
Test of a Habitat Suitability Index for Black Bears in the Southern Appalachians
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Test of a habitat suitability index for black bears in the southern Appalachians

Michael S. Mitchell, John W. Zimmerman, and Roger A. Powell

Abstract We present a habitat suitability index (HSI) model for black bears (*Ursus americanus*) living in the southern Appalachians that was developed a priori from the literature, then tested using location and home range data collected in the Pisgah Bear Sanctuary, North Carolina, over a 12-year period. The HSI was developed and initially tested using habitat and bear data collected over 2 years in the sanctuary. We increased number of habitat sampling sites, included data collected in areas affected by timber harvest, used more recent Geographic Information System (GIS) technology to create a more accurate depiction of the HSI for the sanctuary, evaluated effects of input variability on HSI values, and duplicated the original tests using more data. We found that the HSI predicted habitat selection by bears on population and individual levels and the distribution of collared bears were positively correlated with HSI values. We found a stronger relationship between habitat selection by bears and a second-generation HSI. We evaluated our model with criteria suggested by Roloff and Kernohan (1999) for evaluating HSI model reliability and concluded that our model was reliable and robust. The model's strength is that it was developed as an a priori hypothesis directly modeling the relationship between critical resources and fitness of bears and tested with independent data. We present the HSI spatially as a continuous fitness surface where potential contribution of habitat to the fitness of a bear is depicted at each point in space.

Key words Appalachian Mountains, black bear, fitness surface, habitat selection, habitat suitability index, North Carolina, *Ursus americanus*

Habitat and habitat quality are terms that often are poorly defined and therefore are reduced to jargon (Hall et al. 1997, Mitchell and Powell 2002). Ambiguities notwithstanding, these concepts are commonly employed by managers and researchers working with wild animal populations. A common technique of defining habitat and habitat quality in such cases is the habitat suitability index (HSI; United States Fish and Wildlife Service [USFWS] 1981). HSI models have received considerable criticism, largely because they are rarely "validated" (i.e., tested with independent data; Brooks 1997, Roloff and Kernohan 1999, but see criticism by Garshelis 2000 and Hilborn and Mangel 1997 on use of the term "validate"). Tests of HSI models are rare in the literature (Lancia et al. 1982, Thomasma et al. 1991, Brooks 1997, Roloff and Kernohan 1999). HSI models also commonly suffer from effects of arbitrary classification schemes in which habitat suitability is defined without a theoretical or empirical relationship to animal fitness (Mitchell and Powell 2002). In light of criticism that we and others have leveled at HSI models, we present an evaluation of an HSI for black bears (*Ursus americanus*) living in the southern Appalachian mountains (Zimmerman 1992, Mitchell 1997, Powell et al. 1997).

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The HSI model for southern Appalachian black bears was developed by Zimmerman (1992) and pertinent details were presented by Powell et al. (1997). The HSI was developed a priori by reviewing the literature and modeling the value of important, potentially limiting resources to bears (i.e., Live Requisite Variables for food [LRV_F], escape cover [LRV_E], and denning resources [LRV_D]). The modeled relationship for each component of the HSI explicitly depicted a hypothesized contribution of a critical resource to bear fitness (sensu Fisher 1930, Stearns 1992). Unlike many HSI models, the one presented by Powell et al. (1997) was spatially informed, meaning that spatial orientation and configurations of key habitat components (e.g., the interspersion and juxtaposition of food and escape resources, spatial extent of available habitat, distance to roads) were important. Further, arbitrary classification of habitat suitability based on classes (e.g., forest cover type) was minimal, with most components emphasizing specific resources important to bears rather than assuming an association between vegetation classification schemes and resource distributions (Mitchell and Powell 2002). Because most of the components were distributed continuously in space independent of each other, the combination of components forming the HSI could only be portrayed as a continuous surface rather than a collection of distinct polygons (Figure 2*a*). This portrayal has intuitive appeal because in reality many critical resources for animals are distributed continuously over a landscape and are not conveniently isolated to patches.

After the HSI's development, Powell et al. (1997) tested its ability to predict behavior and distribution of collared black bears living in the Pisgah Bear Sanctuary in western North Carolina. To portray the HSI for the sanctuary, they sampled HSI components at 59 evenly distributed, systematically located sites in 1983-1984, and values for each component were interpolated between sites. Combining all components resulted in an HSI map of the sanctuary with HSI values potentially ranging from 0 (poor suitability) to 1 (high suitability; Figure 2*a*). Home range data from 19 bears (9 males and 10 females) in 1983-1985 were used to test how HSI values predicted 1) habitat selection of the bear population (i.e., across the 19 bears sampled and presumed to represent all bears living in Pisgah), 2) habitat selection of individual bears, and 3) number of bear home ranges that would incorporate a given habitat patch (Powell et al. 1997). HSI values correctly predicted habitat use for the population (r^2=0.21, P<0.05) but poorly predicted individual selection. The HSI value assigned to a patch also was correlated positively with the number of home ranges that would include that patch, suggesting that areas with abundant patches of high HSI could support more bears than areas without. We emphasize that these analyses constituted a true test (sensu Platt 1964) of the HSI because the model was evaluated with data not used to generate it. Even though some model components were

