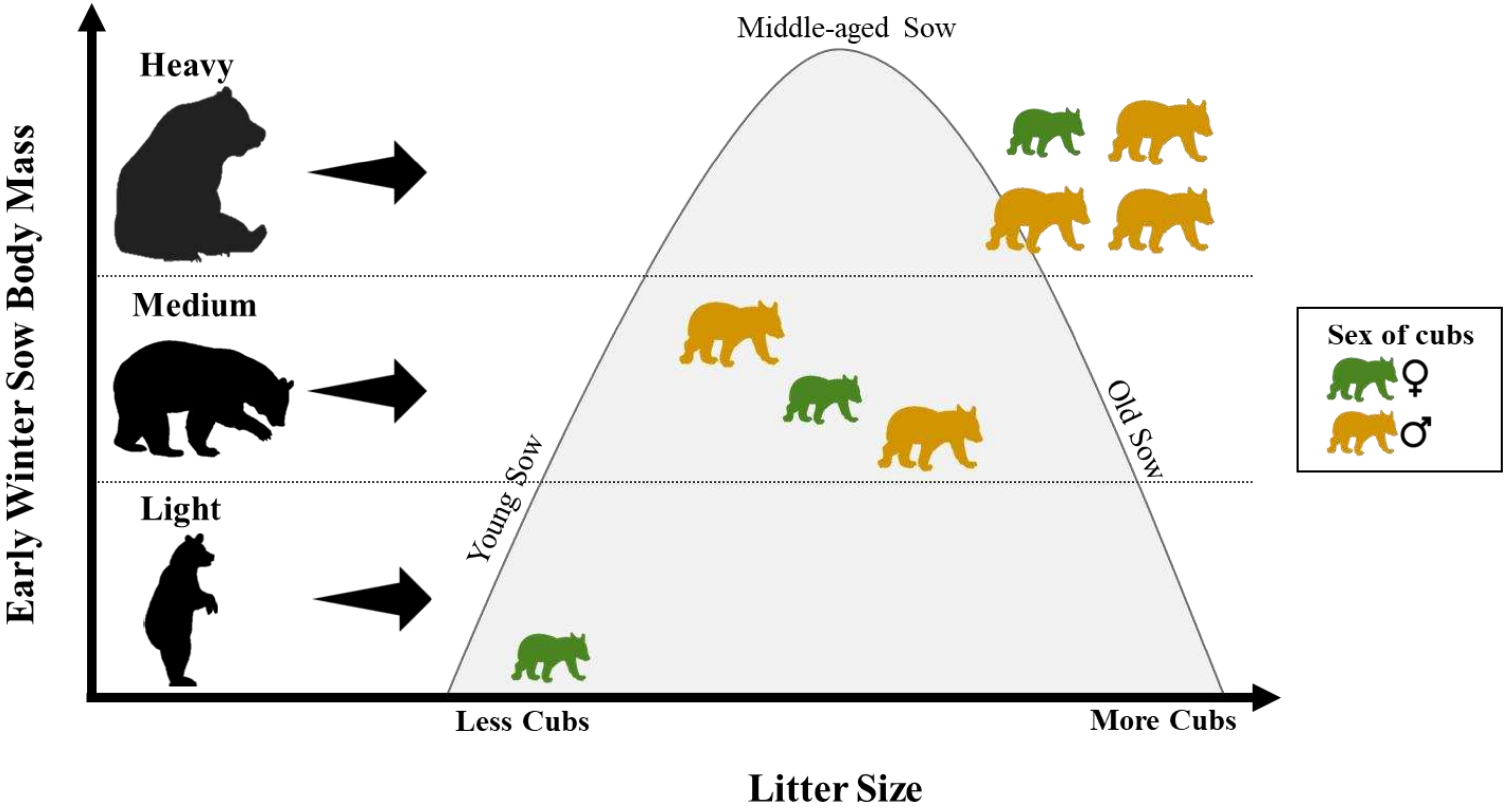

Figure 3.2. Hypothesized relationships between maternal condition [e.g., age, early winter body mass – categorized as light, medium, and heavy] in female (sow) American black bears (*Ursus americanus*) in northern New Jersey, and expected litter size (number of cubs), litter sex ratio (female-dominated, male-dominated, same sex), and cub mass. Differences in size of cubs, depicts cubs that have larger body mass. We predict heavier sows should produce more male-dominated litters, with heavier male cubs relative to female cubs, whereas lighter sows should produce more female cubs, particularly females of lower fitness (e.g., lower cub mass, Trivers-Willard hypothesis).

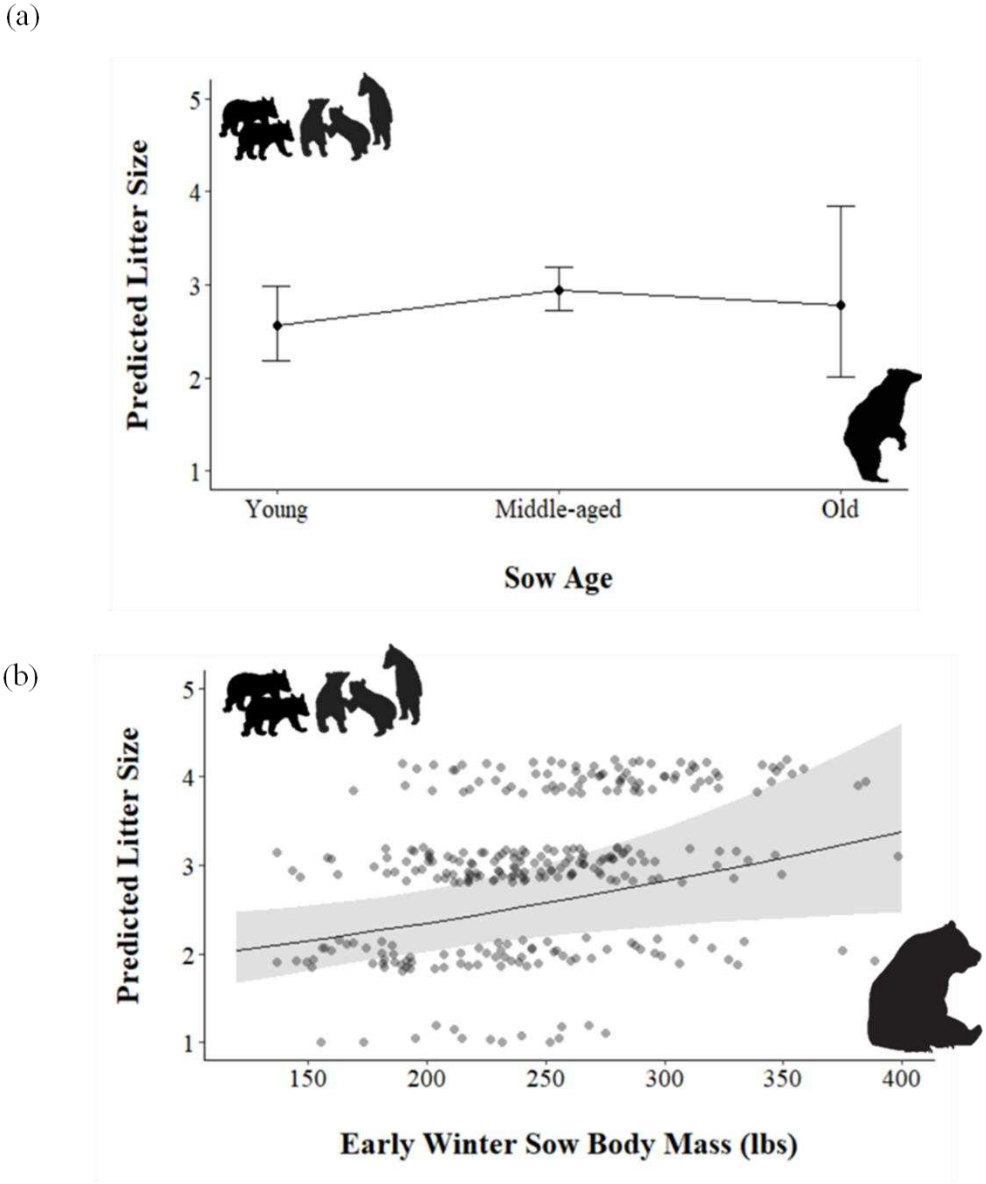

Figure 3.3. Predicted litter size (number of cubs) of female American black bears (*Ursus americanus*) in northern New Jersey relative to maternal effects: (a) sow age [young (3 – 4 years old), middle-aged (5 – 13 years old), old (14+ years old)], and (b) early winter sow body mass (lbs), in our baseline generalized linear mixed-effects model (GLMM). Plots show the estimated marginal means (holding the other covariates at their mean) and associated 95% confidence intervals from the fitted model, using the *emmeans*, *ggpredict*, and *ggplot2* packages in R.

