


RESEARCH ARTICLE

Differential habitat use between demographic states of black bears in managed timber forests

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Abstract

The long-term effects of intensive forest harvest on sensitive demographic stages of the American black bear (*Ursus americanus*) have been often overlooked. Much of Maine, USA, is covered in forests that are hospitable to bears and commercial timber harvest. To investigate the potential effects of differing intensities of disturbance on black bears, and on females with cubs particularly, we designed a large-scale natural experiment with 197 motion-sensitive camera sites dispersed over representative forest stands in northern and central Maine. Using multi-state occupancy models, we distinguished the overall trends in space use by females with young versus adult bears without young. Forest disturbance at large spatial scales was positively associated with the probability of use for both demographic groups and the availability of hardwood trees was an additional important factor for habitat use by females with young. Our study illustrates the use of motion-sensitive cameras to monitor and understand habitat use by distinct life-history stages of animals living in human-modified landscapes, and results indicate that managers can maintain black bear habitat in areas of active forest harvest by ensuring the availability of hardwood species.

KEYWORDS

forest disturbance, forest management, land-use change, motion-sensitive cameras, multi-state occupancy, silviculture, *Ursus americanus*

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One way that animals improve their fitness is by making optimal use of resources across a landscape (Rettie and Messier 2000). Landscapes are often heterogeneous in terms of the distribution of high-quality resources, areas of increased predation risk, and locations where intra- and inter-specific competition are highest (Gaillard et al. 2010, Gaynor et al. 2019, Brehm and Mortelliti 2021). Individuals must therefore select and use habitat in a way that minimizes the risks associated with predation and competition, while maximizing resource acquisition (Martin et al. 2010, Latif et al. 2011). This behavioral tradeoff between resource selection and mortality-risk avoidance is most important to sensitive demographic stages, like females with dependent young, as gestation and lactation greatly increase energetic demands on mothers (Dahle and Swenson 2003, Ayers et al. 2013), and young may be especially vulnerable to predation and anthropogenic mortality risks (i.e., vehicle collisions; Rachlow and Bowyer 1998, Duquette et al. 2017).

American black bears (*Ursus americanus*) are an ideal species for studying how maternal trade-offs may be reflected in habitat segregation. Black bears are abundant in a wide array of landscapes across North America, and are slow to reach sexual maturity, with females typically producing first litters from 3–5 years of age, and usually biannually thereafter (Garshelis 1994, Garshelis et al. 2016, Clark et al. 2021) because young spend an entire year foraging with their mother. Understanding what constitutes suitable areas for females to rear young, and whether habitat use by females with young differs from non-reproductive adult bears, is important for the long-term management of bears, especially in regions that rely on natural resources for recreation and tourism and where bear hunting is economically important, such as Maine, USA (Honey et al. 2016, Maine Department of Inland Fisheries and Wildlife [MDIFW] 2017). An additional complexity, and reason for understanding patterns of habitat use by reproductive female bears in Maine, is that the majority of Maine's forests are managed for timber and other resource extraction. Of the 71,000 km² of forest in the state, 65,000 were designated as commercial land in 2017 (Butler 2018). Forest disturbance has direct and indirect effects on native wildlife species by introducing anthropogenic mortality risks (e.g., vehicle collisions) and fragmenting resources across the landscape (Reynolds-Hogland and Mitchell 2007, Waller et al. 2014) and gives a unique opportunity to assess the effect of disturbance on maternal trade-offs.

Research has primarily focused on the effects of human disturbances on several facets of bear behavior, with varying results (Mitchell and Powell 2003). In some cases, human disturbance has resulted in increased access to food sources (Samson and Huot 1995, Etcheverry et al. 2005), whereas other researchers have reported that black bears avoided recently cleared areas and that denning females preferred older mature stands and areas of increased cover (Brodeur et al. 2008, Vitale et al. 2018). There is limited knowledge regarding the specific effect of silvicultural activities on the behavior of reproductive black bears in managed forests (Koehler and Pierce 2003) and whether the degree of disturbance versus stand composition may influence female segregation.

Several habitat requirements are necessary for female bears to successfully produce and rear young. Hard mast from deciduous tree species is linked to several components of reproduction (e.g., age of first reproduction, the proportion of adult females producing litters; Schooley et al. 1994, McLaughlin 1999) because hard mast provides an abundant supply of high-quality food during fall hyperphagia prior to hibernation (Elowe and Dodge 1989, Samson and Huot 1995, Costello et al. 2003). Notably, in areas of Maine where American beech (*Fagus grandifolia*) is the dominant hardwood, the cycle of alternate-year masting leads to synchronous reproductive success or failure in the black bear population (McLaughlin et al. 1994, Jakubas et al. 2005). The sensitivity of cub production and survival to hardwood tree species abundance and diversity warrants attention particularly in temperate forests in the northeastern United States, where one notable hardwood species has already been lost entirely (American chestnut [*Castanea dentata*], which became ecologically extinct in the early 1900s; Paillet 2002), and another important hardwood, the American beech, is experiencing widespread mortality due to beech bark disease (Kasson and Livingston 2012). Understanding the sensitivity of black bears, and especially adult female black bears with young, to the current and future availability of hardwoods is an important issue for ecologists and managers, and adult females with young may

be more sensitive to environmental changes or more selective about habitat requirements because of the varied investment tradeoffs unique to this demographic stage.