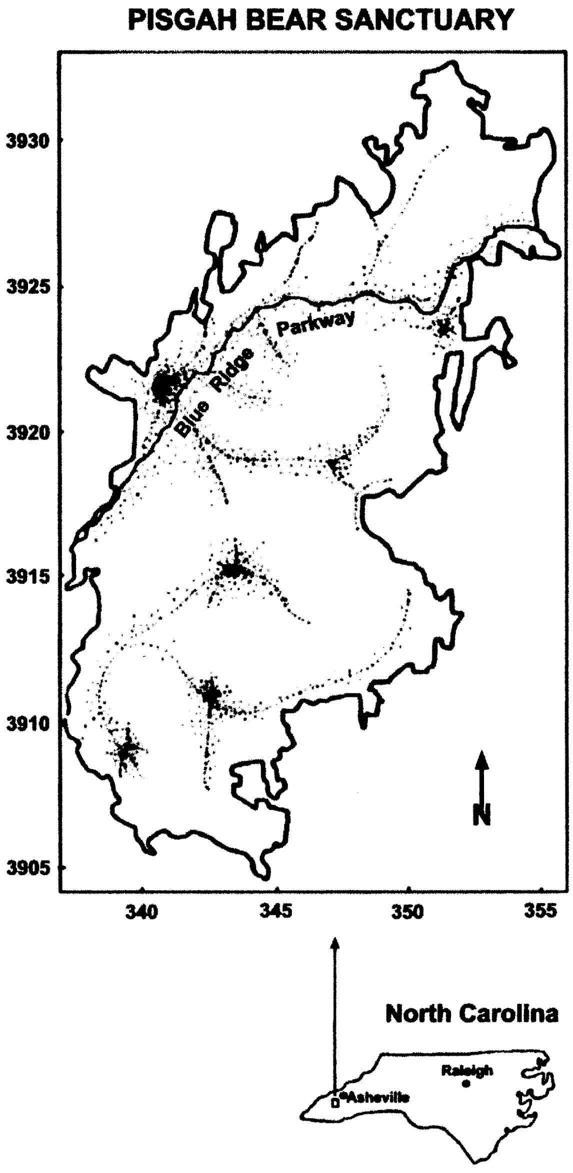

Figure 1. Pisgah Bear Sanctuary, North Carolina, and its Universal Transverse Mercator (UTM) coordinates. Dots on the map indicate major mountains and ridges. Courtesy of C. Powell.

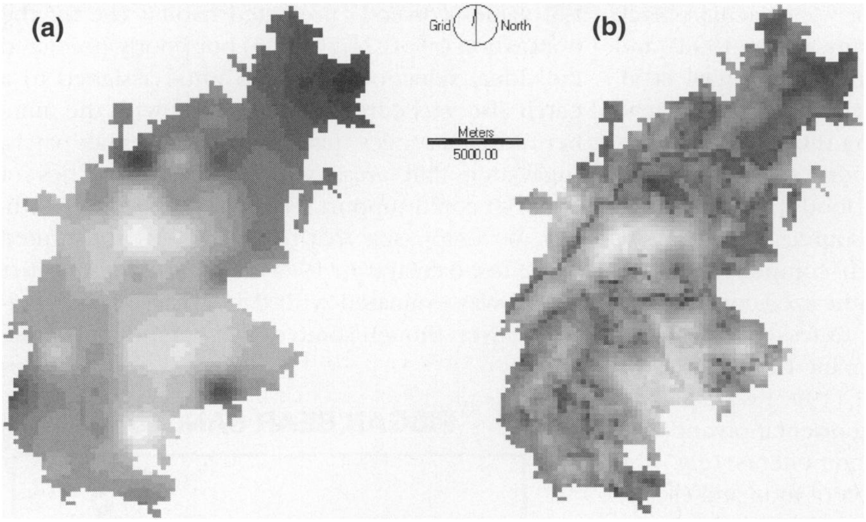

Figure 2. Habitat suitability index (HSI) values for black bears in the Pisgah Bear Sanctuary, Pisgah National Forest, North Carolina, 1994. Figure 2*a* depicts the HSI as originally modeled by Zimmerman (1992) and Powell et al. (1997), using only interpolation of data between systematically located sampling points. Figure 2*b* depicts the HSI as modeled by Mitchell (1997) using landform, roads, and forest cover data; data collected in field sampling at systematically located sampling points and mapped using landform modeling and interpolation; and data collected from selected stands of regenerating forest.

estimated or at times modeled arbitrarily in the absence of reliable information, the assumed relationships were tested (Powell et al. 1997). Had they been modeled incorrectly, it was unlikely (though not impossible) they would have predicted bear behavior and the number of bears including a given patch in their home range. Based on results of their analyses, Powell et al. (1997) also evaluated a variation of the HSI model, HSI_2, which contained only the food and denning components of the HSI. They found that HSI_2 better predicted habitat selection by bears on a population scale ($r^2=0.73$, $P<0.05$). Because HSI_2 was a second-generation model developed in response to analyses of the HSI, its relationship to bear behavior was correlative and therefore hypothetical and untested.