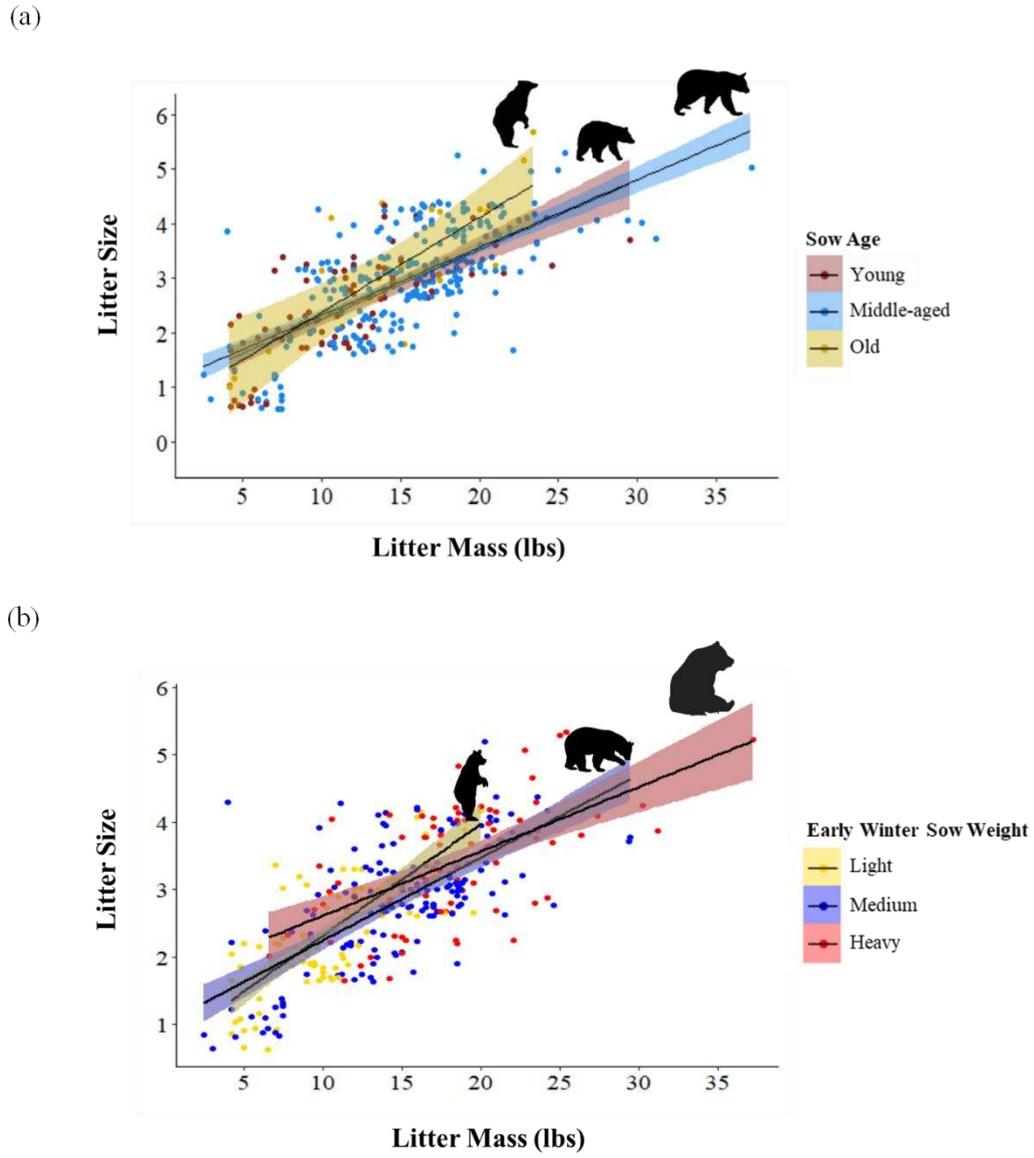

Figure 3.4. Relationship between litter size (number of cubs) and litter mass (lbs) of female (sow) American black bears (*Ursus americanus*) in northern New Jersey relative to: (a) sow age [young (3 – 4 years old), middle-aged (5 – 13 years old), old (14+ years old)], and (b) early winter sow body mass (lbs, categorized as light, medium, heavy). Litter size was obtained from den surveys during late January to early April, between 1984 – 2019.

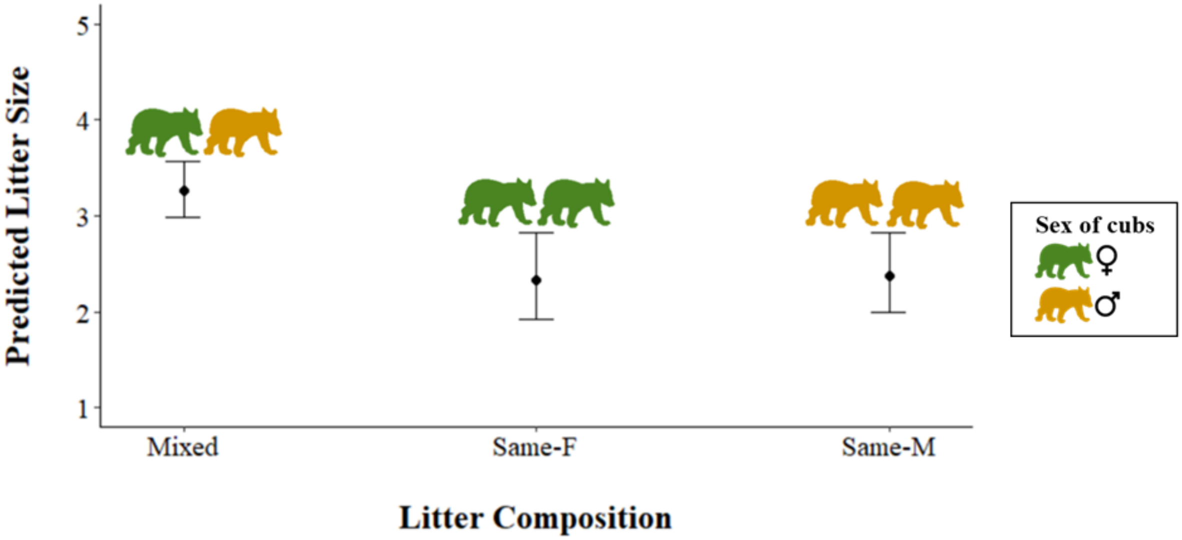

Figure 3.5. Predicted litter size (number of cubs) of female American black bears (*Ursus americanus*) in northern New Jersey relative to litter composition (mixed sex, same sex – female, same sex – male), in our supported generalized linear mixed-effects model (GLMM). Plots show the estimated marginal means (holding the other covariates at their mean) and associated 95% confidence intervals from the fitted model, using the *emmeans*, *ggpredict*, and *ggplot2* packages in R.

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CONCLUSIONS

Black bear management across the U.S. is quite complex, particularly in New Jersey (Johnson and Sciascia 2013), stemming from disputes and contention surrounding human-black bear conflicts (Decker et al. 1985), bear harvest (Beck et al. 1994), and bear habitat conservation (BBCC 1992). Indeed, as human and black bear populations continue to grow and spatially expand in the northeastern U.S., the increase in human-black bear interactions, and more importantly conflicts, is inevitable. Thus, understanding the factors regulating black bear populations and resilience in anthropogenic areas is vital to black bear management and conservation in New Jersey and surrounding states. For my dissertation, I used a combination of long-term human-black bear interaction, a female metric of fitness (e.g., sow body mass) and reproductive output (e.g., litter size) data to identify the factors contributing to robust black bear populations in New Jersey. Each of my chapters contributes novel findings to black bear research and (or) expands upon current knowledge of black bear demography and interactions with humans.

First, human-black bear interaction (HBI) severity and frequency, and thus black bear behavior, differed considerably by bear life cycle stage (Chapter 1). Other studies have analyzed bear behavior in terms of space use and activity patterns (Baruch-Mordo et al. 2014) and resource selection (Lewis et al. 2015) by bear life cycle stage, yet those studies focused on pre-hyperphagia and hyperphagia, rather than across the four main life cycle stages (e.g., denning, den emergence, breeding and summer activity, hyperphagia) that I examined here. In Chapter 1, I demonstrated there were higher odds of nuisance HBI, and more specifically garbage conflicts, occurring when bears were emerging from winter denning in the spring, and in anthropogenic areas. During the breeding and summer activity period I found there were higher odds of both benign (e.g., sightings of bears traveling through a neighborhood) and more severe HBI (e.g., home and vehicle entries) occurring. I also showed higher odds of more severe (e.g., attacks on protected livestock) and nuisance HBI (e.g., bears lying on deck) occurring during hyperphagia, a critical part of the yearly cycle of black bears when they actively gain fat reserves prior to winter denning.

I recommend management strategies focus on specific life cycle events by limiting anthropogenic stimuli during specific periods (e.g., access to garbage, birdfeeders, barbeque grills, pet food) to help reduce the likelihood of HBI escalating to a more severe category (i.e., Category I). During den emergence, management should invest in bear-proof containers or provide access to landowner and residents, particularly in developed-open space, low intensity areas where the majority (83%) of overall HBI occurred. During the breeding period, public outreach should focus on campaigns that help reduce attractants to decrease home and vehicle entries, which could in turn decrease the likelihood of sightings (Category III) turning into nuisance HBI (Category II, e.g., bear lying on porch). During hyperphagia, management should help increase awareness for the protection of domestic livestock and areas surrounding homes (e.g., gardens, apiaries). Management efforts could consist of other measures beyond electric fencing around domestic livestock (e.g., chicken coops, rabbit hutches). For example, non-lethal taste aversion has been successful in reducing black bear damage and deterring black bears from human foods [e.g., thiabendazole (TBZ), Polson 1983, McCarthy and Seavoy 1994, Ternent and Garshelis 1999]. Management should mandate garbage and attractant control throughout the entire year but especially during den emergence and the breeding period, coupled with distributing fines to homeowners and business for violating ordinances to ensure effectiveness (Baruch-Mordo et al. 2011, Taylor and Phillips 2020). While there is much debate about the efficacy of aversive conditioning in black bears (Mazur 2010), black bear managers in New Jersey found aversive conditioning did not eliminate nuisance behavior of adult sows, and all bears regardless of being aversively conditioned, returned to urban environments within 17 days (NJOAL 2015). Therefore, black bear managers in New Jersey may also consider intensifying aversive conditioning at the site of conflict *and* throughout a two-week window to deter bears from returning to anthropogenic areas and resources. We also recommend bear managers in New Jersey increase the number of conflict and non-conflict bears they collar, while ensuring a balanced sample across age and sex classes, to better understand how bears use the landscape and resources. This increase in sample size of collared individuals is also important in determining whether specific behaviors related to HBI are transferred from sows to offspring (Mazur and Seher 2008) or among conspecifics (Schulte 2016).

My results also revealed anthropogenic-dominated areas, especially with agricultural land cover, supported the highest odds of more severe HBI (e.g., corn depredation, orchard damage). The New Jersey Division of Fish and Wildlife (NJDFW) already employs a variety of useful tactics that allow landowners opportunities to alleviate black bear damage to their property (e.g., through depredation permits for agricultural or livestock damage, education on electric fencing to protect crops or livestock). However, the NJDFW may benefit from transferring a larger portion of this responsibility to residents and landowners (e.g., homeowner responsible for reducing or securing attractants, allowing more residents to legally kill nuisance bears rather than wait for bear managers or law enforcement to respond, extending the hunting season for specific hunters to target crop depredating bears, Garshelis et al. 2020). Thus, we also suggest regulated harvest continue to overlap with hyperphagia and early denning, given its effectiveness in reducing nuisance bear behavior in New Jersey (Raithel 2017). Additionally, the NJDFW could provide alternative education measures to landowners to protect their crops and livestock (e.g., through permanent electric fencing, yearly crop rotation, plant non-preferred crops in high-risk conflict areas, livestock protection dogs, synchronized and (or) penned birthing of livestock, Taylor and Phillips 2020). Future HBI management and research in New Jersey could also benefit from categorizing existing and future HBI reports to include the history of conflict the reporter has experienced as well as the residents' perception of how prior conflict was previously controlled (e.g., Madden and McQuinn 2014). This additional categorization of HBI events could help management isolate reporting bias and areas where tolerance for bears may be low (e.g., Suryawanshi et al. 2013, Dickman and Hazzah 2016). Black bear managers in New Jersey should also explore additional factors that may be better at explaining the variability in HBI (e.g., human population density, distance from dense forest and heavily urbanized areas, Hagani et al. 2021).