Our goal was to understand more fully the patterns of space use by adult female bears with young so that managers may ultimately clarify the degree to which black bears could be affected by forest disturbance versus the composition of the forest stand. We asked 2 questions: how do the degree of forest disturbance and composition (specifically, percent hardwood versus softwood) influence the probability of use by adult black bears and how do these variables influence the probability of use by females with young? We hypothesize that use patterns will differ between adult bears with and without young because of differences in habitat preferences between these 2 demographic stages. We predict the following, reflecting differences in habitat preferences depending on demographic stage: the space use of adult bears will be positively correlated with disturbance, as early seral stage forest stands may provide additional food resources (Hugie 1982, Costello 1992), while the space use of females with young will be negatively correlated with disturbance, and positively correlated with the proportion of hardwood trees, as this life stage is more sensitive to predation risk and has high caloric intake needs during fall masting season (McLaughlin et al. 1994, Laufenberg et al. 2018).

STUDY AREA

Our study took place in Maine, which is in a humid continental climate regime with warm summers (May–Oct) and cold winters (Nov–Apr), and falls at the junction of temperate forest and boreal forest ecoregions (Figure 1; Hasbrouck and Connors 1987, Gawler et al. 1996, National Oceanic and Atmospheric Administration [NOAA] 2020). In Maine, black bears occur in all but the farthest south (and most urbanized) areas, and are managed as a big game species (McLaughlin 1999). Our data were collected from June 2017 to October 2020, in the geographic area between 44.15968°N and 47.42166°N latitude, and -70.55842°W and -67.62582°W longitude. Our 67,730-km² study area covers all of the northern region of the state and much of the interior region (Fernandez et al. 2020). In this area, daily temperature averages 18.6°C in July (which is the warmest month annually, and has seen averages ranging from 15.9°C to 21.1°C from 1895 to 2021) and averages -10.2°C in January (the coldest month, ranging from -15.7°C to -5.2°C; NOAA 2021). Precipitation typically falls as rain in warmer months (May–Oct, 55 cm average) and as snow in colder months (Nov–Apr, 51 cm average; NOAA 2020). The topography of our study area is relatively flat with mountainous areas in the center and west, and elevations ranging from 31 m to 1,590 m (Hollister 2020).

The landscape is primarily forested with many areas experiencing human-caused clearing and subsequent re-forestation since the 1700s and the majority is now managed for commercial timber production (Maine Forest Service 1995, Butler 2018). Timber harvesting and natural disturbances have resulted in a mosaic of mixed-age stands, and tree communities often contain maples (*Acer* spp.), birches (*Betula* spp.), and American beech (*Fagus grandifolia*) as dominant hardwoods and white pine (*Pinus strobus*), firs (*Abies* spp.), eastern hemlock (*Tsuga canadensis*), and spruces (*Picea* spp.) as dominant conifers (Gawler et al. 1996, McWilliams et al. 2005). Terrestrial mammalian herbivores in the region included 2 ungulates, moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*), and smaller species such as snowshoe hare (*Lepus canadensis*), porcupine (*Erethizon dorsatum*), beaver (*Castor canadensis*), and ground hog (*Marmota monax*). In addition to American black bear, there was a rich carnivore community including fisher (*Pekania pennanti*), American marten (*Martes americana*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), Canada lynx (*Lynx canadensis*), bobcat (*Lynx rufus*), American ermine (*Mustela richardsonii*), long-tailed weasel (*Neogale frenata*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), North American river otter (*Lontra canadensis*), and American mink (*Neovison vison*). Small mammals present included, but were not limited to, American red squirrel (*Tamiasciurus hudsonicus*), flying squirrels

