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Comparison of behaviors of black bears with and without habituation to humans and supplemental research feeding

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Humans interact with wildlife regularly, mostly without conflict. Interactions between humans and bears, however, have a history of conflict. Using data from female black bears in two populations, we compared behaviors related to a series of hypotheses about habituation and food supplementation via research feeding. We livetrapped bears in the southern boreal forests and cove forests of the Pisgah National Forest, North Carolina, in barrel traps or modified leg-hold snares and outfitted them with very high frequency (VHF) transmitters, for 95 bear-years of data. In the southern boreal forests of Superior National Forest, Minnesota, we habituated bears and outfitted them with VHF collars supplemented with GPS units, for 42 bear-years. Some human residents of the Superior study area fed local black bears and we established a research feeding site. Bears in both populations avoided roads and habituated: Superior bears avoided houses where they were not fed; the study site for Pisgah bears (no habituation or feeding) had too few houses to test for avoidance. Bears in both populations gained weight faster during their active seasons when wild foods were abundant. Habituated, supplemented Superior bears averaged a smaller proportion of a day active, longer activity bouts, and less sinuous movements than did not-habituated or supplemented Pisgah bears. The bears in the two populations did not differ with respect to distances traveled per 2 h or mean lengths of activity bouts. The abundance of wild foods affected time active, distance traveled, and sinuosity of travel by not-habituated or supplemented Pisgah bears. Females in breeding condition in both populations were more active, had longer activity bouts, traveled further, and had more linear travel in spring and early summer while females with cubs pushed these activities into late summer and autumn. This timing pattern for bout length, distance moved, and sinuosity was less pronounced for habituated and research-fed Superior bears than for not-habituated or supplemented Pisgah bears. Thus, habituation to a small number of researchers appeared to not affect many behaviors of bears in our habituated and research-fed Superior population; research feeding appeared to affect some behaviors in a manner consistent with a food supply that had low annual variance. Because we have samples of one for each treatment (one site with habituation and feeding, one site without), our results do not establish that differences documented between the populations were caused by the differences in habituation and feeding. The effects of habituation, research feeding, or other forms of food supplementation on backcountry behaviors of black bears need broader testing across the range of black bears.

Key words: black bear, foraging, habituation, movement, supplementation, *Ursus americanus*

Los seres humanos interactúan rutinariamente con fauna silvestre, mayormente sin conflictos. Sin embargo, las interacciones entre humanos y osos históricamente sí tienen un historial de conflicto. Usando datos de hembras en dos poblaciones de oso negro, comparamos comportamientos relacionados con una serie de hipótesis sobre habituación a seres humanos y suplementación alimenticia por medio de alimentación durante programas de investigación. Usando trampas de barril o trampas de lazo para piernas, capturamos osos de forma no letal en el sur de los bosques boreales y en bosques de ensenada del ecosistema Apalache, y les pusimos collares con transmisores de muy alta frecuencia (transmisores VHF), los cuales resultaron en datos sobre 95 años-oso. Sometimos a los osos del sur de los bosques boreales en Minnesota a un régimen de habituación y les pusimos collares VHF suplidos con aparatos GPS, resultando en datos sobre 42 años-oso. Los osos de ambas poblaciones evitaron las carreteras. Los osos bajo régimen de habituación y con alimentos suplementados evitaron aquellas casas sin alimentación suplementaria. El ámbito de estudio de los osos independientes (sin habituación o alimentación suplementaria) tenía demasiadas pocas casas para poder llevar a cabo un análisis con respecto al comportamiento de evitar casas. Los osos de ambas poblaciones aumentaron de peso más rápidamente en su temporada activa, cuando abundaban los alimentos silvestres. Los osos alimentados pasaban en activo una menor parte del día en promedio, pero recorrían mayores distancias por periodos de dos horas, evidenciaron periodos de actividad más largos y recorridos más sinuosos que los osos independientes. La abundancia de alimentos silvestres afectó el tiempo pasado en activo, la distancia recorrida, y la sinuosidad de los recorridos de los osos independientes; sin embargo, nuestros análisis carecieron de poder estadístico suficiente para aceptar las hipótesis nulas predicando la falta de efectos en los osos con comida suplementada. Las hembras en condición reproductiva de ambas poblaciones eran más activas, mostraron periodos de actividad más largos y recorridos más largos y más lineales durante la primavera y comienzo del verano, mientras las hembras con oseznos extendieron estas actividades hasta el final del verano y otoño. Este patrón de periodos de actividad, distancia recorrida y sinuosidad de recorrido era menos marcado en los osos con alimentación suplementada que en osos independientes. Así, la habituación a un reducido número de investigadores no parece haber afectado el comportamiento de los osos, mientras que la alimentación con propósitos de investigación pareció afectar algunos comportamientos de una manera que es consistente con un suministro de alimentos de baja variación anual. Nuestros resultados no establecen una relación efecto-causa porque teníamos muestras de uno para cada tratamiento distinto (un sitio con habituación y alimentación suplementada, un sitio sin ellos). Los efectos de la habituación, la alimentación por investigación u otras formas de suplementación alimentaria en los comportamientos de los osos negros en zonas campestres requieren pruebas más amplias en toda la distribución de osos negros.

Palabras clave: buscar, habituar, movimiento, oso negro, suplementaciôn, *Ursus americanus*

Many people interact with wildlife on a daily basis, from feeding birds, to observing wildlife while driving, to observing wildlife in wilderness areas. Most such interactions are benign and most conflicts are minor, such as people being irritated by squirrels who raid bird feeders. Indeed, researchers have a history dating back nearly a century of habituating and following study animals in the field (Carpenter 1934).

Clearly, however, not all interactions are benign: predators kill livestock (Treves 2009, 2017; Lozano 2019) and humans hunt and kill game animals. The 2020 United States census documented that urban areas are expanding (Census 2020) and, as human populations expand, people interact with wildlife more often (Kobilinsky 2020a, 2020b; Abrahms 2021). Into the 20th century, humans of European descent generally killed large carnivorans, while many people, though clearly not all, now wish to share environments with large carnivorans (Craighead et al. 1995; Treves 2009, 2017; Johnson et al. 2015; Gilbert 2019; Gould 2020; De Angelis et al. 2021). Many indigenous peoples maintained mutually nonaggressive relationships with large mammalian predators for millennia (e.g., Clark 1904; Thomas 1990; Shepard 1996).

Conflicts between European humans and black and brown bears (*Ursus americanus*, *U. arctos*) have a long history in North America (Botkin 1995; Clark and Rutherford 2005; Artelle et al. 2016; Lischka et al. 2018; Gilbert 2019). Notorious conflicts in Yosemite, Yellowstone, and Great Smoky Mountains national parks in the United States (Craighead et al. 1995; Pelton and van Manen 1996; Rutherford and Clark 2005; Mazur 2015; Gilbert 2019) led to the catchphrase "a fed bear is a dead bear." This phrase was popularized by the US National Park Service to educate park visitors not to feed bears (Garshelis et al. 2017) because human–bear conflicts usually involve food (Craighead et al. 1995; Spencer et al. 2007; Merkle et al. 2013; Johnson et al. 2015; Mazur 2015; Garshelis et al. 2017; Lozano et al. 2019). Bears are adept at discovering new and novel food sources and are better than most other carnivorans at devising ways to access foods that are hard to reach (Benson-Amram et al. 2016; Stringham et al. 2017). Some bears learn from their mothers that food can be available near people (Hopkins 2013). Many bears appear to have learned independently that, when wild foods are scarce, fruits and vegetables may be available in towns or in other areas of human development. Also, bears learn that foods located near humans can change in availability just as can wild foods (Merkle et al. 2013; Hopkins et al. 2014; Johnson et al. 2015). Most bears avoid foraging near people when wild foods are abundant (Zack et al. 2003; Mansfield 2007; Merkle et al. 2013; Johnson et al. 2015).