Second, I found sow body mass to be influenced by *both* individual bear features and the environmental context they experience in the study area (Chapter 2). Other black bear research has made specific connections between body mass gains and feeding on anthropogenic resources (e.g., *unpublished data*, K. Noyce, Minnesota Department of Natural Resources; Baruch-Mordo et al. 2013), and contributions of anthropogenic resources and human-bear conflicts to assimilated diets of black bears (e.g., Welfelt 2018). In Chapter 2, I showed sow body mass increased with cultivated crop and developed-low density land covers. I also demonstrated a prior history of nuisance conflict with humans explained heavier sow body mass. Furthermore, my work indicates a return on maternal investment (e.g., Hargrove et al. 2018), in that sows may be taking more risks to acquire resources in these agricultural and anthropogenic landscapes, which is reflected in their increased body mass (Chapter 2) and litter size and mass (Chapter 3). Given the majority of HBI events occur during the breeding season and summer activity period (Chapter 1), it appears those risks to acquire resources are setting up females for not only higher success (e.g., increased body mass, Chapter 2) throughout the year and when they enter dens, but also greater reproductive output (e.g., larger litter sizes, Chapter 3) that translates into higher offspring fitness (e.g., litter mass, Chapter 3). However, further research should follow offspring throughout their lives to determine if this fitness benefit persists as they age, and transfers to their future progeny as well.

While our research highlights the factors contributing to the success of black bears in New Jersey, it also underscores where future research can contribute. A logical next step would be to combine the findings of Raithel (2017) and the results of this dissertation to quantify how variability in vital rates (e.g., survival, reproductive success, litter size) influences black bear population dynamics in our study area. An additional step would be to study the social dimensions and cultural carrying capacity (Peyton et al. 2007) for black bears (Cleary et al. 2021) in New Jersey, to help mitigate future contention and limit human-bear conflicts. Human perception of HBI can be individual-based (e.g., values, attitudes, expectations), but can also be shaped by collective social units (e.g., demographic, socio-economic, neighborhood attitudes towards wildlife) whereby feedback of HBI can be disseminated within social groups (Lischka et al. 2018). To determine current and future efficacy of HBI management in New Jersey, systematic surveys should assess the public's perception of black bear managers in New Jersey (e.g., are they a capable entity of handling HBI) and how this perception relates to the public's likelihood of controlling attractants (e.g., Lischka et al. 2018). For example, similar surveys have linked skepticism of the management agency to increased likelihood of securing garbage (Lischka et al. 2018). Nevertheless, my results will help guide management so that black bears can continue to be thrive in the northeastern U.S., while minimizing human-bear conflicts and the costs associated with them, and thus maximizing human-black bear coexistence in this human-dominated landscape.

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APPENDICES

APPENDIX 1

We first assessed known natural resources important to black bears throughout their life cycle, with particular focus on female bears (Fig. A1.1). Given hard and soft mast are extremely important to black bears (Inman and Pelton 2002), especially for reproduction (Eiler et al. 1989), we searched for available data collected on hard and soft masting species important to black bears in the northeastern U.S. Unfortunately, mast data were limited in New Jersey, thus we searched for both hard and soft mast data collected from neighboring states that we could use as proxies to masting data within our study area(s). We compared ecoregions of northern New Jersey (due to frequency of sites sampled – see Chapter 2, and Table A1.1 and Fig. A1.2) to nine nearby states: Connecticut, Maryland, New Hampshire, North Carolina, Pennsylvania, Rhode Island, Tennessee, Virginia, West Virginia, where hard and soft mast data were available based on literature reviews and information provided by local state agencies (Table A1.2). Ecoregions represent areas where environmental conditions (e.g., species assemblages, climate patterns, natural vegetation, soil type, landforms, geology, land use) are typically ecologically homogenous (Omernik 1987). Given ecoregions are defined hierarchically and their homogeneity depends upon the scale of observation (Omernik 1987, Cleland et al. 1997), we first compared the finest scale ecoregion: Level IV (EPA 2021) between northern New Jersey, where the bulk of our data comes from, and the nine states listed above (Table A1.1). In addition, climatic factors (e.g., temperature, precipitation, drought) play important roles in influencing both hard and soft mast production (Sharp and Sprague 1967, Sork et al. 1993). Notably, mast variability and failure often occur in conjunction with climatic constraints (e.g., frost or drought, Sork et al. 1993). Therefore, we compared climate metrics [e.g., county-level average daily temperature and precipitation (PRISM 2020), and state-level monthly Palmer Z-Drought Indices (NOAA 2020)], using a Pearson's correlation coefficient, to provide insight into the degree of association between climate in each state and the state of New Jersey (Table A1.3). While spring frost can hinder plant development and growth (Inouye et al. 2000), frost and freeze events have been described as more localized phenomena that can be quite variable across smaller areas (Seneviratne et al. 2012); thus, we did not compare spring frost for any of the states (Table A1.3).

Table A1.1. U.S. Environmental Protection Agency (EPA) Level III and IV ecoregions comparing northern New Jersey (NJ) to nine surrounding states: Connecticut (CT), Maryland, New Hampshire (NH), North Carolina (NC), Pennsylvania (PA), Rhode Island (RI), Tennessee (TN), Virginia (VA), West Virginia (WV). An "X" demonstrates Level III and IV ecoregions that match northern Northern New Jersey ecoregions.

NJ		**CT**	**MD**	**NH**	**NC**	**PA**	**RI**	**TN**	**VA**	**WV**
Level III: Northeastern Highlands		X		X		X			X	
Level IV:	Glaciated Reading Prong/Hudson Highlands									
	Reading Prong					X				
Level III: Northern Piedmont			X		X	X			X	
Level IV:	Hackensack Meadowlands									
	Trap Rock and Conglomerate Uplands		X			X			X	
Level III: Ridge & Valley			X			X			X	X
Level IV:	Northern Glaciated Limestone Ridges, Valleys, and Terraces					X				
	Northern Glaciated Limestone Valleys					X				
	Northern Glaciated Ridges					X				
	Northern Glaciated Shale and Slate Valleys					X				
	Northern Limestone/Dolomite Valleys		X			X			X	X

Table A1.2. State-level rankings of U.S. Environmental Protection Agency (EPA) Level III ecoregions comparing northern New Jersey (NJ) to nine surrounding states: Connecticut (CT), Maryland, New Hampshire (NH), North Carolina (NC), Pennsylvania (PA), Rhode Island (RI), Tennessee (TN), Virginia (VA), West Virginia (WV), and the associated mast data available for each state, ranked from highest to lowest shared Level III ecoregions.

State	**Ranking of Shared Level III Ecoregions with NJ**	**Level III Ecoregions Shared with NJ**	**Years of Data**	**Mast Type**	**Masting Species**	**Data Type**	**Data Source**
VA	3	Northeastern Highlands, Northern Piedmont, Ridge, and Valley	2007 – 2018	Hard Mast	Red Oak (*Quercus rub*ra) and White Oak (*Q. alba*)	Annual production by oak spp.: weight (kg) of well-developed acorn production	VDGIF 2022
PA	2	Northern Piedmont, Ridge, and Valley	1983 – 1984, 2002 – 2018	Hard and Soft Mast, and other plants	Red and White Oaks (*Q.* spp.), Apple (*Malus* spp.), Beech (*Fagus* spp.), Blackberry and Raspberry (*Rubus* spp.), Black Cherry (P*runus serotina*), Blueberry (*Vaccinium* spp.), Chokecherry (*Pyrus* spp.), Dogwood (*Cornus* spp.), Elderberry (*Sambucus* spp.), Gooseberry (*Ribes* spp.), Grapes (V*itis* spp.), Hawthorn (*Crataegus* spp.), Hickory (*Carya* spp.), Pokeberry (*Phytolacca* spp.), Sassafras (*Sassafras* spp.), Serviceberry (A*melanchier* spp.), Strawberry (*Frageria* spp.)	Subjective rankings (e.g., Trace to None, Poor, Below Average, Average, Above Average, Excellent)	Ternent 2022

Table A1.2 continued.

State	Ranking of Shared Level III Ecoregions with NJ	Level III Ecoregions Shared with NJ	Years of Data	Mast Type	Masting Species	Data Type	Data Source
MD	2	Northern Piedmont, Ridge, and Valley	1983 – 2000, 2004 – 2018	Hard Mast	Red and White Oaks (*Q*. spp.)	Counts of acorns per transect; Average number of acorns per branch; Proportion of Trees Bearing Acorns (PBAs); Subjective Rankings (e.g., Failure, Good, Bumper)	Fearer et al. 2008, Duda et al. 2019, VDGIF 2022
CT	1	Northeastern Highlands	2007 – 2018	Hard Mast	Red and White Oaks (*Q*. spp.)	Average number of acorns per branch; Proportion of Trees Bearing Acorns (PBAs); Subjective Rankings (e.g., Failure, Good, Bumper)	VDGIF 2022
NC	1	Northern Piedmont	1983 – 2018	Hard and Soft Mast	Red and White Oaks (Q. alba), Hickory (*Carya* spp.) Beech (*Fagus* spp.), Blueberry (*Vaccinium* spp.), Huckleberry (*Gaylussacia* spp.), Blackberry (*Rubus* spp.), Pokeberry (*Phytolacca* spp.), Cherry (*Prunus* spp.), Grapes (*Vitus* spp.)	Numerical Rating from Percent Crown With Acorns (PCAs) and Subjective Ranking of Crop Quality (e.g., 0.0 to 2.0 = Poor; 2.1 to 4.0 = Fair; 4.1 to 6.0 = Good; 6.1 to 8.0 = Excellent)	NCWRC 2022

Table A1.2 continued.

State	Ranking of Shared Level III Ecoregions with NJ	Level III Ecoregions Shared with NJ	Years of Data	Mast Type	Masting Species	Data Type	Data Source
NH	1	Northeastern Highlands	2005 – 2018	Hard Mast	Red and White Oaks (*Q*. spp.)	Average number of acorns per branch; Proportion of Trees Bearing Acorns (PBAs); Subjective Rankings (e.g., Failure, Good, Bumper)	VDGIF 2022
WV	1	Ridge and Valley	1983 – 2018	Hard Mast	Red and White Oaks (*Q*. spp.)	Mast Index = [Abundant Observations/Total Observations + ((Common Observations × 0.5/Total Observations)] × 100	WVDNR 2021
RI	0	NA due to no shared Level III ecoregions with New Jersey					
TN	0	NA due to no shared Level III ecoregions with New Jersey					

Table A1.3. Pearson's correlation coefficients (r) between the state of New Jersey and shared Level III ecoregions between 1984 and 2018 (the time period of our study) with respect to drought (monthly Palmer Z-Drought Indices, NOAA 2020), average daily precipitation (PRISM 2020), and average daily temperature covariates (PRISM 2020). r values close to ±1.00 indicate strong linear associations between variables from a specific state and northern New Jersey, while values close to zero indicate no such association.