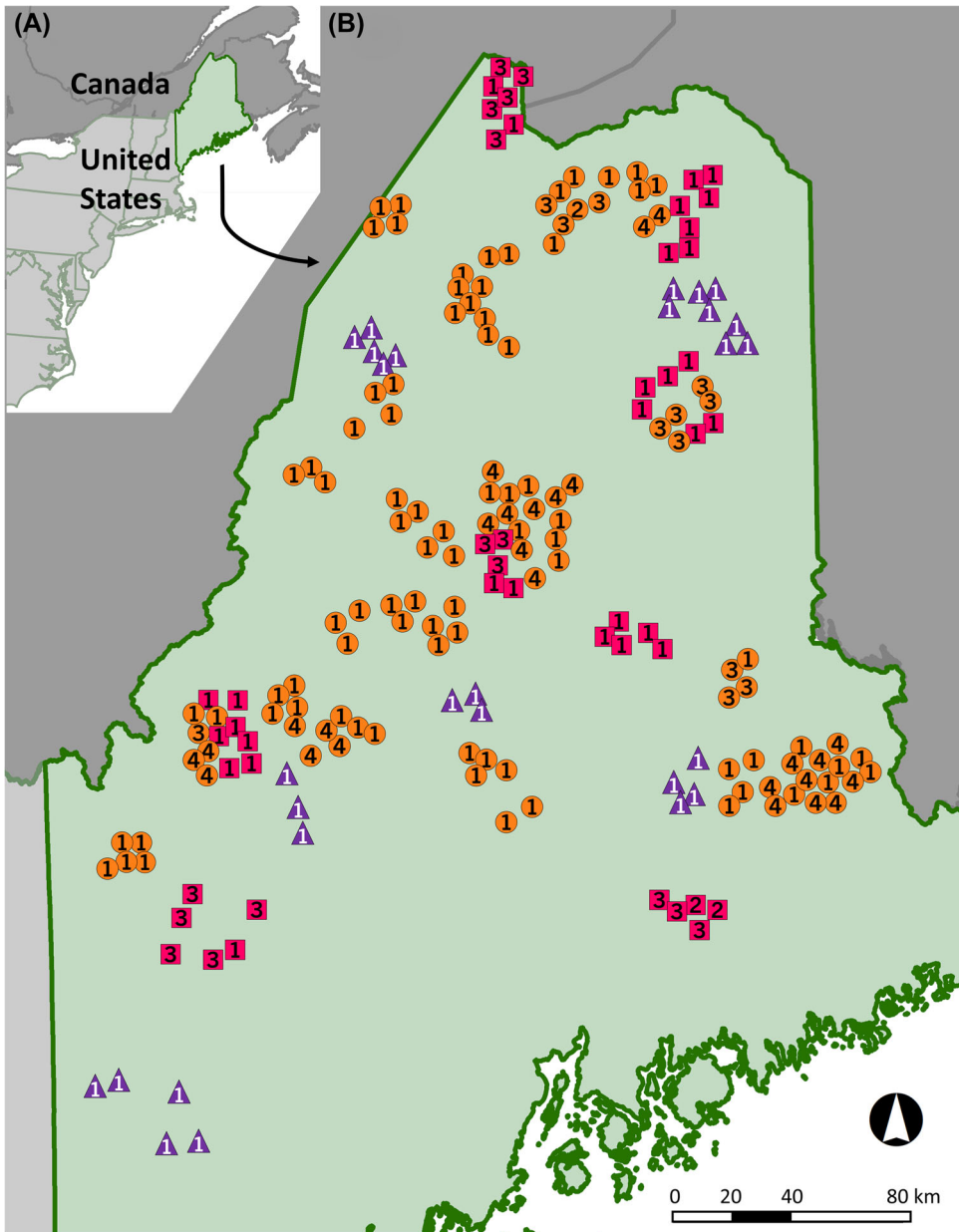


FIGURE 1 Study area located in Maine, in the northeastern United States (A) and survey sites visited with transects of motion-sensitive cameras to detect American black bears from 2017 to 2020 (B). Orange circles indicate sites that were first set in summer 2017, pink squares were first set in 2018, and purple triangles were set in 2019. The numbers indicate the number of years each site was sampled (1–4).

(*Glaucomys* spp.), eastern chipmunk (*Tamias striatus*), and southern red-back voles (*Clethrionomys gapperi*), and the avian community included songbirds (e.g., black-capped chickadee [*Poecile atricapillus*]), corvids (e.g., Canada jay [*Perisoreus canadensis*]), raptors (e.g., bald eagle [*Haliaeetus leucocephalus*]), and galliformes (e.g., ruffed grouse [*Bonasa umbellus*]).

METHODS

Study design

To study large-scale patterns of use by black bears both with and without young, we implemented a natural experiment over northern Maine (Garton et al. 2011). We collected data using motion-sensitive camera surveys (Fisher et al. 2014, Gould et al. 2019), and balanced survey effort along a gradient of forest disturbance intensities from the very lowest (e.g., Baxter State Park) to the very highest (recently harvested commercial timber properties). We then replicated study areas in different disturbance categories across the latitude range of our study area (Figure S1.1, available in Supporting Information; Mortelliti et al. 2022, Evans and Mortelliti 2022a). Disturbance in our study refers to any tree loss event, mainly associated with timber harvest activity but also with natural tree loss. We measured tree loss from Landsat image data processed using novel change-detection algorithms developed specifically for New England forests (Kilbride 2018, Wulder et al. 2019). We discretized 2 raster layers: one that included the year of the most recent disturbance event experienced at each 30-m pixel and another for the magnitude of the event (i.e., lower magnitude scores may correspond to a partial harvest occurring, where higher magnitude scores can result from clearcut activity; Kilbride 2018). We then combined these to create a single raster layer where each pixel had a value for our disturbance index (combination of temporal recency and severity) that we could then average at different spatial scales. Initially working at the township scales, which is a municipal delineation of quadrats of roughly 100 km² across the entire state, we selected areas in proportion to availability that had the highest disturbance scores, the lowest disturbance scores, and intermediate values of disturbance (Figure S1.1). We distributed survey effort in regions of large contiguous areas of a similar forest disturbance history, defined as ≥ 3 townships all with the same approximate disturbance index, and smaller, disjunct patches, where 1–2 townships of a given disturbance index were surrounded by all higher or all lower scoring townships. We then replicated these criteria in the north and south of our overall study region (Figure S1.2, available in Supporting Information). Our study design included areas that, prior to the start of our surveys, fell along a gradient of disturbance from never harvested to harvested as recently as 2 years before our surveys, but sites were not harvested between seasons of our surveys.

Once we selected townships for inclusion in our study, we randomly generated target points spaced 6 km apart at which to establish survey sites (Figure 1). After we deployed camera stations as close as possible to these target points, we calculated the disturbance index data and remote-sensed forest composition data (LANDFIRE 2016) within a set of circular buffers that ranged in their radius around each site: 300 m, 1 km, and 3 km for disturbance and forest composition and 6 km for disturbance only. These scales allowed us to assess the influence of disturbance and forest composition on detection (at the immediate survey location or microsite; Niedballa et al. 2015, Hofmeester et al. 2019) and on space use at a gradient of areas within the home range for female bears in Maine (1-km radius encompassing a core area and 3-km radius encompassing the majority) to the entire landscape around a home range (6-km radius; Alt et al. 1980, Hugie 1982). The largest scale used for landscape disturbance had the same radius as the distance between independent sites, which creates some overlap in the pixels assigned to >1 detection history. When checked for spatial autocorrelation using spline correlograms for detection history and top-ranked model residuals (Figures S2.1, S2.2, available in Supporting Information; R package ncf; Bjornstad 2018, R Core Team 2022), and we did not find evidence of spatial autocorrelation. Therefore, we continued using the 6-km scale of disturbance because this large-scale buffer provides information on the landscape-level effect of human disturbance on black bears.