Bears must gain enough weight each year during their active season to survive winter denning and food scarcity in spring, a time period that includes parturition and lactation for many females (Pelton 2003). Local, annual food production affects reproductive output of females (Rogers 1976; Eagle and Pelton 1983; Eiler et al. 1989; Elowe and Dodge 1989; Costello et al. 2003; Laufenberg et al. 2018) and affects home-range size (Powell et al. 1997). Long-term, regional levels of food production and patchiness determine whether black bears defend territories or tolerate extensive home-range overlap (Powell et al. 1997).

In recent decades, most major national parks in the United States and Canada have managed bears with some significant success by attempting to minimize feeding of bears and to minimize bear–human interactions (Hopkins et al. 2014; Garshelis et al. 2017). The fed bear–dead bear argument implies that, once bears have learned about food available from, and have become habituated to, humans, their behavior has been altered permanently (Craighead et al. 1995; Garshelis et al. 2017), though biology is seldom that simple. If the implication is true, then purposefully feeding bears, even diversionary feeding (feeding to divert bears from conflict with humans; Garshelis et al. 2017), would make bears depend on humans permanently, would affect their abilities to forage for wild foods, and would, therefore, affect behaviors such as home-range use and foraging (Garshelis et al. 2017). In contrast, extensive recent research on urban black bears and on brown bears suggests that giving bears access to food from humans does not affect their abilities to forage for wild foods (Craighead et al. 1995; Baruch-Mordo et al. 2014; Johnson et al. 2015; van Manen et al. 2019; Blair et al. 2020; Gould 2020). Supplemental feeding can affect nutritional status of bears (Partridge et al. 2001) and, thus, reproduction and survival. Bears generally can obtain more food faster at supplemental feeding sites than when foraging in the backcountry but need to forage in the backcountry to balance their diets (Welch et al. 1997; Rode and Robbins 2000). Diversionary feeding can prevent black bears from foraging on tree bark in spring, thereby reducing damage to timber crops (Fersterer et al. 2001; Ziegltrum 2004, 2006) and may lead black bears to avoid campgrounds (Rogers 2011). Nonetheless, comparisons are few of backcountry behavior of bears unaccustomed to people versus behavior of bears habituated to humans and to human food (Massé et al. 2014).

Like bears, wild, free-living primates come into conflict with humans in many public settings (Sapolsky 2001; Grossberg et al. 2003; Medhi et al. 2007; Sengupta and Radhakrishna 2020; Leca et al. 2021). At the Uluwatu Temple in Bali, long-tailed macaques (*Macaca fascicularis*) steal possessions, such as cameras, glasses, and purses from tourists and then barter the return of the stolen items for food (Brotcorne et al. 2017; Leca et al. 2021). Nonetheless, habituating and following primates for field research has a history that dates back nearly a century (Carpenter 1934) and that is accepted as the norm for the study of primates (e.g., Carpenter 1934; DeVore 1963; Goodall 1963; Altmann and Altmann 1970; Altmann 1980; Altmann 1998; Sapolsky 2001; Merrick 2014; and hundreds more). Although black bears are not primates, they are outstanding at problem-solving, and are able to identify individual people who are neither a danger to them nor a source of food (Mansfield 2007; Vonk and Beran 2012; Benson-Amram et al. 2016). Consequently, no reason exists that black bears who are not exposed to the general public consistently but who are habituated to a small group of researchers should necessarily not behave the same as bears who are not-habituated. Such habituation allows collection of detailed behavior data otherwise impossible to collect.

We tested whether the backcountry behaviors of wild female black bears in two widely separated populations differed. The bears in a population in the southern boreal forests of the Superior National Forest in northern Minnesota were habituated to a small number of people and had access to supplemental food provided by those people (hereafter "hab-sup Superior bears"). We call this feeding "research feeding," as defined by Garshelis et al. (2017): "providing food for bears to habituate them to human presence so they can be approached closely for scientific study." The bears of a population in the southern boreal forests and cove forests of the Pisgah National Forest in the southern Appalachian Mountains of North Carolina obtained no food from humans and had few, if any, interactions with humans ("not-hab-sup Pisgah bears"; Tables 1 and 2).

We acknowledge that, with sample size of one site for each treatment (habituated and supplemented vs. not habituated or supplemented), we can not test directly for differences in behavior related to the treatments. We also acknowledge that differences exist between our two study sites, as is always the case for any two study sites. Such differences highlight the need for ≥3 replicates of each treatment in an experiment. Nonetheless, few research projects on large mammals, especially carnivorans, are able to muster two independent study sites, let alone six. We test for differences in behavior between the bears in the two populations and we believe that the overlap in habitats at the two sites provided a basis for assessing the effects of feeding and habituation, though we could not formally test hypotheses related to feeding and habituation.

We compared data on 10 behaviors and four seasonal patterns of behavior across the active seasons of the bears. First, we developed several hypotheses assuming the "fed bear–dead bear" logic. The logic that habituation and research feeding cause bears to lose fear of humans leads to two hypotheses: (1) hab-sup Superior bears approach all houses no less often than expected by chance of proximity while not-hab-sup Pisgah bears approach houses significantly less often than expected; (2) hab-sup Superior bears approach paved and major gravel roads no less often than expected, given that roads are associated with humans (Reynolds-Hogland and Mitchell 2007; Ditmer et al. 2018), while not-hab-sup Pisgah bears approach roads less often than expected. Losing fear of humans is not the same as being attracted to them and, thus, hab-sup Superior bears may be indifferent to houses and roads, and neither avoid them nor be attracted.

Research feeding means that bears do not have to move across large areas to obtain sufficient food when wild foods are scarce, leading to four hypotheses: (3) use of research food supplements by hab-sup Superior bears is not affected by the abundance of wild foods; (4) the rates of weight gain by hab-sup Superior bears during the active season do not change with abundance of wild foods while the rate of weight gain for not-hab-sup Pisgah bears varies positively with wild food abundance. Because home ranges do not need to be large enough to include enough wild foods for years with scarce wild foods (Massé et al. 2014), (5) home ranges of hab-sup Superior bears are smaller than those for not-hab-sup Pisgah bears, and (6) home-range sizes of hab-sup Superior bears do not change with abundance of wild food while home ranges of not-hab-sup Pisgah bears are large during years of food shortage but small in years with abundant food.

Activity is a multidimensional set of behaviors that can be quantified using (i) the proportion of time that an animal is active, (ii) the lengths of activity bouts, (iii) the distances traveled while active, and (iv) the sinuosity or circuity of travel

Table 1.—Test results for hypotheses about behaviors of female black bears that were habituated and food-supplemented via research feeding on the Superior National Forest in Minnesota versus those that were not-habituated or supplemented on the Pisgah National Forest in North Carolina. Hypotheses are reworded as results under the appropriate column. Numbers for hypotheses match numbers used to present hypotheses in the Introduction.