New Jersey vs. State	**Climate Variables**		
	Drought	**Precipitation**	**Temperature**
Connecticut	0.82	0.84	0.97
Maryland	0.84	0.83	0.98
North Carolina	0.50	0.41	0.85
New Hampshire	0.68	0.72	0.92
Pennsylvania	0.81	0.82	0.97
Virginia	0.70	0.71	0.93
West Virginia	0.71	0.70	0.89

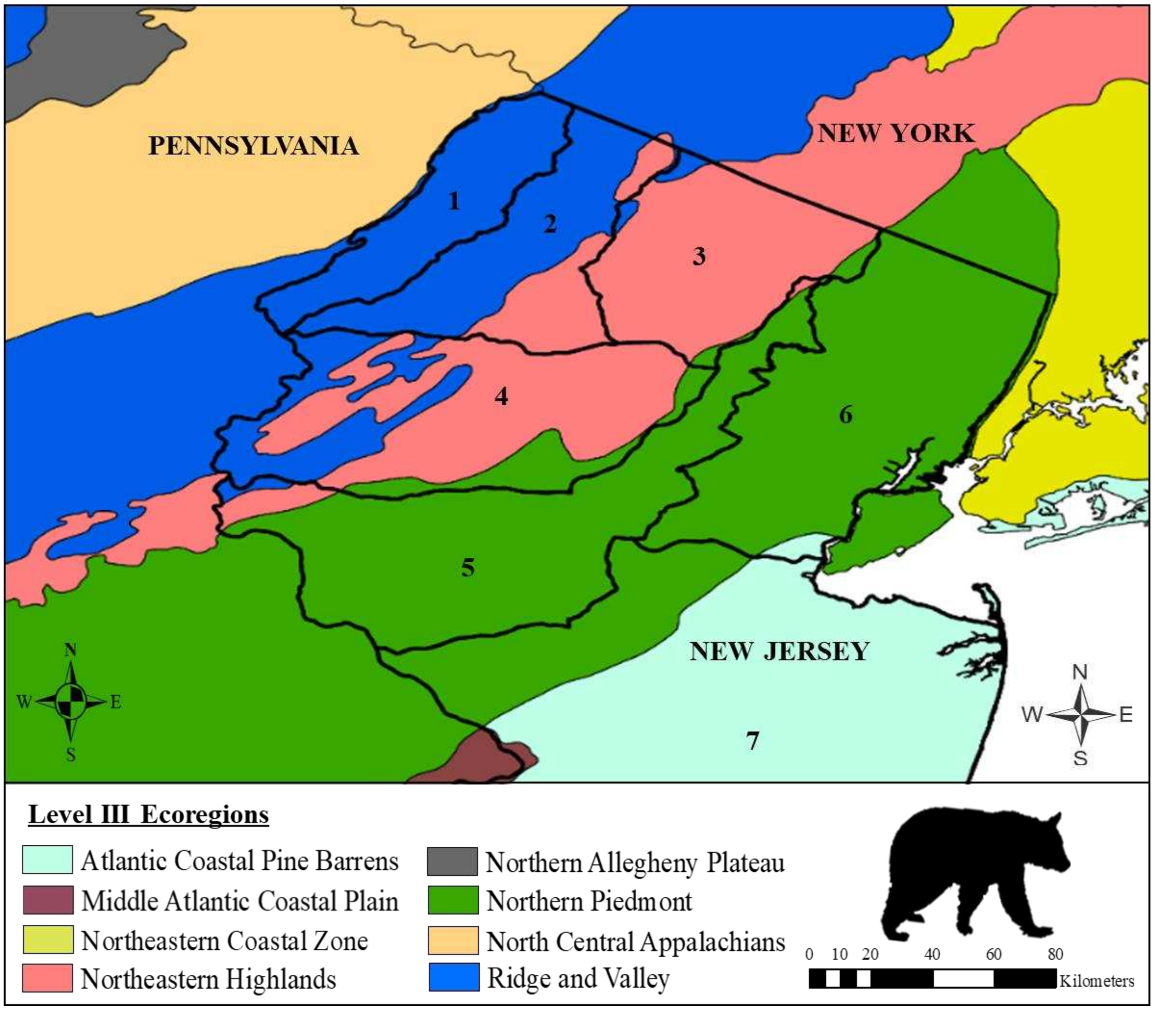

Figure A1.1. U.S. Environmental Protection Agency designated Level III Ecoregions of New Jersey, Pennsylvania, and New York. Numbers presented represent the current seven designated Bear Management Zones (BMZs) 1 – 7 in New Jersey.

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APPENDIX 2

Table A2.1. Number of human-black bear (*Ursus americanus*) interactions (HBI) by land cover type throughout the state of New Jersey, 2001 – 2017.

Land cover Type	**2001 – 2006**	**2007 – 2010**	**2011 – 2017**	**Total**
Agriculture	154	111	148	413
Anthropogenic	7,671	7,639	10,973	26,283
Natural	636	573	906	2,115
Total	**8,461**	**8,323**	**12,027**	**28,811**

Table A2.2. Number of human-black bear (*Ursus americanus*) interactions (HBI) by bear life cycle stage and HBI category (I – III) throughout the state of New Jersey, 2001 – 2017.

Bear Life Cycle Stage	**HBI Category**	**Observed**	**Expected**	**Proportion by HBI Category**
Denning (1 Dec – 31 Mar)	I	116	153	0.06
	II	1,006	996	0.55
	III	722	694	0.39
	Total	**1,844**	**1,843**	**1.00**
Den Emergence (1 Apr – 31 May)	I	515	595	0.07
	II	4,064	3,860	0.57
	III	2,566	2,691	0.36
	Total	**7,145**	**7,146**	**1.00**
Breeding & Summer Activity (1 Jun – 31 Aug)	I	1,147	1,098	0.09
	II	6,841	7,124	0.52
	III	5,200	4,966	0.39
	Total	**13,188**	**13,188**	**1.00**
Hyperphagia (1 Sep – 30 Nov)	I	620	552	0.09
	II	3,653	3,584	0.55
	III	2,361	2,498	0.36
	Total	**6,634**	**6,634**	**1.00**
Total		**28,811**	**28,811**	

Table A2.3. Number and relative proportion of human-black bear (*Ursus americanus*) interactions (HBI) by land cover type and HBI category (I – III) throughout the state of New Jersey, 2001–2017.

Land cover Type	**HBI Category**	**Observed**	**Expected**	**Proportion by HBI Category**
Agriculture	I	291	56	0.43
	II	230	366	0.34
	III	156	255	0.23
	Total	**677**	**677**	**1.00**
Anthropogenic	I	1,855	2,159	0.07
	II	14,143	14,010	0.55
	III	9,936	9,766	0.38
	Total	**25,934**	**25,935**	**1.00**
Natural	I	252	183	0.12
	II	1,191	1,188	0.54
	III	757	828	0.34
	Total	**2,200**	**2,199**	**1.00**
Total		**28,811**	**28,811**	

Table A2. 4. Number of human-black bear (*Ursus americanus*) interactions (HBI) by bear life cycle stage and main and refined HBI category throughout the state of New Jersey, 2001 – 2017.

Bear Life Cycle Stage	HBI Category	Refined HBI Category	Observed	Expected	Proportion by Refined HBI Category
Denning (1 Dec – 31 Mar)	I	Aggressive	9	17	0.00
		Agricultural Damage	5	24	0.00
		Entry	27	63	0.01
		Human Attack	0	1	0.00
		Property Damage >$1,000	5	5	0.00
		Protected Livestock	64	40	0.03
		Unprovoked Dog Attack	6	3	0.00
	II	Campsite/Tent	0	10	0.00
		Garbage	348	404	0.19
		Nuisance	469	440	0.25
		Property Damage <$1,000	118	101	0.06
		Provoked Dog Attack	6	8	0.00
		Unprotected Livestock	65	33	0.04
	III	Birdfeeder	204	70	0.11
		Sighting	511	613	0.28
		Urban Bear	7	12	0.00
		Total	1,844	1,844	1.00
Den Emergence (1 Apr – 31 May)	I	Aggressive	50	65	0.01
		Agricultural Damage	1	92	0.00
		Entry	220	246	0.03
		Human Attack	4	3	0.00
		Property Damage >$1,000	29	19	0.00
		Protected Livestock	201	156	0.03
		Unprovoked Dog Attack	10	13	0.00
	II	Campsite/Tent	18	39	0.00
		Garbage	1,897	1,567	0.27
		Nuisance	1,498	1,705	0.21
		Property Damage <$1,000	465	390	0.07
		Provoked Dog Attack	28	29	0.00
		Unprotected Livestock	158	129	0.02
	III	Birdfeeder	361	270	0.05
		Sighting	2,138	2,375	0.30
		Urban Bear	67	46	0.01
		Total	7,145	7,144	1.00

Table A2.4 continued.

Bear Life Cycle Stage	HBI Category	Refined HBI Category	Observed	Expected	Proportion by Refined HBI Category
Breeding (1 Jun – 31 Aug)	I	Aggressive	137	120	0.01
		Agricultural Damage	229	170	0.02
		Entry	566	453	0.04
		Human Attack	6	6	0.00
		Property Damage >$1,000	29	35	0.00
		Protected Livestock	154	289	0.01
		Unprovoked Dog Attack	26	23	0.00
	II	Campsite/Tent	134	73	0.01
		Garbage	2,600	2,892	0.20
		Nuisance	3,341	3,148	0.25
		Property Damage <$1,000	586	720	0.04
		Provoked Dog Attack	52	54	0.00
		Unprotected Livestock	128	238	0.01
	III	Birdfeeder	357	498	0.03
		Sighting	4,749	4,383	0.36
		Urban Bear	94	85	0.01
		Total	13,188	13,187	1.00
Hyperphagia (1 Sep – 30 Nov)	I	Aggressive	67	61	0.01
		Agricultural Damage	137	86	0.02
		Entry	177	228	0.03
		Human Attack	4	3	0.00
		Property Damage >$1,000	14	18	0.00
		Protected Livestock	212	145	0.03
		Unprovoked Dog Attack	9	12	0.00
	II	Campsite/Tent	7	37	0.00
		Garbage	1,474	1,455	0.22
		Nuisance	1,569	1,583	0.24
		Property Damage <$1,000	403	362	0.06
		Provoked Dog Attack	32	27	0.00
		Unprotected Livestock	168	120	0.03
	III	Birdfeeder	167	251	0.03
		Sighting	2,177	2,205	0.33
		Urban Bear	17	43	0.00
		Total	6,634	6,636	1.00
		Grand Total	28,811	28,811	

Table A2.5. Number and type of human-black bear (*Ursus americanus*) interactions (HBI) by landcover type throughout the state of New Jersey, 2001 – 2017.