Field methods

We used motion-sensitive trail cameras to collect detection, non-detection, and demographic data on black bears at each of our sites. All independent survey sites were set a minimum of 6 km apart, and each site was composed of a transect of 3 camera stations. These stations each had one Bushnell Trophy Cam E2-E3 (Overland Park, KS, USA)

attached to a live tree and set across a clear area from a bait tree. Each bait tree included beaver meat enclosed in a suet cage attached with wire at the same height as the camera (~20–40 cm) and Vaseline-based scent lure containing skunk (*Mephitis* spp.) essence and beaver castor (J. E. Braley, Kenduskeag, ME, USA) applied just below the bait and 3–4 m up the trunk of the bait tree (Buyaskas et al. 2020). The 3 camera stations were spaced in a linear transect 100 m apart, and we pooled the image data collected from these 3 stations for that site (Evans et al. 2019). A validation of the effectiveness of our monitoring protocol is available in Mortelletti et al. (2022). At each survey site, we collected data on the composition of the forest stand via 2 variable-radius basal area plots from which we calculated the percentage of hardwoods among live trees at the stand level.

We first deployed cameras in summer 2017 for a minimum active period of 2 weeks. In the following summers 2018–2020, we revisited a subset of these locations to collect data across multiple years at the same locations ($n = 59$), and in summers 2018–2019 we also established new locations to expand geographic coverage (sites with ≥ 1 season of data = 197; Figure S3.1 and Table S3.1, available in Supporting Information). We did not include winter data in this study because black bears in Maine typically hibernate from November to April (Schooley et al. 1994). In total, 121 sites were active for 14 to 33 days between June and September 2017, 88 sites were active from June to September 2018, 84 sites were active from June to September 2019, and 44 sites were active from June to October 2020. Our allocation of survey effort followed the rotating panel design described by MacKenzie et al. (2017:218) to collect the spatially independent site information and the time-series data needed to fit dynamic occupancy models.

Occupancy models

We tagged all camera images to the level of species or other cause of the motion-trigger event (e.g., false-triggers or crew while setting up and taking down cameras), and we further reviewed all images containing bears and classified them by the number of individuals present and the age classes detected. We pooled the images recorded at all 3 camera stations in each survey site to create a single detection history, wherein each 24-hour period was classified as an occasion, and 1 of 3 possible occupancy states was recorded: no bears detected (0), ≥ 1 adult bear detected (1), or a female with young detected (2 - typically both the mother and young were observed together, but the presence of a female was assumed in rare cases where ≥ 1 young-of-the-year cubs were visible but a female was not observed [$n = 4$]). If we detected multiple states in a 24-hour period, we classified the occasion at the highest level; for example, if we observed a single adult and then later in the same day observed an adult with young, we classified the entire occasion as 2.

We conducted multi-season, multi-state occupancy modeling in Program PRESENCE (Hines 2006) with data from 197 sites (the 59 sites that were deployed for 2 to 4 seasons and 138 sites that were deployed for a single season). Because our study system is in continuous habitat and is not geographically closed, we define our variables of interest as the probability of use of the landscape surrounding our camera transects by black bears (Efford and Dawson 2012, Latif et al. 2016). From these models, we estimated the probabilities of initial use by adult bears (state 1, or Ψ) or by bears including females with young (state 2, or R), the likelihood of transition of a site from one state to another between seasons ($C\Psi$ and CR), and the probabilities of detection given different states of use by bears (p_1 , p_2 , and δ). Multi-state models were originally designed with the assumption of exclusivity in states, where if the highest state is observed all lower states cannot be occurring while incorporating imperfect detection. Though this is a reasonable assumption for territorial species such as the California spotted owl (*Strix occidentalis*; MacKenzie et al. 2009), it does not apply to our study system, where state 2 (presence of a female with young) does not preclude state 1 (presence of an adult bear without young) from also occurring. Therefore, we focus our analyses only on the highest state and do not make any claims regarding subsuming space use by adult bears when a site transitions from state 1 into state 2. Rather than looking at local colonization and local extinction of the species as a whole, we are interested in the change in reproductive status of a site: whether it becomes or remains

used by a female with young, transitions back to only adults bears present, or has no bears using the site. The models assume that false positives do not occur, such that bears in any state are never observed when the true state is 0, and young are never observed when the true state is 0 or 1 (Table 1).

We conducted a sequential-by-submodel strategy to first model the detection processes, then the initial state, and finally the transition probabilities (Morin et al. 2020). In phase 1 we held occupancy and transition parameters constant while modeling detection. We treated the probability of detection when the true state is either occupied by adult bear only (p_1) or occupied by female with young (p_2) as co-varying with the same covariates, while we treated the probability of identifying the presence of young, given a detection occurs and the true state is occupied by female with young (δ) separately. We tested the following covariates: disturbance index at the 300-m spatial scale, proportion of hardwood trees at the stand level and the 300-m scale (proxies for microsite features that could influence detection), the year of the survey, and the days within the survey period (to account for decaying attractant potency). We ranked the resulting models via Akaike's Information Criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002) and considered the top-ranked converging model and any other models within $2 \Delta AIC_c$ to be informative for model performance. We first established the top-ranking models for p_1 and p_2 , then repeated the process for δ , and then tested models that combined the top-ranking covariates for all detection parameters (Morin et al. 2020).