Hypotheses	Habituation and supplementation have an effect	Habituation and supplementation have no effect
1		Habituated Superior bears avoided houses (study site for not-habituated Pisgah bears had too few houses to test)
2		Bears of both populations avoided roads
3		Habituated, supplemented Superior bears decreased use of food supplements when wild foods were abundant
4		Bears of both populations increased rate of weight gain with abundance of wild foods
5		Habituated, supplemented Superior bears had larger home ranges than did not-habituated or supplemented Pisgah bears
6	Not-habituated or supplemented Pisgah bears decreased home-range size with increasing abundance of wild autumn foods but habituated, supplemented Superior bears did not	
7	Not-habituated or supplemented Pisgah bears averaged more time active per day than did habituated, supplemented Superior bears	
	Not-habituated or supplemented Pisgah bears increased time active with increasing abundance of wild foods but habituated, supplemented Superior bears did not	
8		Not-habituated or supplemented Pisgah bears averaged shorter lengths of activity bouts than did habituated, supplemented Superior bears
		Abundance of wild foods did not affect activity bouts of lactating bears in either population or breeding not-habituated or supplemented Pisgah bears
9		Bears in the two populations did not differ for average distances traveled per 2 h
	Not-habituated or supplemented Pisgah bears traveled shorter distances in 2 h when wild foods were abundant did habituated, supplemented Superior bears did not change	
10	Not-habituated or supplemented Pisgah bears had more sinuous travel that did habituated, supplemented Superior bears	
		Abundance of wild foods did not affect sinuosity of travel by habituated, supplemented Superior bears

Table 2.—Test results for hypotheses about changes in behaviors of breeding versus lactating female black bears across their active season and whether the patterns are the same for bears that were habituated and food-supplemented via research feeding on the Superior National Forest in Minnesota versus those that were not-habituated or supplemented on the Pisgah National Forest in North Carolina. Hypotheses are reworded as results under the appropriate column.

Hypotheses	Habituation and supplementation have an effect	Habituation and supplementation have no effect
Proportion day active		Breeding female bears were most active early in year, lactating females late in both populations
	Habituated, supplemented Superior bears had earlier peaks in activity than did not-habituated or supplemented Pisgah bears	
Activity bout length		Peaks for activity bout lengths did not differ in timing between breeding and lactating female bears in either population
	Habituated, supplemented Superior bears had earlier peaks in lengths of active bouts than did not-habituated or supplemented Pisgah bears	
Distance moved/2 h		Breeding female bears traveled longer distances per 2 h early in year, lactating females late in both populations
		Timing of peak travel distances did not differ between the two populations
Sinuosity of movements		Sinuosity of travel did not differ between breeding and lactating female bears
		Sinuosity did not differ among bears in the two populations

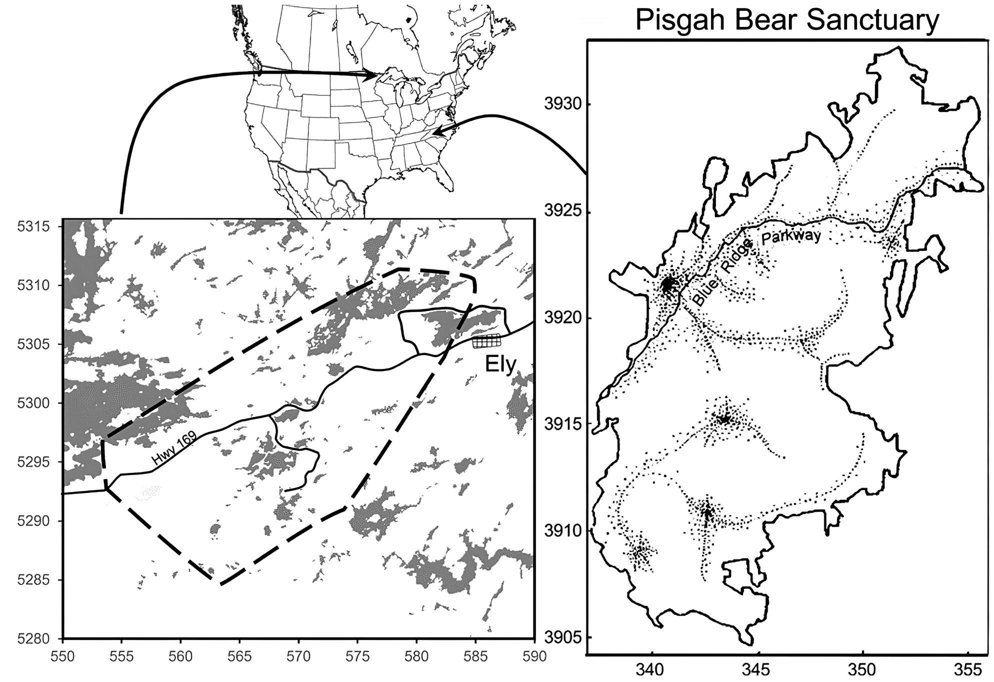

Fig. 1.—Locations of the two study sites. The borders for the two sites show their UTM (Universal Transverse Mercator) units (×1,000).

(Turchin 1998; Favreau 2006). We quantified these behaviors for breeding and lactating female black bears averaged across their annual active season. Because fed bears do not need to forage far and wide to obtain food nor do they need to forage for long periods when wild foods are scarce, we hypothesized the following: (7) hab-sup Superior bears spend less time active; (8) have shorter activity bouts; (9) travel shorter distances when active (Massé et al. 2014); and (10) have more sinuous travel than do not-hab-sup Pisgah bears.

Within their 2-year reproductive cycle, female black bears live under different conditions with different responsibilities every other year. Because breeding females are potentially seeking mates, and because they are not tethered with small cubs, we hypothesize that breeding females spend more time active in spring and early summer, in longer activity bouts, and travel further and more in straight lines than do lactating females, who have cubs. Later in the active season of a bear, lactating females have elevated food requirements to fuel lactation and to provide cubs with fruits, nuts, colonial insects, and other wild foods. Therefore, later in their active season, lactating females spend more time active, in longer activity bouts, and travel further and more in straight lines than do breeding females. We hypothesize that these differences in behavior between breeding and lactating females are less pronounced for hab-sup Superior bears. Anecdotal evidence noted while collecting VHF (very high frequency) telemetry data in the southern Appalachian Mountains supported these deductions (Powell et al. 1997).

Materials and Methods

Bears not habituated or supplemented.—The Pisgah Bear Sanctuary, our study site in the Southern Blue Ridge Mountains, was south to southwest of Asheville, North Carolina (Fig. 1). The approximately 235-km^2 sanctuary was within the Pisgah National Forest, managed by the USDA Forest Service, and was bisected from northeast to southwest by the Blue Ridge Parkway, managed by the US National Park Service (Fig. 1). The North Carolina Wildlife Resources Commission managed wildlife within the unfenced Sanctuary and hunting of black bears was not allowed either within the Sanctuary or within the Parkway. Elevation ranged from 650 m to nearly 1,900 m; southern boreal forests were at high elevations with mixed conifer–northern hardwood forest at lower elevations, and with mixed conifer–cove hardwood forest in low elevation valleys (Powell et al. 1997). Spring and summer temperatures were mild and annual precipitation was high (~250 cm/year), falling as snow at moderate to high elevations in winter. Human uses of the area included logging, hiking, biking, camping, fishing, and hunting of species other than black bears (Powell et al. 1997). The study area had few private inholdings and, after extensive driving and hiking, we located only one hunting shack.