Land Cover Type	**HBI Category**	**Refined HBI Category**	**Observed**	**Expected**	**Proportion by Refind HBI Category**
Agriculture	I	Aggressive	5	6	0.01
		Agricultural Damage	267	9	0.39
		Entry	11	23	0.02
		Human Attack	0	0	0.00
		Property Damage > $1000	0	2	0.00
		Protected Livestock	7	15	0.01
		Unprovoked Dog Attack	1	1	0.00
	II	Campsite/Tent	0	4	0.00
		Garbage	70	148	0.10
		Nuisance	129	162	0.19
		Property Damage < $1000	24	37	0.04
		Provoked Dog Attack	1	3	0.00
		Unprotected Livestock	6	12	0.01
	III	Birdfeeder	21	26	0.03
		Sighting	133	225	0.20
		Urban Bear	2	4	0.00
		Total	677	677	1.00
Anthro–pogenic	I	Aggressive	244	237	0.01
		Agricultural Damage	2	335	0.00
		Entry	916	891	0.04
		Human Attack	13	13	0.00
		Property Damage > $1000	67	69	0.00
		Protected Livestock	565	568	0.02
		Unprovoked Dog Attack	48	46	0.00
	II	Campsite/Tent	1	143	0.00
		Garbage	5,848	5,688	0.23
		Nuisance	6,319	6,190	0.24
		Property Damage < $1000	1,386	1,415	0.05
		Provoked Dog Attack	100	106	0.00
		Unprotected Livestock	489	467	0.02
	III	Birdfeeder	1,002	980	0.04
		Sighting	8,759	8,619	0.34
		Urban Bear	175	167	0.01
		Total	25,934	25,934	1.00

Table A2.5 continued.

Land Cover Type	HBI Category	Refined HBI Category	Observed	Expected	Proportion by Refined HBI Category
Natural	I	Aggressive	14	20	0.01
		Agricultural Damage	103	28	0.05
		Entry	63	76	0.03
		Human Attack	1	1	0.00
		Property Damage > $1000	10	6	0.00
		Protected Livestock	59	48	0.03
		Unprovoked Dog Attack	2	4	0.00
	II	Campsite/Tent	158	12	0.07
		Garbage	401	483	0.18
		Nuisance	429	525	0.20
		Property Damage < $1000	162	120	0.07
		Provoked Dog Attack	17	9	0.01
		Unprotected Livestock	24	40	0.01
	III	Birdfeeder	66	83	0.03
		Sighting	683	731	0.31
		Urban Bear	8	14	0.00
		Total	2,200	2,200	1.00
		Grand Total	28,811	28,811	

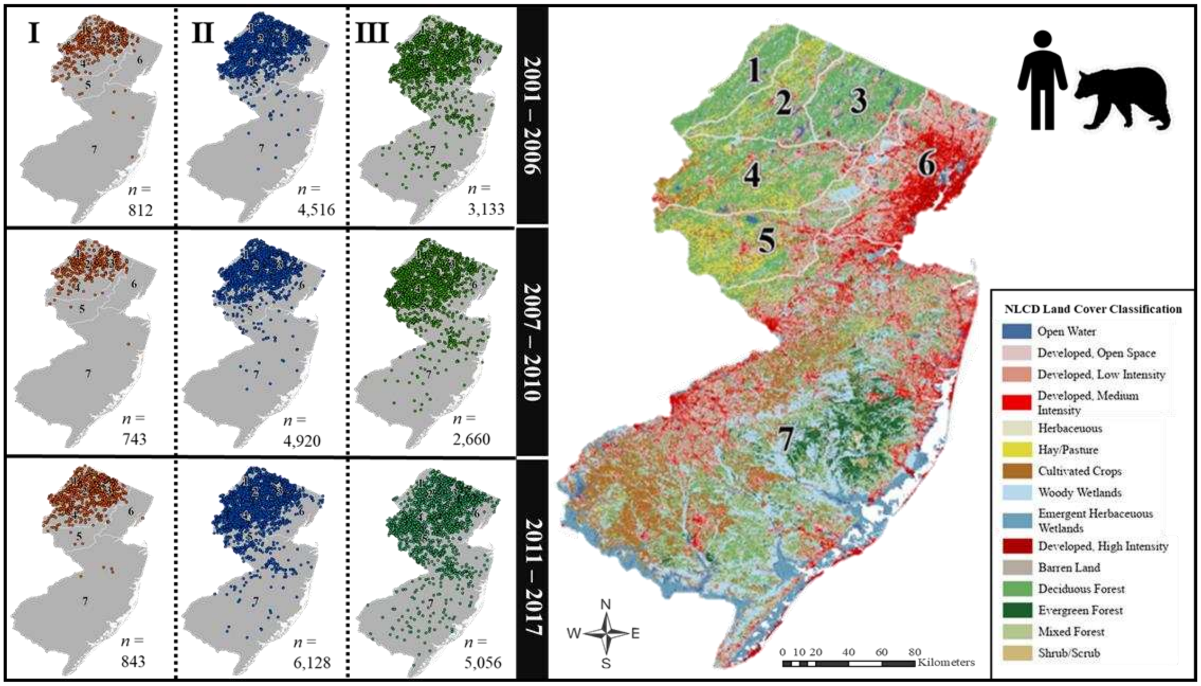

Figure A2.1. Spatial distribution of human-black bear interactions ‘HBI’ (*n* = 28,811) throughout the state of New Jersey, where points represent HBI locations by category: I (most severe), II (moderate severity), and III (least severe), across various land cover types over time periods: (a) 2001 – 2006 (*n* = 8,461); (b) 2007 – 2011 (*n* = 8,323); (c) 2012 – 2017 (*n* = 12,027).

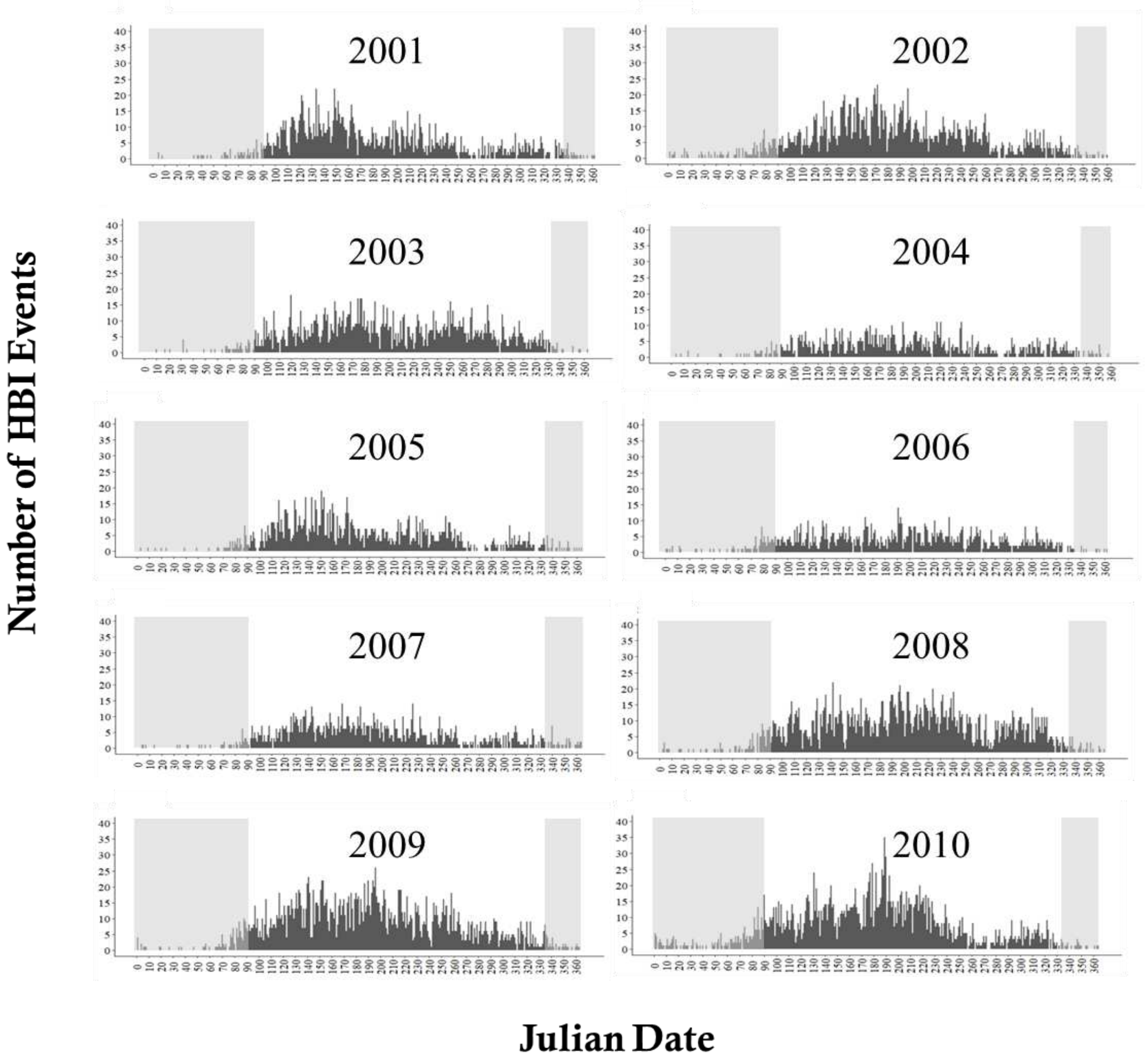

Figure A2.2. Annual variation in human-American black bear (*Ursus americanus*) interactions (HBI) counts between 2001 and 2017 by Julian date. Julian dates in the grey sections represent the denning period (1 December – 31 March; Julian date = 001 – 090 and 335 – 365).