In phase 2, we compared models including covariates for the probability of use by adult bears (Ψ), then the probability of use by females with young (R), and finally a model with the top-ranked covariates for both. We retained the top-ranking covariates for the detection process from the previous step and tested the following covariates for occupancy: disturbance at 1-km, 3-km, and 6-km spatial scales, the proportion of hardwood

TABLE 1 Parameters of dynamic multi-state occupancy models applied to American black bear detection histories from 197 sites over 4 summers, 2017–2020, Maine, USA. In each summer season, a site can be in 1 of 3 states: 0, no bears present; 1, only adult bears present; and 2, female with young present (MacKenzie et al. 2009).

Parameter	Description
Ψ	Probability a site is used by an adult bear or bears in the first season (but not females with young)
R	Probability a site is used by bears, and at least one female with young is present in the first season (does not exclude overlapping use by non-reproductive bears)
$C\Psi_0$	Probability of local colonization by an adult bear or bears at a site that was not used in the previous season (state 0 \rightarrow 1)
$C\Psi_1$	Probability of consistent use by an adult bear or bears, without dependent young (state 1 \rightarrow 1)
$C\Psi_2$	Probability of a change in state, going from occupied by a female with young to occupied by adult bears only (state 2 \rightarrow 1)
CR_0	Probability of local colonization by a female with young at a site that was not used by bears at all in the previous season (state 0 \rightarrow 2)
CR_1	Probability of a change in state, going from occupied by adults only to occupied by a female with young (note that there may still be non-reproductive bears overlapping in the area; state 1 \rightarrow 2)
CR_2	Probability of consistent use by a female or females with young over 2 seasons (state 2 \rightarrow 2)
p_1	Probability of detecting a bear or bears on an occasion during a season when the true state is 1
p_2	Probability of detecting a bear or bears on an occasion during a season when the true state is 2. This detection event may be either an observation of an adult bear only or an observation that includes young
δ	Probability of successfully observing young on an occasion when bears are detected given the true state is 2

at 1-km and 3-km scales, and the latitude of the site as a proxy for winter snow severity and any confounding climatic or vegetative clines. We did not model different spatial scales of the same variable together, but we tested them against each other to determine the most relevant scale. In the third and final phase, we modeled the transition probabilities $C\Psi$ (between-year transition to being used by adult bears only from any of the 3 states) and CR (transition to being used by female with young) as a function of the same covariates as initial occupancy. We retained top-ranking covariates for detection and initial occupancy state, and first tested models that allowed $C\Psi$ and CR to vary between the state from which transition occurred or varied by years, then candidate models including covariates for $C\Psi$ to assess if any improved model performance, then candidate models with covariates for CR , and finally tested a model including top-ranked covariates from the preceding steps.

RESULTS

We collected trail camera data from 197 sites, active for 15–33 days ($\bar{x} = 26.2 \pm 4.6$ [SE]) during 1 to 4 summers from 2017 to 2020 (Supporting Information S3). We cataloged >800,000 images and identified bears in >65,000. Our final dataset comprised 1,121 detections of bears (a detection defined as ≥ 1 observation of >1 bear at any of the 3 camera stations in a site within a 24-hr period). Of these 1,015 (90%) were categorized as adult bears only and 106 (10%) were categorized as a female with young (36 events with 1 cub or yearling observed, 60 events with 2 cubs or yearlings observed, and 10 events with 3 cubs or yearlings observed; Figures S4.1–S4.4, available in Supporting Information). Across all 336 site-surveys (which includes each summer of data collected at revisited sites; Table S3.1), the highest observed state was 0 (no bears detected) 51 times (15%), state 1 (only adult and non-reproductive bears) 222 times (66%), and state 2 (females with young) 63 times (19%). Adult bears were detected at least once at 168 out of 197 sites (naïve occupancy rate = 85%) and bears with cubs were detected at 52 sites (26%).

The top-ranked occupancy model included year and disturbance at a smaller spatial scale (300 m) for detection probabilities, disturbance at a larger spatial scale (6 km) and hardwood forest at 3 km for occupancy probabilities, and disturbance at 3 km and latitude for the probabilities of transition into state 2 (females with young; Table 2). No covariates were informative for transitions into state 1 (adult bears only; Tables S5.1–S5.3, available in Supporting Information).

Detection of bears varied by year, with summers 2017 and 2019 having daily detection probabilities twice as high as summers 2018 and 2020, and the probability of observing cubs or yearlings at sites in state 2 increased with the disturbance score at the stand scale (300-m buffer; Table 3). The estimated probabilities of detecting bears on a given survey occasion ranged for p_1 from 0.03 to 0.07 (occupied by adults only, true state 1), for p_2 from 0.13 to 0.25 (detecting an adult at sites occupied by both adults and young, true state 2), and for δ from 0.02 to 0.03 (successfully detecting young on an occasion when the true state is 2; Table 3).