Between 1983 and 2002, we visited 225 sites evenly spaced across the study area to document vegetation. At each sampling site we established five subsites of 10-m radius and located at the center and at 100 m in each cardinal direction; except for boundary sites, each of the four outside subsites was 800 m from a subsite of an adjacent site. At each subsite, we documented species and dbh of all trees, proportion of subsite covered by berry bushes, and ground cover. Pine (*Pinus* spp.), pine-hardwood, and oak (*Quercus* spp.) forests predominated, with southern boreal spruce-fir (*Picea rubens*, *Abies fraserii*) above 1,650 m. The forest understory was patchy with berry bushes (*Vaccinium* spp., *Gaylussacia* spp., and *Rubus* spp.) at all elevations and rhododendrons (*Rhododendron* spp.) and mountain laurel (*Kalmia latifolia*) at low to intermediate elevations (Powell et al. 1997).

The fruits of bear corn (*Conopholis americana*), a nonphotosynthesizing parasite of mostly oak roots, were eaten by bears in spring. During fruiting of 9 years, we visited vegetation sampling sites readily accessible from trap checking trails or roads (n = 13 + 0.6/year, *SD*), harvested and weighed all bear corn at each site (Powell and Seaman 1990; Powell et al. 1997). We sampled berries as they ripened from late June through early September 1986–1990 and 1993–2002, visiting the 19 subsites with >25% berry cover approximately weekly until production ceased, picking and weighing all ripe berries. We determined gross energy of berries using bomb calorimetry (Powell and Seaman 1990) and berries did not differ by species in percent dry weight or energy content. Therefore, all berries at each subsite were combined to calculate the mean production ± *SD* (kg/ha of berry plants), which we extrapolated across the study area using the mean ± *SD* for berry plant coverage at our sampling sites (Powell et al. 1997).

The North Carolina Wildlife Resources Commission surveyed hard mast annually from August through September starting in 1983 (to which we contributed) and based index values (range 0–8) on visual estimates of the percentage of masting tree crowns with nuts (Greenberg and Warburton 2007). We converted index values to kg/ha using analyses of Beck (1977) and Beck and Olson (1968), whose research was done in a representative part of our study area.

We used barrel traps and leg-hold snares modified for bear safety (Cattet et al. 2008; Powell 2005) to livetrap black bears during 1981–2002 (Powell et al. 1997). Most trapping occurred from late May through early July each year. We livetrapped 248 bears and outfitted 57 adult females with VHF, activity-monitoring collars (Telonics, Mesa, Arizona; SirTrack, Havelock North, New Zealand; Lotek, Newmarket, Ontario, Canada). To locate bears, we drove a pickup truck outfitted with a rotatable 8-element antenna mounted through the roof and anchored on a compass rose in the cab. We drove the Parkway and other roads, stopping at sites with good radio reception, to record azimuths for collared bears. A well-experienced team could obtain azimuths for triangulation for up to a dozen bears within a 2-h period, which we repeated for blocks of 4, 6, or 12 two-h periods before taking a 32-h break (balancing autocorrelation among blocks; Swihart and Slade 1985; Powell et al. 1997). We obtained a mean of 134 ± 86 (*SD*) location estimates for 95 bear-years with >30 location estimates with at least 10 locations in each season (spring, summer, autumn). Activity switches incorporated within the telemetry packages indicated when bears were active or resting. Median error for location estimates was approximately 250 m (Zimmerman and Powell 1995). We estimated 95% home-range areas from utilization distributions generated by a fixed kernel estimator with band width h = 250 m (matching telemetry error) and using Silverman's k_2 as the kernel.

Habituated and research-fed bears.—This study area was in southern boreal forest in northeastern Minnesota centered in Eagles Nest Township (hereafter "Eagles Nest"; Mansfield 2007), approximately 15 km southwest of Ely, Minnesota (Fig. 1). White Spruce (*Picea glauca*)–Fir (*Abies balsamia*)–Hardwood (*Populus* spp., *Betula papyrifera*) forest, bog forest (*Picea mariana*, *Larix laricina*), scattered pine forest, and open water predominated across the patchwork of Superior National Forest, state forests, and private property (Robison 2018). Only 1% of the study area was developed.

The Minnesota Department of Natural Resources surveyed food abundances for bears each summer and autumn and calculated index values by multiplying species abundance ratings (0–10) × fruit production ratings (0–10) for 14 foods that included summer and autumn berries and autumn nuts.

Some human residents of the study area had fed local black bears for over 50 years before our study. During our research, 17 households fed bears purposefully during at least a portion of the bears' active seasons and some did habituate bears to members of the households. We established an additional feeding site and habituated local bears to human activities at that site. To habituate bears to our presence, we offered nuts and acclimated some bears to our touch. Starting in 2009, habituated bears that came to our site and that stepped onto a digital scale to obtain food were weighed and photographed automatically, with data saved by computer. During the years of this study, this system functioned without interruption during the entirety of July and August each year, the months during which the most bear foods ripened (Rogers 1987).

Between 1999 and 2014, we placed VHF transmitter collars (Telonics, Mesa, Arizona) on a total of 44 bears without the use of traps or immobilizing drugs. By using these methods, we avoided the short- and long-term problems caused by traps and drugs (Powell 2005; Cattet et al. 2008; Gilbert 2019). Most study bears were initially transmitter-collared as yearlings with known kinship prior to family breakup. These habituated bears fell into three categories: bears comfortable with us around our feeding stations but who did not allow us to approach them in the woods; bears who allowed us to join them in the woods but left us if we tried to walk with them; bears who allowed us to walk with them in the woods (Mansfield et al. 2022).

To obtain additional location data on study bears, during 2009–2013 we attached modified SPOT Personal Tracker GPS (global positioning system) units (Spot Image Corporation, Chantilly, Virginia) to the VHF collars of 14 female bears who allowed us to join them in the woods. These bears all belonged to one clan descended from a matriarch born in 1987 and the bears ranged from 2 to 13 years old while wearing GPS units (mean = 7 ± 3 years). We obtained 42 bear-years of movement data. The SPOT units had their 911 alerts disabled, were programmed to operate continuously until their batteries died, and located themselves every 10 min. The SPOT units transmitted locations to a website, enabling us to observe movements of study bears on our computers in real time and to intercept bears in accessible locations to change batteries every 8–10 days. To change batteries, a member of our research team homed on a target bear using VHF telemetry, calling to the bear when approaching. Some bears continued their activities, some waited for the team member, while others approached. The team member offered the bear a handful of nuts in exchange for access to her transmitter-collar and SPOT unit. Feeding of bears was limited to the minimum needed to change batteries (Mansfield et al. 2022).

We considered bears to be resting if five consecutive locations were all within 30 m of each other. Otherwise, we considered them to be active.