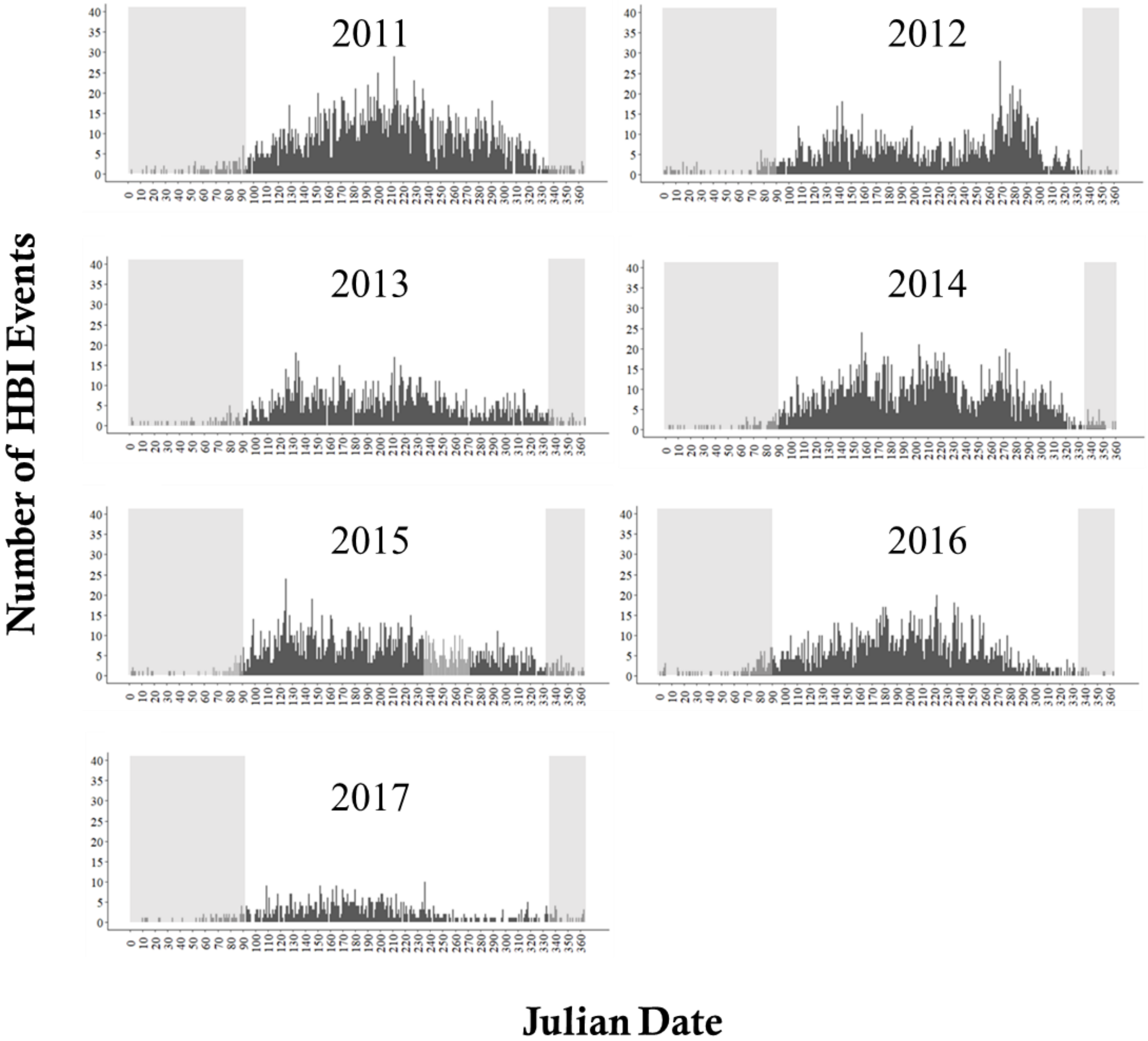

Figure A2.2 continued.

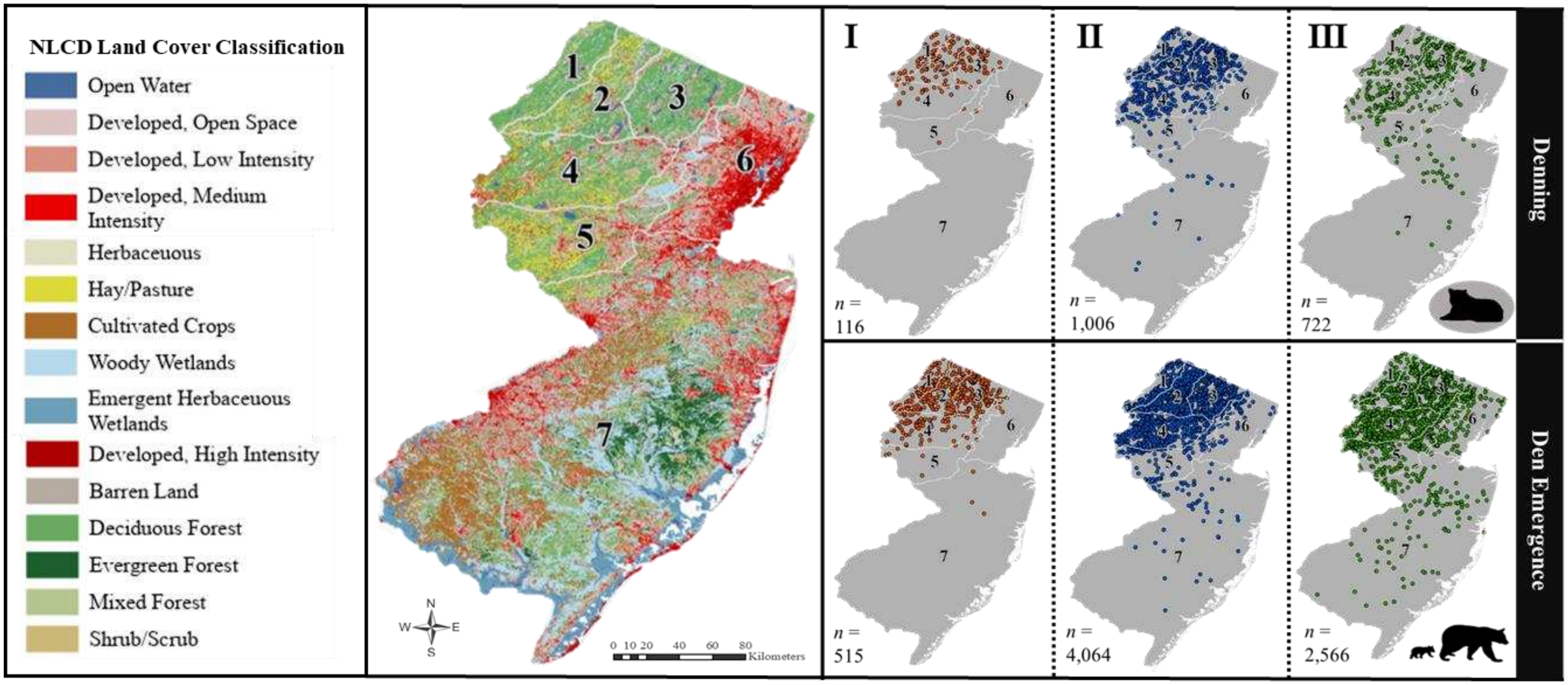

Figure A2.3. Spatial distribution of human – black bear interactions 'HBI' (n = 28,811) throughout the state of New Jersey, where points represent "conflict" locations between humans and American black bears (*Ursus americanus*) by category: I (most severe), II (moderate severity), and III (least severe) across various landcover types over bear life cycle stages: Denning (1 December – 31 March; n = 1,844), Den Emergence (1 April – 31 May; n = 7,145), Breeding and Summer Activity (1 June – 31 August; n = 13,188), and Hyperphagia (1 September – 30 November; n = 6,634).

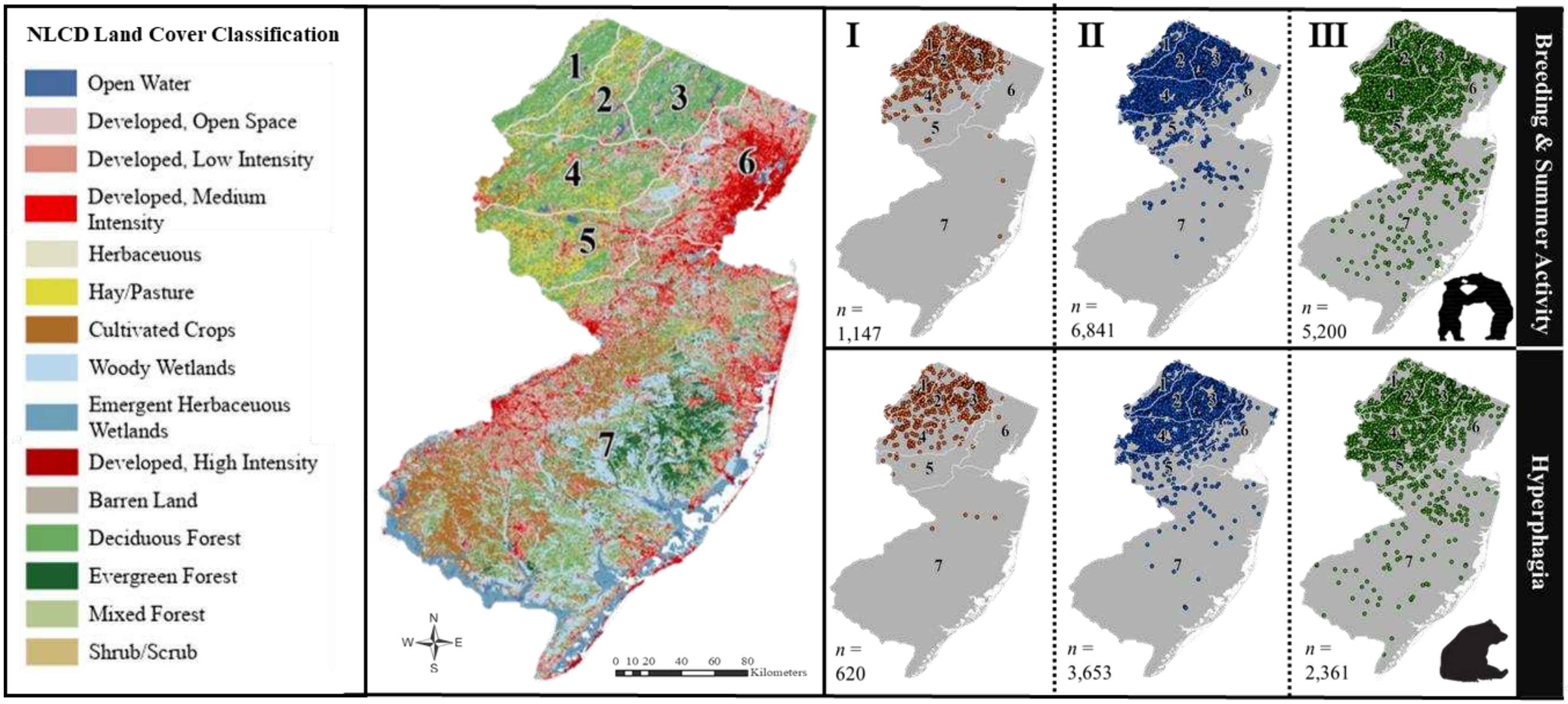

Figure A2.3 continued.