Initial use by adult, non-reproductive bears was positively associated with increasing forest disturbance at the landscape scale (represented by a radius of 6 km around the survey sites). The probability of initial use by females with cubs increased roughly 50% as the proportion of hardwood trees at the largest home-range scale (3-km radius) increased from a minimum of 1% to a maximum of 77% hardwood species (Table 4; Figure 2A). Black bears occupied 95.22% (95% CI = 68.36–99.46%, SE = 0.05) of study sites, and were in a reproductive state at 48.87% (CI = 36.64–61.24%, SE = 0.10) of sites.

The probability of a site used by only non-reproductive bears in a season transitioning to being used by females with young in the next season was roughly 40% higher in sites with the maximum disturbance index at a 3-km radius (minimum score 1.3 to maximum score 5.6; Figure 2B), while the probability that a site used by bears with young in a season would remain so in a following season was 50% higher at the highest latitudes (minimum latitude 44.1578, maximum 47.4216; Table 4; Figure 2C).

TABLE 2 Model ranking based on Akaike's Information Criterion corrected for small sample sizes (AIC_c) for the final step of parameterizing dynamic, multi-state occupancy models on American black bear data collected at 197 sites over 4 summers, 2017–2020, in Maine, USA. In this final step we compared the importance of different habitat covariates on predicting the probability of a site being used by a female with cubs given the state in the prior summer: $CR(0,1,2)$ where state 0 is no bears present in prior summer, state 1 is used by only adult and non-reproductive bears, and state 2 is used by bears including a female with young. Model ranking was performed in earlier steps on the probability of adult bear use in the first season (Ψ), the probability of use by reproductive females in the first season (R), the probability of transitions to use by adult and non-reproductive bears from other states ($C\Psi$), the probability of detecting bears when the true state is 1 and when the true state is 2 ($p[1,2]$), and the probability of observing dependent young during a detection at a site in state 2 (δ). Covariates included in top models were the disturbance index (DI) within 300-m, 3-km, and 6-km radii buffers; the proportion of forest composed of hardwood trees (HW) at a 3-km radius; and the latitude of the site (lat). We included the corrected model ranking score (AIC_c), the difference in score from the top-ranking model (ΔAIC_c), the model weight (w_i), and the number of parameters (K).

Model	AIC_c	ΔAIC_c	w_i	K
$\Psi(DI\ 6\text{-km}), C\Psi(.), R(HW\ 3\text{-km}), CR(.,\ DI\ 3\text{-km},\ lat), \delta(DI\ 300\text{-m}), p(\text{year},\ \text{year})$	7,002.96	0.00	0.203	17
$\Psi(DI\ 6\text{-km}), C\Psi(.), R(HW\ 3\text{-km}), CR(.,\ lat), \delta(DI\ 300\text{-m}), p(\text{year},\ \text{year})$	7,002.99	0.03	0.200	16
$\Psi(DI\ 6\text{-km}), C\Psi(.), R(HW\ 3\text{-km}), CR(.,\ DI\ 3\text{-km},.), \delta(DI\ 300\text{-m}), p(\text{year},\ \text{year})$	7,003.24	0.28	0.177	16
$\Psi(DI\ 6\text{-km}), C\Psi(.), R(HW\ 3\text{-km}), CR(.,\ lat), \delta(DI\ 300\text{-m}), p(\text{year},\ \text{year})$	7,003.49	0.53	0.156	15
$\Psi(DI\ 6\text{-km}), C\Psi(.), R(HW\ 3\text{-km}), CR(.,\ HW\ 3\text{-km}), \delta(DI\ 300\text{-m}), p(\text{year},\ \text{year})$	7,003.69	0.73	0.141	16
$\Psi(DI\ 6\text{-km}), C\Psi(.), R(HW\ 3\text{-km}), CR(.,\ DI\ 6\text{-km}), \delta(DI\ 300\text{-m}), p(\text{year},\ \text{year})$	7,005.61	2.65	0.054	16

TABLE 3 Detection probabilities for American black bears in Maine, USA, from data collected at 197 motion-sensitive camera sites from 2017 to 2020. Parameters included are the probability of detecting bears when the true state is 1 (used by only adult bears without young) within a 24-hour period (p_1), the probability of detecting bears when the true state is 2 (used by bears including a female with young; p_2), and the probability of observing cubs or yearling bears during a detection at a site where they are present (δ). Thus, $p_2 \times \delta$ is the probability of observing young on an occasion when the true state is 2, and $p_2 \times (1 - \delta)$ is the probability of observing only adults when the true state is 2.

Summer	p_1 (SE)	p_2 (SE)	δ (SE) ^a	$p_2 \times \delta$	$p_2 \times (1 - \delta)$
2017	0.073 (0.009)	0.277 (0.018)		0.031	0.247
2018	0.038 (0.005)	0.162 (0.012)	0.112 (0.011)	0.019	0.144
2019	0.066 (0.007)	0.257 (0.015)		0.028	0.229
2020	0.034 (0.005)	0.148 (0.015)		0.016	0.132

^a δ was constant across years. This is the estimate at an average value of disturbance within a 300-m buffer of the site.

DISCUSSION

We examined the habitat use of American black bears in a forested landscape across north and central Maine to help understand how 2 components of forest structure and composition (forest disturbance caused by timber harvest, the proportion of hardwood to softwood trees) can affect the probability that bears, and particularly females with dependent young, will use the area. Black bears in Maine were widely distributed, using 95% of the land in our study area, and different habitat features predicted where females with cubs were observed in comparison to adults without young. Adult bears' initial probability of use increased with forest disturbance, whereas female with young use increased with the proportion of hardwood forest. The differences in forest

TABLE 4 Untransformed parameter intercepts and beta values for any top-ranking covariates for the top-ranked dynamic, multi-state model occupancy model of American black bears in Maine, USA. Data were collected at 197 motion-sensitive camera sites, over 4 summers from 2017 to 2020. Covariates included in top models were the disturbance index (DI) within 300-m, 3-km, and 6-km radii buffers; the proportion of forest composed of hardwood trees (HW) at a 3-km radius; and the latitude of the site.