To test the accuracy and precision of the SPOT Personal Trackers, we placed collars at four forested test locations and located those sites precisely on GoogleEarth. At two test areas, we used multiple units placed in different locations within 35 m of each other and left the units in place for days to weeks. We placed one unit at each of the other two test locations and left them for 4 months. We wrapped these collars around logs of bear neck size and at bear height above ground. We calculated the spatial mean for each collar reported by the spot units and compared that mean GPS location to the known location. All mean GPS locations were within 3 m of the known locations. Individual GPS locations for the test collars ranged, however, up to 300 m from the GoogleEarth locations. The closest 25% of GPS locations were within 9 ± 4 m of the test locations; the closest 50% were within 14 ± 6 m; the closest 75% were within 24 ± 11 m; and the closest 90% were within 36 ± 11 m.

We estimated 95% home-range areas from utilization distributions generated by a fixed kernel estimator with band width h = 100 m (based on the abilities of bears to smell, hear, and see their surroundings; Powell 2012) and using Silverman's k_2 as the kernel.

Analyses.—We divided the behaviors we compared into those related to habituation effects (avoidance of humans by avoiding roads and houses where bears were not fed) and those that showed effects of research feeding (behaviors of bears when they were not near humans). Reynolds-Hogland and Mitchell (2007) documented avoidance of roads by our not-hab-sup Pisgah black bears. To test for avoidance of roads by hab-sup Superior bears, we quantified for each bear the nearest distance to paved roads for every 100 × 100 m cell within her 95% utilization distribution constructed to have no disjunct units. We calculated distances around large lakes but used straight-line distances elsewhere. We compared the number of locations for each bear within or further than 183 m (the distance from roads at which black bears in Minnesota exhibit elevated heart rates; Ditmer et al. 2018) of a road to the expected number of locations using chi-square. We made the same comparison for distances to houses where bears were not fed. This test was hampered by some houses where bears were not fed being <183 m from houses where bears were fed. In the end, this bias did not affect our results.

We used the glm (general linear model) procedure in SAS to test for a relationship between abundance of wild foods at our Minnesota study site and bear visitation to our feeding sites.

We tested for differences in the mean annual sizes of 95% utilization distributions for hab-sup Superior bears and not-hab-sup Pisgah bears, and the changes in sizes of utilization distributions regressed against changes in wild food production using glm in SAS (Statistical Analysis System). Also, we used glm to test for differences in annual proportion of time active, bout lengths, distances moved/2 h, and sinuosity.

To quantify the differences in annual behavior patterns of breeding versus lactating females, we divided the active season for bears at each site into 34 periods starting at 1 April. Because the active season for hab-sup Superior bears was shorter (because of being further north) than that for not-hab-sup Pisgah bears, we set each period to be 6.1 days for hab-sup Superior bears (to make 34 periods). For each bear each year, we calculated per period the values of four variables: (1) proportion 24 h active, (2) mean length of activity bouts during 24 h, (3) mean distanced moved per 2 h per day, and (4) mean sinuosity per day. Values for the first three variables all were 0 when bears were in dens, rose during the active season, and again reached 0 when bears entered dens. We quantified sinuosity using the fractal dimension D for travel bouts. When travel is linear, $D = 1$; for random walk, $D = 2$; and as travel bends back on itself more and more, D increases above 2.

For each of the four activity variables and each female at each study site in each year, we calculated the per-period means and fit a quadratic regression to the means, defining the intercept as 0 (except sinuosity). We used quadratic regression because the values for three behaviors rose from 0 as bears left dens, peaked, and then descended to 0 when bears entered dens. Like proportions of time that black bears are active, lengths of activity bouts, and distances traveled per 2 h, sinuosity of travel bouts goes through an annual pattern of changing values. Unlike the other characteristics of activity, however, sinuosity does not start the year at 0 because sinuosity is not defined for the activities of bears in their dens. Therefore, for sinuosity we allowed the intercept to vary. For each regression we found the constants of proportionality for period (β_{period}) and for period^2 (β_{period2}). We then used the manova option of glm in SAS to test for differences in β_{period} and β_{period2} between breeding and lactating female bears, blocking by study site when study site differences existed. Finally, for illustration, we calculated the grand per-period means for travel distances across all females of both reproductive classes, calculated the five-period running means, and calculated the mean βs to plot the grand mean regression (Fig. 2; Supplemental Data SD1 and SD2).

Because we have used many statistical tests, we set $\alpha = 0.01$ to avoid spurious significance. When we were unable to reject a null hypothesis, we used Proc GLMPower in SAS to calculate the power of the test. We set $1 - \beta = 0.80$ to have confidence that not rejecting a hypothesis was supported by the data.

Results

Numbers of visits to our Eagles Nest feeding sites regressed negatively on abundance of summer foods (glm; $F_4 = 13.09$, $P < 0.001$). The abundance of summer berries did not affect the rate of weight gain in either population (glm; not-hab-sup Pisgah bears: $F_1 = 1.91$, $P > 0.05$, $1 - \exists > 0.95$; hab-sup Superior bears: $F_1 = 0.78$, $P > 0.05$, $1 - \exists > 0.95$) but for bears in both populations the weight gain increased with increasing abundance of autumn foods (glm; not-hab-sup Pisgah bears: F_1

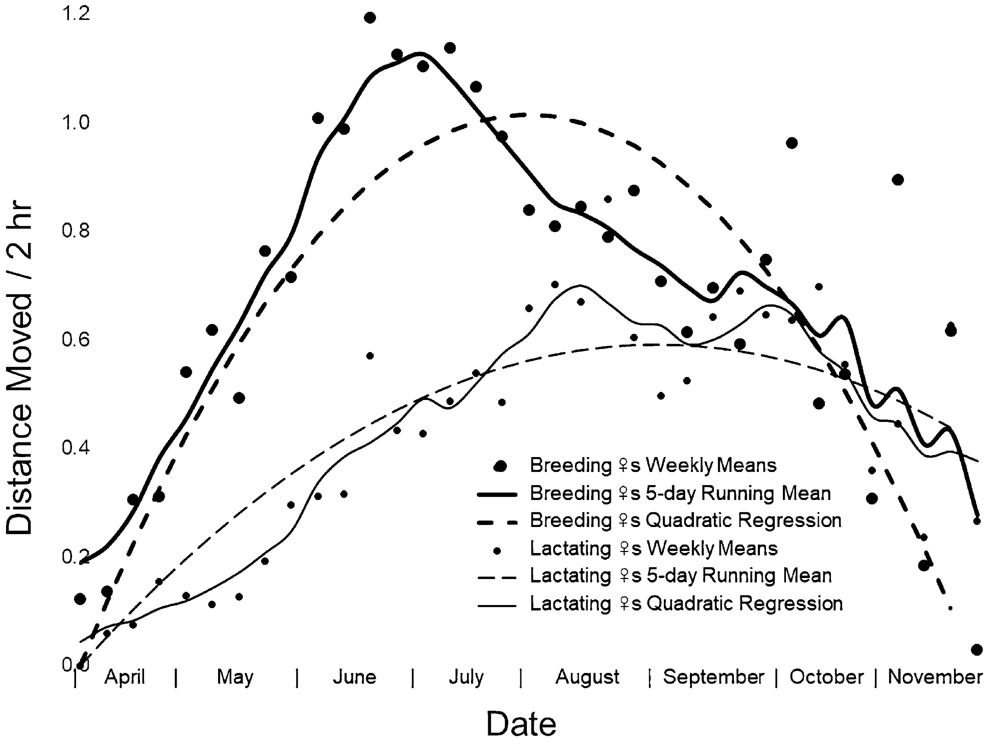

Fig. 2.—Example of analyses of how activity varied across their active season for breeding and lactating female black bears. The example is for distances moved per 2 h by breeding and lactating female bears that were habituated to research personnel and had supplemental food available at our study site on the Superior National Forest in northeastern Minnesota. The grand per-period means are for travel distances across all years and all females of both reproductive classes, the five-period running means, and the grand mean regression. This example shows how well the regressions summarized the per-period data and shows the typical differences between seasonal activity of breeding and lactating females. Breeding females tended to be more active early in their active season while lactating females tended to be more active late in their active season.