APPENDIX 3

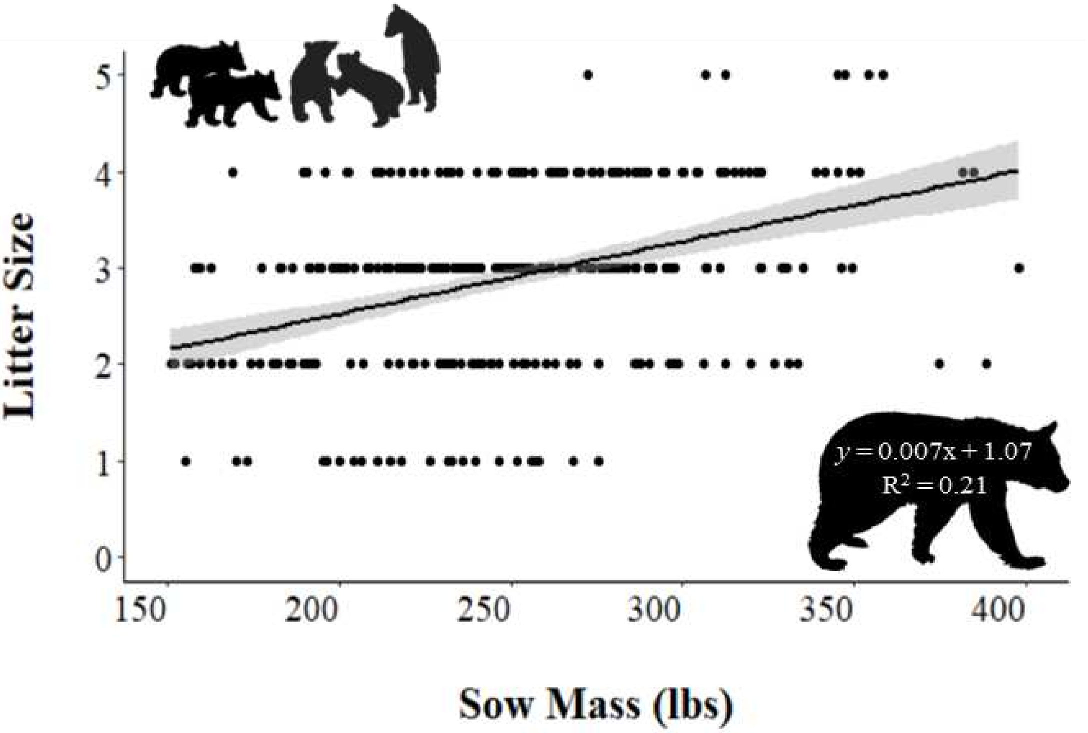

Figure A3.1. Relationship between female American black bear (*Ursus americanus*) body mass (lbs) and litter size (number of cubs) in the study area. Sow body mass measurements (black dots, *n* = 317) were obtained from den surveys that ranged from late January to early April, between 1984 – 2019. The line represents the fitted, positive relationship between sow mass and litter size, along with 95% confidence intervals in light grey [$\beta = 0.007$, (0.005, 0.009)].

APPENDIX 4

Table A4.1. Results from the “baseline” generalized linear mixed-effects model testing for the effect of maternal characteristics on litter size of female American black bears (*Ursus americanus*) in the study area between 1984 – 2019 (*n* = 419 den surveys, *n* = 214 individuals). We present regression coefficient estimates (*β*), standard errors (SE), 95% upper and lower confidence intervals (CI).

Covariate	***β***	**SE**	**95% CI**
Intercept (Young Sow)	0.94	0.08	(0.74, 1.10)
Middle-aged Sow	1.08	0.04	(–0.04, 0.32)
Old Sow	0.93	0.17	(–0.29, 0.46)
Early Winter Sow Body Mass	0.09	0.04	(0.02, 0.17)

Table A4.2. Results from generalized linear mixed-effects models testing for maternal characteristics, litter characteristics, environmental covariates, and population characteristics on litter size (number of cubs) of female American black bears (*Ursus americanus*) in the study area between 1984 – 2019 (n = 419 den surveys, n = 214 individuals). We present regression coefficient estimates (β), standard errors (SE), 95% upper and lower confidence intervals (CI).

Covariate Category	**Covariate Sub-Category**	**Covariate**	β	**SE**	**95% CI**
Maternal Characteristics	Den Type Selection	Intercept (Ground Den and Young Sow)	0.97	0.09	(0.79, 1.15)
		Manmade Den	–0.18	0.14	(–0.47, 0.10)
		Rock Den	–0.01	0.08	(–0.16, 0.14)
		Tree Den	0.001	0.11	(–0.22, 0.22)
		Middle-aged Sow	0.13	0.09	(–0.06, 0.31)
		Old Sow	0.04	0.19	(–0.34, 0.42)
		Early Winter Sow Body Mass	0.10	0.04	(0.03, 0.18)
	Legacy of Conflict	Intercept (Legacy of Category II and Young Sow)	0.99	0.14	(0.43, 1.24)
		Legacy of Category I Human-Bear Conflict	–0.12	0.27	(–0.66, 0.42)
		Middle-aged Sow	0.16	0.26	(–0.36, 0.68)
		Old Sow	–0.54	0.68	(–1.88, 0.80)
		Early Winter Sow Body Mass	0.20	0.12	(–0.04, 0.44)
Litter Characteristics	Litter Sex Ratio	Intercept	0.94	0.09	(0.76, 1.12)
		Male-Dominated Litter	–0.04	0.08	(–0.15, 0.14)
		Female-Dominated Litter	0.002	0.10	(–0.19, 0.19)
		Middle-aged Sow	0.14	0.09	(–0.04, 0.32)
		Old Sow	0.08	0.19	(–0.29, 0.46)
		Early Winter Sow Body Mass	0.09	0.04	(0.02, 0.17)

Table A4.2 continued.

Covariate Category	**Covariate Sub-Category**	**Covariate**	***β***	**SE**	**95% CI**
Litter Characteristics	Litter Mass	Intercept (Above Average Litter Mass and Young Sow)	1.15	0.09	(0.96, 1.33)
		Below Average Litter Mass	–0.32	0.08	(–0.48, –0.16)
		Middle-aged Sow	0.06	0.10	(–0.13, 0.24)
		Old Sow	0.07	0.19	(–0.31, 0.44)
		Early Winter Sow Body Mass	0.03	0.04	(–0.05, 0.11)
	Litter Composition	Intercept (Mixed Sex Litter and Young Sow)	1.05	0.08	(0.89, 1.21)
		Same Sex Litter – Female	–0.39	0.10	(–0.54, –0.14)
		Same Sex Litter – Male	–0.32	0.09	(–0.50, –0.01)
		Middle-aged Sow	0.13	0.09	(–0.05, 0.31)
		Old Sow	0.11	0.19	(–0.27, 0.49)
		Early Winter Sow Body Mass	0.07	0.04	(–0.004, 0.15)
Environmental Context	Trash Production	Intercept (High Trash Production and Young Sow)	0.95	0.01	(0.76, 1.14)
		Low Trash Production	–0.03	0.08	(–0.18, 0.12)
		Middle-aged Sow	0.13	0.10	(–0.08, 0.33)
		Old Sow	0.04	0.21	(–0.36, 0.44)
		Early Winter Sow Body Mass	0.11	0.04	(0.02, 0.19)
	Hard Mast Production ($t-1$)	Intercept (Below Average Hard Mast Year and Young Sow)	0.93	0.09	(0.74, 1.13)
		Average Hard Mast Year	0.01	0.08	(–0.14, 0.23)
		Good Hard Mast Year	0.05	0.08	(–0.16, 0.15)
		Middle-aged Sow	0.14	0.09	(–0.04, 0.32)
		Old Sow	0.08	0.19	(–0.30, 0.45)
		Early Winter Sow Body Mass	0.09	0.04	(0.02, 0.17)

Table A4.2 continued.

Covariate Category	**Covariate Sub-Category**	**Covariate**	***β***	**SE**	**95% CI**
Environmental Context	Hard Mast Production ($t-2$)	Intercept (Poor Hard Mast Year and Young Sow)	0.91	0.09	(0.73, 1.09)
		Average Hard Mast Year	0.05	0.08	(–0.10, 0.21)
		Good Hard Mast Year	0.04	0.08	(–0.12, 0.21)
		Middle-aged Sow	0.14	0.09	(–0.05, 0.33)
		Old Sow	0.08	0.19	(–0.30, 0.46)
		Early Winter Sow Body Mass	0.09	0.04	(0.02, 0.17)
	Bear Management Zone	Intercept (BMZ 1 and Young Sow)	0.97	0.09	(0.79, 1.16)
		BMZ 2	–0.12	0.12	(–0.35, 0.11)
		BMZ 3	–0.03	0.08	(–0.19, 0.12)
		BMZ 4	0.05	0.11	(–0.17, 0.26)
		Middle-aged Sow	0.13	0.09	(–0.06, 0.31)
		Old Sow	0.06	0.19	(–0.31, 0.44)
		Early Winter Sow Body Mass	0.10	0.04	(0.02, 0.17)
	County	Intercept (Morris and Young Sow)	0.91	0.14	(0.63, 1.19)
		Passaic	0.03	0.18	(–0.32, 0.37)
		Sussex	0.02	0.13	(–0.24, 0.27)
		Warren	0.06	0.14	(–0.21, 0.34)
		Middle-aged Sow	0.14	0.09	(–0.04, 0.32)
		Old Sow	0.08	0.19	(–0.29, 0.46)
		Early Winter Sow Body Mass	0.09	0.04	(0.02, 0.17)
Population Characteristics	Bear Population Size ($t-1$)	Intercept	0.98	0.16	(0.67, 1.29)
		Below Average Bear Population Size	–0.05	0.13	(–0.31, 0.21)
		Middle-aged Sow	0.07	0.17	(–0.27, 0.40)
		Old Sow	0.27	0.30	(–0.31, 0.86)
		Early Winter Sow Body Mass	0.14	0.07	(0.002, 0.28)

Table A4.2 continued.