Parameter ^a	Untransformed model estimates		
	Intercept (SE)	Covariate	β (SE)
ψ	2.982 (1.127)	DI 6-km	0.957 (0.661)
$C\psi$			
R	-0.045 (0.256)	HW 3-km	0.419 (0.245)
$CR0$			
$CR1$	-0.358 (0.378)	DI 3-km	0.499 (0.341)
$CR2$	0.687 (0.331)	Latitude	0.381 (0.246)
δ	-2.071 (0.114)	DI 300-m	0.418 (0.114)
$p1$	-2.546 (0.136)	Year 2017	
		Year 2018	-0.684 (0.122)
		Year 2019	-0.103 (0.117)
		Year 2020	-0.793 (0.151)
$p2$	-0.959 (0.088)	Year 2017	
		Year 2018	-0.684 (0.122)
		Year 2019	-0.103 (0.117)
		Year 2020	-0.793 (0.151)

^aParameters include the probability of adult bear use in the first season (ψ); the probability of transitions to use by adult and non-reproductive bears from other states ($C\psi$); the probability of use by reproductive females in the first season (R); the probability of a site being used by a female with cubs given the state in the prior summer (CR) where state 0 is no bears present in prior summer, state 1 is used by only adult and non-reproductive bears, and state 2 is used by bears including a female with young; the probability of observing dependent young during a detection at a site in state 2 (δ); and the probability of detecting bears when the true state is 1 ($p1$) and when the true state is 2 ($p2$).

structure and composition predicting the presence of non-reproductive bears versus females with young suggests that these 2 demographic stages make different decisions regarding trade-offs between resource selection and mortality risk (Duquette et al. 2017).

Changes in timber harvesting practices that promote younger and denser forests (Bose et al. 2016, 2021) and the growth of economically valuable tree species like white spruce (*Picea glauca*; Nelson et al. 2012) could have lasting effects on Maine's black bear population. Our top-ranking models revealed that females with young were more likely to use a site as the proportion of hardwoods in the 3-km area surrounding the site increased. We did not have data on the different species of hardwood present at our sites, and thus cannot assess if there are tree-species-specific trends in black bear reproductive probability (as seen in synchronous breeding success linked to beech in some areas of Maine; Spencer 1961, McLaughlin et al. 1994, Schooley et al. 1994). Further research and monitoring should examine which hardwood species may be particularly important, as the species composition of hardwoods in Maine has already changed and will continue to do so with land-use and climate change (Kelly and Goulden 2008). This is particularly important because hardwood tree species that produce fall hard mast food are important for female reproductive success (McLaughlin et al. 1994, Jakubas et al. 2005, Seger et al. 2013); we