= 10.4, $P = 0.01$, effect size = 0.63; hab-sup Superior bears: $F_1 = 14.11$, $P < 0.001$, effect size = 0.28).

Road and house avoidance.—Although some individual hab-sup Superior bears did not avoid roads and did not avoid houses where they were not fed, as a population the hab-sup Superior bears avoided both roads (glm blocked by bear-year; $F_{85} = 828$, $P < 0.0001$, effect size = 0.12) and houses (glm blocked by bear; $F_{85} = 675$, $P < 0.0001$, effect size = 0.10).

Home-range size.—Home ranges for hab-sup Superior bears (19 ± 10 km^2) were larger than those for not-hab-sup Pisgah bears (10 ± 4 km^2; glm: $F_1 = 55.2$, $P < 0.0001$). Not-hab-sup Pisgah bears did not adjust spring home-range areas significantly (glm, $F_1 = 5.10$, $P > 0.01$, $1 - \exists = 0.80$, $n = 19$ bear-years) or summer home-range sizes (glm, $F_1 = 0.0$, $P > 0.05$, $1 - \exists = 0.80$, $n = 18$ bear-years) in response to variation in seasonal food production, but did decrease autumn home-range sizes with increasing production of hard mast (glm, $F_1 = 9.05$, $P < 0.01$, effect size = 0.08). Hab-sup Superior bears did not adjust home-range sizes to annual or seasonal changes in food production (glm; annual: $F_1 = 0.9$; $P > 0.05$, $1 - \exists > 0.90$; summer: $F_1 = 1.22$, $P > 0.05$, $\exists > 0.90$; autumn: $F_1 = 0.01$, $P > 0.05$, $1 - \exists > 0.90$).

Proportions of day active.—Across all years for their whole annual, active period, not-hab-sup Pisgah female black bears were active for a larger proportion of each day than were fed females (Fig. 3; glm: $F_1 = 258$, $P < 0.0001$, effect size = 0.17), which was also true specifically for breeding females (glm: $F_1 = 106$, $P < 0.0001$) and for lactating females (glm: $F_1 = 160$, $P < 0.0001$, effect size = 0.22). In addition, not-hab-sup Pisgah females increased their time active with increasing annual production of foods (glm: $F_1 = 9.51$, $P = 0.002$, effect size = 0.02), which was true for breeding females (glm: $F_1 = 106$, $P < 0.0001$, effect size = 0.13) but not for lactating females (glm: $F_1 = 3.21$, $P > 0.05$, $1 - \exists > 0.95$). We reject the hypothesis that fed females changed the amount of time active as food supply changed (glm: $F_1 = 0.06$, $P > 0.05$, $1 - \exists > 0.95$), which was also true specifically for breeding females (glm: $F_1 = 0.17$, $P > 0.05$, $1 - \exists > 0.95$) and for lactating females (glm: $F_1 = 0.00$, $P > 0.05$, $1 - \exists > 0.95$).

Lengths of active bouts.—Not-hab-sup Pisgah female black bears had shorter bout lengths when active than did fed females (Fig. 3; glm: $F_1 = 20.4$, $P < 0.0001$, effect size = 0.01). Across all bears, breeding and lactating females did not differ for lengths of active bouts (glm: $F_1 = 3.24$, $P > 0.05$, $1 - \exists > 0.95$), blocking by site showed that breeding females had longer activity bouts at each site (glm: $F_3 = 8.59$, $P < 0.0001$, effect size = 0.01). Only breeding hab-sup Superior females changed the lengths (decreasing them) of their activity bouts with increasing production of annual foods (breeding fed females: $F_1 = 9.00$, $P < 0.003$, effect size = 0.02; lactating fed females: $F_1 = 0.11$, $P > 0.05$, $1 - \exists > 0.95$; breeding not-hab-sup Pisgah females: $F_1 = 1.70$, $P > 0.05$, $1 - \exists > 0.95$; lactating not-hab-sup Pisgah

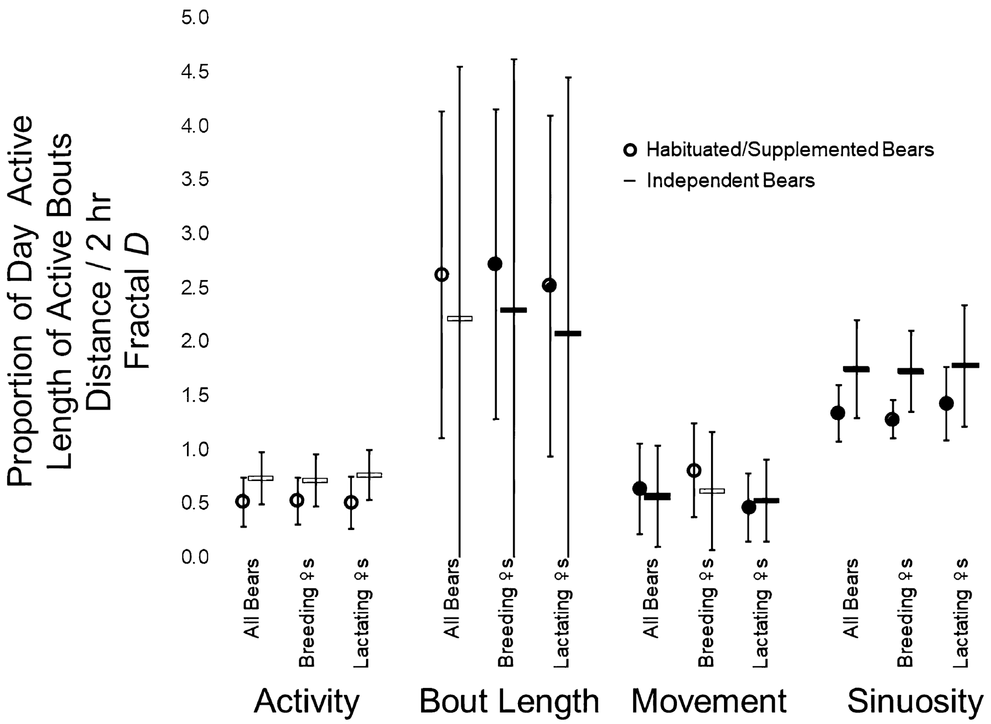

Fig. 3.—Summary activity data for entire active seasons for habituated, supplemented Superior bears and not-habituated or supplemented Pisgah bears. Hollow symbols indicate significant difference.

females: $F_1 = 1.27$, $P > 0.05$, $1 - \exists > 0.95$. The low effect sizes of the significant results suggest that differences between bears in the two populations might not be biological significant.