Covariate Category	**Covariate Sub-Category**	**Covariate**	***β***	**SE**	**95% CI**
Population Characteristics	Bear Population Size (*t* – 2)	Intercept (Above Average Bear Population Size and Young Sow)	0.90	0.16	(0.58, 1.21)
		Below Average Bear Population Size	0.03	0.15	(–0.27, 0.33)
		Middle-aged Sow	0.21	0.18	(–0.14, 0.56)
		Old Sow	0.43	0.39	(–0.34, 1.20)
		Early Winter Sow Body Mass	0.07	0.07	(–0.07, 0.20)
	Total Bears Harvested (*t* – 1)	Intercept (Above Average Harvested and Young Sow)	0.98	0.13	(0.72, 1.23)
		Below Average Harvested	–0.08	0.14	(–0.35, 0.19)
		No Bears Harvested	–0.03	0.13	(–0.28, 0.22)
		Middle-aged Sow	0.14	0.09	(–0.04, 0.32)
		Old Sow	0.09	0.19	(–0.30, 0.46)
		Early Winter Sow Body Mass	0.09	0.04	(0.02, 0.17)
	Total Bears Harvested (*t* – 2)	Intercept (Above Average Harvested and Young Sow)	0.92	0.13	(0.68, 1.17)
		Below Average Harvested	0.07	0.14	(–0.21, 0.34)
		No Bears Harvested	0.01	0.12	(–0.23, 0.25)
		Middle-aged Sow	0.14	0.09	(–0.04, 0.32)
		Old Sow	0.09	0.19	(–0.29, 0.47)
		Early Winter Sow Body Mass	0.09	0.04	(0.01, 0.17)
	Total Male Bears Harvested (*t* – 1)	Intercept (Above Average Harvested and Young Sow)	1.02	0.16	(0.71, 1.34)
		Below Average Harvested	–0.12	0.16	(–0.43, 0.18)
		No Male Bears Harvested	–0.07	0.15	(–0.35, 0.22)
		Middle-aged Sow	0.13	0.09	(–0.05, 0.31)
		Old Sow	0.07	0.19	(–0.31, 0.45)
		Early Winter Sow Body Mass	0.10	0.04	(0.02, 0.17)

Table A4.2 continued.

Covariate Category	**Covariate Sub-Category**	**Covariate**	***β***	**SE**	**95% CI**
Population Characteristics	Total Male Bears Harvested ($t - 2$)	Intercept (Above Average Harvested and Young Sow)	0.95	0.16	(0.63, 1.26)
		Below Average Harvested	0.03	0.17	(–0.31, 0.36)
		No Bears Harvested	–0.02	0.16	(–0.33, 0.30)
		Middle-aged Sow	0.15	0.09	(–0.04, 0.33)
		Old Sow	0.10	0.19	(–0.28, 0.47)
		Early Winter Sow Body Mass	0.09	0.04	(0.01, 0.17)

Table A4.3. Results from generalized linear mixed-effects models testing for the effects of maternal characteristics, litter characteristics, and environmental covariates on litter size (number of cubs) of female American black bears (*Ursus americanus*) in the study area between 1984 – 2019 (*n* = 419 den surveys, *n* = 214 individuals). We report on regression coefficient estimates (*β*), standard errors (SE), 95% upper and lower confidence intervals (CI).

Covariate Sub-Category	**Covariate**	***β***	**SE**	**95% CI**
	Intercept (Above Average Litter Mass and Young Sow)	1.17	0.15	(0.87, 1.47)
Litter Mass	Below Average Litter Mass	–0.35	0.18	(–0.71, 0.005)
	Middle-aged Sow	0.04	0.16	(–0.28, 0.35)
×	Olde Sow	–0.03	0.26	(–0.53, 0.47)
	Early Winter Sow Body Mass	0.03	0.04	(–0.05, 0.11)
Sow Age	Below Average Litter Mass × Middle-aged Sow	0.02	0.20	(–0.36, 0.40)
	Below Average Litter Mass × Old Sow	0.27	0.37	(–0.45, 1.00)
	Intercept (Above Average Litter Mass and Young Sow)	1.15	0.10	(0.95, 1.34)
Litter Mass	Below Average Litter Mass	–0.32	0.08	(–0.48, –0.16)
	Middle-aged Sow	0.06	0.010	(–0.13, 0.25)
×	Old Sow	0.07	0.19	(–0.31, 0.45)
Early Winter	Early Winter Sow Body Mass	0.03	0.05	(–0.07, 0.14)
Sow Body Mass	Below Average Litter Mass × Early Winter Sow Body Mass	–0.01	0.08	(–0.16, 0.15)
	Intercept (Poor Hard Mast Year and Young Sow)	0.93	0.09	(0.76, 1.10)
Hard Mast	Average Hard Mast Year	0.01	0.08	(–0.16, 0.16)
Production ($t - 1$)	Good Hard Mast Year	0.05	0.09	(–0.12, 0.22)
	Middle-aged Sow	0.14	0.09	(–0.04, 0.32)
×	Old Sow	0.07	0.19	(–0.31, 0.45)
	Early Winter Sow Body Mass	0.09	0.05	(–0.01, 0.19)
Early Winter	Average Hard Mast Year × Early Winter Sow Body Mass	0.02	0.08	(–0.15, 0.18)
Sow Body Mass	Good Hard Mast Year × Early Winter Sow Body Mass	–0.001	0.08	(–0.16, 0.16)

Table A4.3 continued.

Covariate Sub-Category	**Covariate**	***β***	**SE**	**95% CI**
Hard Mast Production (t – 2) × Early Winter Sow Body Mass	Intercept (Poor Hard Mast Year, Young Sow)	0.97	0.10	(0.77, 1.17)
	Average Hard Mast Year	–0.01	0.09	(–0.19, 0.16)
	Good Hard Mast Year	–0.06	0.08	(–0.22, 0.10)
	Early Winter Sow Body Mass	0.08	0.06	(–0.04, 0.20)
	Middle-aged Sow	0.14	0.10	(–0.05, 0.33)
	Old Sow	0.08	0.19	(–0.30, 0.46)
	Average Hard Mast Year × Early Winter Sow Body Mass	0.02	0.09	(–0.15, 0.19)
	Good Hard Mast Year × Early Winter Sow Body Mass	0.02	0.08	(–0.14, 0.18)

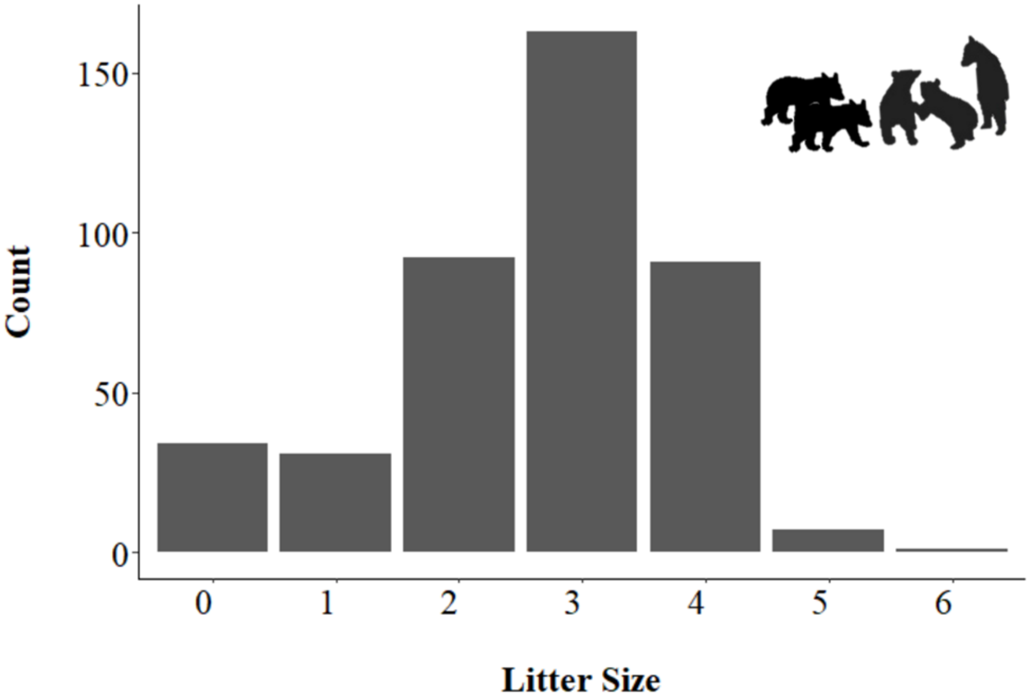

Figure A4.1. Litter size (number of cubs) counts of female American black bears (*Ursus americanus*) in the study area. Litter size was obtained from den surveys that took place between late January and early April, from 1984 to 2019.

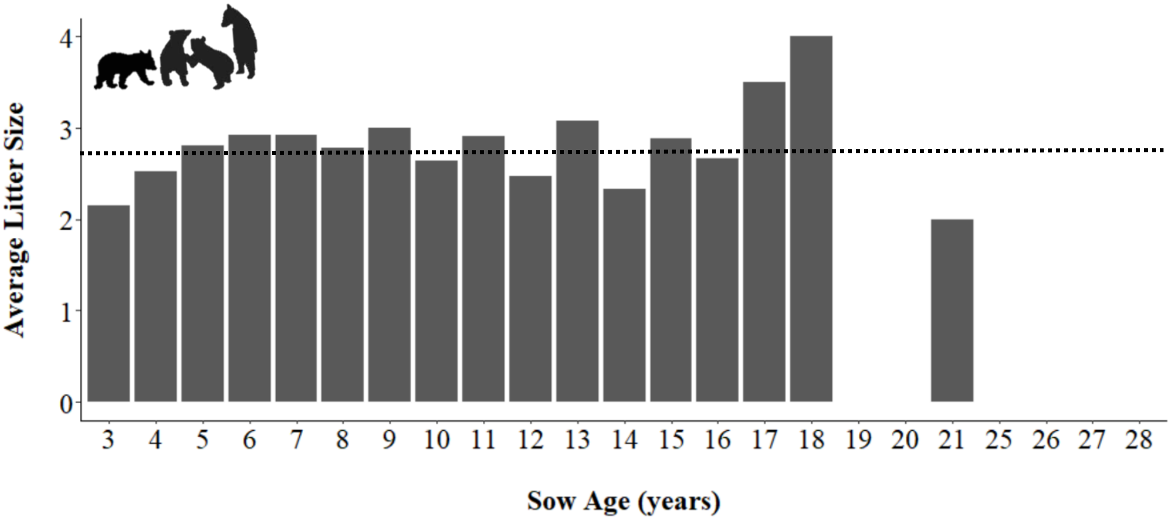

Figure A4.2. Average litter size (number of cubs) of female American black bears (*Ursus americanus*) in the study area. Litter size was obtained from den surveys that ranged from late January to early April, between 1984 – 2019. The dotted line indicates the average litter size over the study period (~2.7 cubs per litter).