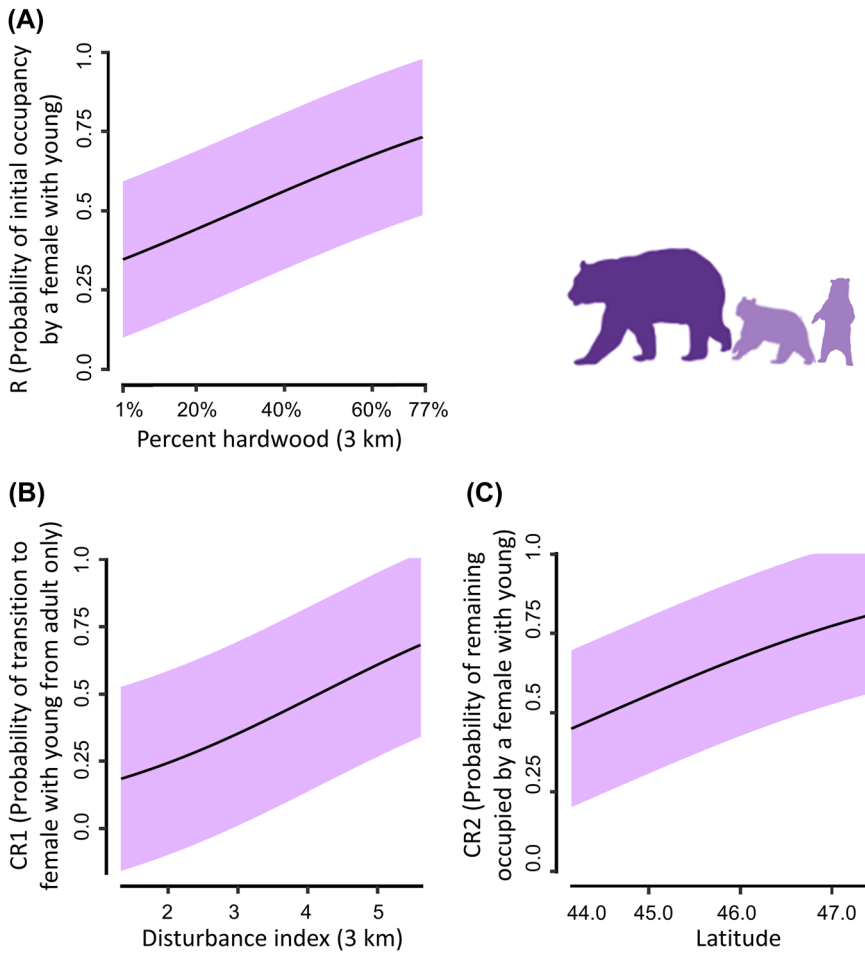


FIGURE 2 Probabilities and standard errors (shaded) from multi-state, multi-season occupancy models of American black bear from motion-sensitive camera data, Maine, USA, 2017–2020. A) The initial probability of use by a female with young as predicted by hardwood (at a spatial scale of a 3-km radius), B) the probability of a site transitioning from used by adult bears only to used by a female with young in the following season, modeled by disturbance in a 3-km buffer, and C) the probability of a site used by a female with young remaining in use the following season, modeled by latitude. Silhouettes are in the public domain, courtesy of M. Michaud and T. A. Heath.

observed a similar trend in summer occupancy patterns of females with young (positive association with hardwood tree cover).

The spatial and temporal patterns of human land-use have complex effects on ecosystems, from the fragmentation of habitat to changes in species composition, and different species respond differently over time since disturbance (Fischer and Lindenmayer 2006, Evans and Mortelliti 2022a, b). In the short-term, the immediate effects of human disturbance and habitat alteration can have acutely negative effects on black bears, such as direct mortality (e.g., road kill) and abandonment of home ranges or den sites leading to cub death (Elowe and Dodge 1989). Longer term effects can be more nuanced such as resetting the natural successional stages of forest stands to provide increased food availability (Costello 1992) and reduced competition from other carnivores (Elbroch et al. 2014). In our study, a remote-sensed disturbance metric including the magnitude and recency of forest disturbance positively predicted the use of an area by adult bears and the probability of colonization by

females with young. That is, areas with relatively high forest disturbance not used by females with young in a given summer had a higher chance of being used in the following summer than relatively less disturbed sites. The spatial scales most supported by the data were large (3-km and 6-km radii). This suggests that disturbance at the landscape (6 km) scale is a biologically meaningful predictor of adult black bear space use, while some history of disturbance at the home-range scale influenced the probability females may come to use an area while rearing young across northern and central Maine. The locations of our survey sites were not being harvested at the time the study took place, so disturbance would have occurred at minimum 2 years prior, and we cannot speculate on how quickly post-disturbance bears will occupy harvested landscapes.

The effect sizes of estimated parameters were not particularly strong and the confidence intervals for transition probabilities into a reproductive state were relatively large (and no covariates were informative for transition into non-reproductive state). This is likely a consequence of the widespread distribution of bears; we observed adults in most sites during the study, and it was rare for them to go undetected in sites that they were present in any season (Table S3). We acknowledge that our dataset contained a relatively limited number of sites with repeated annual visits, which can possibly bias parameter estimates when assessing transitions between states, especially when detection rates are low (McKann et al. 2013). Nonetheless, even with limited repeated surveys per site, we were able to estimate other key state variables such as changes in the use of a site by females with young (the local colonization and extinction parameters in simple multi-season models), which helped us understand the overall effects of forest management on different demographic stages of black bears. We also acknowledge that baiting for hunting is allowed in Maine, and this practice has been suggested as a potential source of bias in home-range selection of bears and may even be responsible for inflating population density in states with long baiting periods like Wisconsin, USA (Kirby et al. 2017). The baiting period in Maine is short relative to that in Wisconsin (30 days prior to hunting season vs. 145) and bait stations are distributed relatively evenly throughout our study area; thus, we are confident that our results were not shaped by the presence of artificial human food sources. American black bears are abundant and have apparently stable populations in Maine, though they were historically over-harvested prior to regulation of hunting activity (McLaughlin 1999). The leading cause of mortality in Maine for adult black bears is hunting, whereas for cubs, yearlings, and juveniles, it is natural causes (e.g., starvation and intraspecific killing; McLaughlin 1999). Our study provides insights into the different habitat requirements for adult bears and females with young, indicating the need to account for the reproductive state in population monitoring. Keeping methodical track of where and how consistently females are raising young at a broad scale can provide key data for population projections and species management without more detailed data on reproductive success for individual bears.

MANAGEMENT IMPLICATIONS

We showed that black bears were widely distributed across the intensively managed landscapes of Maine. Bears in different demographic stages (adult bears vs. females with young) prefer different habitat characteristics at different spatial scales, which indicates that forest management should be carefully designed and implemented to ensure these requirements are satisfied. Specifically, the landscape scale (6-km radius) appeared to be the most suitable for managing disturbance regimes, as this scale affected adult black bear use as a function of forest disturbance. Additionally, higher proportions of hardwood stands at the home-range scale (3-km radius) were associated with use by females with young. Therefore, timber forest practices that emulate natural disturbance at a landscape scale while preserving hardwood forests at a smaller scale can create an overall habitat suitability for black bears in all their demographic stages. Managers should also take advantage of motion-sensitive cameras to understand the spatial and temporal trends of reproductive individuals and young, as it can be a relatively cheaper and non-invasive alternative to other techniques that require more time and funds (e.g., radio-telemetry, global positioning system tracking).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All our methods complied with the American Society of Mammalogists standards for ethical research (Sikes 2016), and were approved by the University of Maine Institutional Animal Care and Use Committee (Protocol A2018-05-06).

DATA AVAILABILITY STATEMENT

The data for this research are provided on Figshare: doi:10.6084/m9.figshare.19157870.

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SUPPORTING INFORMATION

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