Distances traveled per 2 h per day.—Travel distances per 2 h did not differ between fed and not-hab-sup Pisgah female black bears (Fig. 3; glm: $F_1 = 4.33$, $P > 0.01$, $1 - \exists > 0.95$). Across all bears, breeding females traveled further than lactating females (glm: $F_1 = 60.6$, $P < 0.0001$, effect size = 0.07). This difference was not related to research feeding because the likelihood ratio decreased by 3% by blocking the test by Site (glm: $F_3 = 27.7$, $P < 0.0001$, effect size = 0.10). Not-hab-sup Pisgah females moved less in years when food was abundant (glm: $F_3 = 6.04$, $P = 0.01$, effect size = 0.03).

Sinuosity.—Not-hab-sup Pisgah females displayed more sinuous travel than did fed female black bears, averaged across their active periods (Fig. 3; glm: $F_1 = 140$, $P < 0.0001$, effect size = 0.25). Across all bears, lactating females had more sinuous travel than did breeding females (glm: $F_1 = 7.41$, $P < 0.007$, effect size = 0.02). Blocking by site showed that this difference was consistent across both sites (glm: $F_3 = 52.1$, $P < 0.0001$). Hab-sup Superior bears did not change the sinuosity of their movements with changes in wild food productivity (glm: $F_1 = 1.75$, $P > 0.05$, $1 - \exists > 0.95$). For not-hab-sup Pisgah bears, we lacked sufficient movement bouts long enough to calculate Fractal *D* for years when we had data on food productivity.

Seasonal behavior patterns.—Hab-sup Superior female black bears had earlier peaks in activity (proportion of each day active) than did not-hab-sup Pisgah females and the peaks were lower (consistent with annual means; Figs. 3 and 4A; Table 2; glm: $F_1 = 41.0$, $P < 0.0001$). The peaks in activity were earlier for breeding females than for lactating females, as predicted from anecdotal observations (glm: $F_2 = 6.35$, $P < 0.004$). Blocking the site differences by reproductive class showed that the sites did not differ with respect to the reproductive class-specific activity patterns (glm: $F_2 = 3.08$, $P > 0.05$, $1 - \exists > 0.95$). Thus, females of the two reproductive classes did differ in how their activity patterns changed across a year but research feeding or other site differences did not affect those differences.

Hab-sup Superior female black bears had earlier peaks in the lengths of their active bouts and the peaks were lower than for not-hab-sup Pisgah females (Fig. 4B; Table 2; glm: $F_2 = 6.71$, $P < 0.003$). The peaks in bout lengths were not, however, earlier for breeding females than for lactating females (glm: $F_2 = 2.55$, $P > 0.05$, $1 - \exists > 0.95$).

The bears in the two populations did not differ in the timing of their peaks for distances traveled in 2 h (Fig. 4C; Table 2; glm: $F_2 = 4.04$, $P > 0.01$, $1 - \exists > 0.95$) but across both sites, breeding females peaked for distances traveled in 2 h earlier in the year than did lactating females (glm: $F_2 = 11.3$, $P < 0.0001$). Thus, females of the two reproductive classes did differ in how their movement patterns changed across a year but research feeding or other site differences did not affect those differences.

For all classes of female bears except lactating, not-hab-sup Pisgah bears, initial sinuosity of travel was roughly random or intermediate between random and linear (Fig. 4D; Table 2). During summer, travel became more linear but then became more random again by late autumn. For lactating, not-hab-sup Pisgah bears, initial sinuosity was midway between linear and random and then rose steadily to random through autumn.

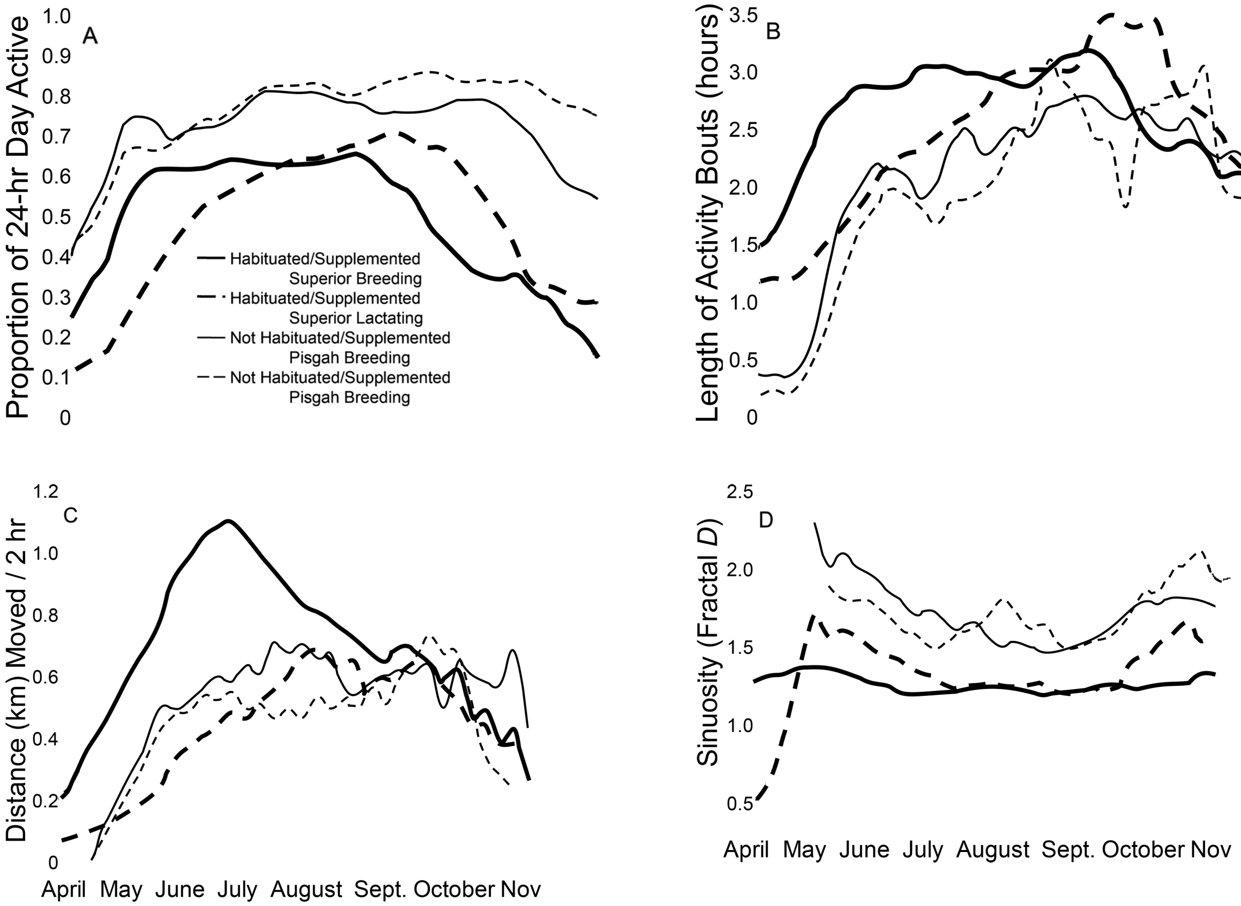

Fig. 4.—Activity levels, shown as the five-period running means, across the active season for habituated, supplemented Superior bears and not-habituated or supplemented Pisgah bears, breeding and lactating females. (A) Per-period means for the proportions of each day active. (B) Per-period means for the lengths of activity bouts (in hours). (C) Per-period means for the distance moved per 2 h when active (in km). (D) Per-period means for sinuosity of travel routes (quantified as the fractal dimension *D*).

Nonetheless, sinuosity did not differ among bears in the two populations (glm: $F_2 = 0.85$, $P > 0.05$, 1 – ∃ > 0.95) nor did it differ between breeding and lactating bears (glm: $F_2 = 0.44$, $P > 0.05$, 1 – ∃ > 0.95) nor differ between bears in the two populations when data were blocked by reproductive class (glm: $F_2 = 0.05$, $P > 0.05$, 1 – ∃ > 0.95).

Discussion

For the female black bears at our two study sites, many backcountry behaviors were similar, although a comparable number of the behaviors differed (Tables 1 and 2; Figs. 3 and 4) suggesting that habituation and research feeding may not alter all foraging behaviors permanently in our hab-sup Superior population. Habituation does affect direct interactions between bears and at least some humans. The bears we studied on the Superior were habituated to some members of our research team and, notably, those bears avoided houses where they were not purposefully fed and avoided roads, just as did our not-hab-sup Pisgah bears (Reynolds-Hogland and Mitchell 2007). The hab-sup Superior bears avoided feeding stations when wild foods were abundant and increased their rates of weight gain during autumn when wild foods were abundant. Thus, the research feeding functioned as diversionary feeding and may have prevented negative human–bear interactions during years with poor production of wild foods (Rogers 2011; Stringham et al. 2017). Diversionary feeding occurs under diverse conditions, sometimes only after bears have established problematic behaviors (Stringham et al. 2017) and, therefore, determining the conditions, if any, that allow diversionary feeding to reduce human–bear conflict is difficult (Garshelis et al. 2017). Nonetheless, clear tests of what conditions allow diversionary feeding to work are badly needed. Even though no two parks or campgrounds or cities are the same, creating challenges to finding absolutely matched sites, researchers at diverse sites can still develop co-operative research programs with important, common treatments that will allow tests across those sites (Cattet et al. 2008).

The behaviors of our hab-sup Superior bears that may have been affected were predominantly behaviors related to research feeding potentially causing bears not to need to forage widely when wild foods were scarce. In contrast to our not-hab-sup Pisgah bears, our hab-sup Superior bears did not exhibit obvious changes in home-range sizes, in proportions of a day active, or in distances moved with changing abundances of wild foods. Nonetheless, though our analyses are suggestive, they are not conclusive because each treatment (fed-habituated and not fed-habituated) had a sample size of one. In addition, our results should not be taken to mean that bear–human conflicts did not occur. They did. The large number of households that fed bears in our hab-sup Superior study site, inevitably, led to unwanted meetings of people and bears at close quarters at times.

Our results are mixed regarding our anecdotal observations that female black bears in breeding condition tend to become active earlier in their active season than females with cubs. Our data showed this pattern for daily time active and distance traveled but not for activity bout length. Habituation and research feeding did not affect this pattern. Females in breeding condition actively seek males and are active in early spring, when food is not plentiful (Kovach and Powell 2003). In contrast, females with cubs may be awake and traveling after leaving their winter dens but are not able to travel far with small cubs and, therefore, confine their activity. Late in the active season, females with cubs have higher food requirements than females without cubs and travel farther to meet those requirements.

Clearly, "habituation" is a general term that includes many different sets of conditions and many bears that are habituated broadly to the general public, such as in national parks, can and do cause serious trouble, damage to property, and, sometimes, injury to people. Other types of habituation, such as habituation to a few researchers with infrequent interactions, need not be so problematic. Bear–human interactions need to be addressed differently depending on how bears apply their natural behaviors to situations that involve humans, by understanding the human behaviors that have preceded the problems, and by understanding how humans perceive the problems. These conditions differ among sites and at any site across time (e.g., Hopkins et al. 2014). Bears that steal food from people concentrated in parks and campgrounds, bears that forage for salmon where they are watched by large numbers of people, bears that steal food from sparsely distributed, backcountry campers, bears whose diets are supplemented to divert them from campgrounds, bears habituated and supplemented where people are sparsely distributed, and bear–human interactions under other conditions all call for different management strategies (Craighead et al. 1995; Merkle et al. 2013; Gilbert 2019). Research on management of bears that are habituated to humans needs to investigate the ranges of conditions that lead to categorically different relationships between bears and humans and the diverse management strategies needed across that range of conditions.

Black bears are excellent problem-solvers (Vonk and Beran 2012; Benson-Amram et al. 2016) and they have evolved abilities to seek and to obtain old and reliable plus diverse new and novel foods and food sources, and to avoid repercussions from humans, often with remarkable abilities (Benson-Amram et al. 2016; Stringham et al. 2017). We expect them to be optimal foragers, meeting their nutritional requirements by maximizing resource acquisition discounted by costs of energy, time, and danger (Emlen 1966; MacArthur and Pianka 1966; Charnov 1976; Pyke et al. 1977; Belovsky et al. 1989; Mitchell and Powell 2004, 2007).

Human–bear interactions are fraught with semantic as well as behavioral confusion (Stringham et al. 2017). Yet, the behaviors of the black bears that we studied appeared predictable and understandable: though foods were associated with people sometimes, the hab-sup Superior bears avoided people when possible (Mansfield 2007). In general, black bears avoid people, especially when they have experienced negative reinforcement, usually via management actions or harassment by home owners (Zack et al. 2003; Merkle et al. 2013; Johnson et al. 2015). Further, black bears learn that foods available from people can change in availability just as can wild foods (Merkle et al. 2013; Hopkins et al. 2014; Johnson et al. 2015) and they can learn to abandon searching for human foods that become unavailable (Hopkins et al. 2014; Mazur 2015; Mazur et al. 2018). Giving black bears access to food from humans does not affect their abilities to forage for wild foods (this study; Craighead et al. 1995; Rode and Robbins 2000; Baruch-Mordo et al. 2014; Johnson et al. 2015; Blair et al. 2020; Gould 2020).

The backcountry behavior of our female black bears appeared not to be much affected by research feeding and habituation to a few specific humans who interacted with the bears mostly less than once per week. Thus, data collected on habituated and food-supplemented wildlife should not summarily be dismissed. Habituation, if done correctly within well-designed research, allows collection of data that is otherwise difficult to impossible to collect. Even GPS telemetry that produces nearly continuous data does not record critically important behavioral details available from direct observations or from snow tracking (Gilbert et al. 2017). Future research with habituated mammals, if done at all, must be designed to address hypotheses that cannot be tested without direct observations of study animals. The long history of habituating free-living research animals shows that such research can be productive when designed well (Altmann 1974).

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Statistics for quadratic equations fit to behavioral data for food-supplemented and habituated black bears on our study site on the Superior National Forest in northeastern Minnesota and for black bears not food-supplemented or habituated on our study site on the Pisgah National Forest in the mountains of western North Carolina.

Supplementary Data SD2.—Annual patterns of four measures of activity (proportion of day active, length of activity bouts, distance traveled per 2 h, and sinuosity of travel indexed by the fractal *D*) for breeding and lactating hab-sup Superior female bears and not-hab-sup Pisgah bears.

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