In this study we undertook a more complete and rigorous evaluation of the HSI than that performed by Powell et al. (1997), following recommendations of Roloff and Kernohan (1999). Powell et al. (1997) did not formally evaluate the sensitivity of the HSI to observed variation in measured habitat characteristics used to calculate its components; thus, the potential for modeled relationships that were inconsequential or disproportionately influential to bias analyses of the HSI was unknown (Roloff and Kernohan 1999). Our first objective therefore was to evaluate the effects of variability within input data on final HSI values to better understand relationships between measured habitat characteristics and the HSI. Powell et al.'s (1997) analyses were based on the home ranges of 19 bears, a small subset of the data we now possess for the Pisgah Bear Sanctuary, where research has been underway since 1981. Additionally, improvements in GIS capabilities and data availability since Powell et al. (1997) was published, combined with additional collection of habitat data in the field, enabled us to substantially improve accuracy and detail in HSI maps over those used by Powell et al. (1997). A larger data set for bears and improved HSI maps enabled a more rigorous test of the HSI than performed by Powell et al. (1997). Our second objective therefore was to replicate the analyses of Powell et al. (1997) by 1) testing relationships between HSI and HSI_2 and habitat selection at population and individual scales, and 2) testing relationships between HSI and HSI_2 values assigned to a patch and the number of bear home ranges including that patch. Because we evaluated HSI_2 using data independent of those used to develop it, our analyses are the first true tests of HSI_2.

Study area

The Pisgah Bear Sanctuary (35°17'N, 82°47'W; Figure 1) was the largest (235 km^2) of 28 bear sanctuaries established in North Carolina in 1971 and was contained completely within Pisgah National Forest. The mountainous terrain ranged in elevation from 650-1,800 m and was dominated by Big Pisgah Ridge, which bisected the sanctuary and along which ran the Blue Ridge Parkway. The region was considered a temperate rainforest, with annual rainfall approaching 250 cm/yr (Powell et al. 1997).

Major forest types in the sanctuary were eastern hemlock (*Tsuga canadensis*), cove hardwoods (*Liriodendron tulipifera*, *Magnolia* spp., *Betula* spp.), oak-hickory (*Quercus* spp., *Carya* spp.), pine (*Pinus* spp.), and pine-hardwood mix. Little primary forest remained in the sanctuary, and mature stands averaged 85±25 (SD) years in age in 1994. The United States Department of Agriculture Forest Service (USDAFS) actively managed for timber production, and as of 1994, timber had been harvested (generally by clearcutting) from a total of 133 sites averaging 7.6±3.8 ha in size. Harvested stands averaged 15±7 years in age. Most stands regenerated naturally after initial site preparation with herbicides and were unmanaged thereafter.

Methods

Estimating HSI values and model analysis

During 1993-1994 we collected data to calculate the 6 ground-survey components of the HSI (Table 1) at 63 new sampling sites located systematically (intersections of odd-numbered 1-km Universal Transverse Mercator [UTM] gridlines) across the sanctuary. We combined these data with those collected by Powell et al. (1997) at 59 similarly located sites (except at even-numbered UTM intersections) in 1983-1984 for a total of 122 sites. Other than forest aging, changes in bear habitat during our study were due primarily to timber harvest and road building. Because these timber management practices were ongoing throughout our study and resulting changes in HSI were potentially important, we incorporated their effects in HSI component maps for each year to ensure the best accuracy possible. No systematically located sampling sites fell within a harvested stand; therefore, effects of timber harvest on the HSI were unknown. To estimate ground-survey components in harvested stands, we collected data in 48 of 133 harvested stands in the sanctuary. Harvested stands fell into 3 broad classes according to age and regenerating forest type: stands ≤10 yr old (n=15), pine stands >10 yr old (n=16), and hardwood stands >10 yr old (n=17). We averaged observations within each class to estimate values for ground-survey components of the HSI for all harvested stands within the sanctuary. We mapped all other HSI components for harvested stands using the same approaches used for systematically located sites.

We used Geographic Information System (GIS) software (IDRISI, Clark University, Worcester, Mass.) to map 11 of the 20 HSI components that could be derived from GIS data and digitized databases (Table 1) and to measure spatial phenomena explicitly (e.g., distance, area). We mapped 7 of the 20 HSI components for which no GIS data existed (Fy_1, Fsp_2, Fsu_1, Ff_2, E_2, D_2, and D_4; Table 1) using regression of field data on landform characteristics (e.g., elevation, slope, aspect, exposure, net curvature of slope; Fels 1994, Mitchell 1997) or interpolation (Mitchell 1997). We hand-digitized and mapped the 2 remaining components (Fy_{2a}, Fy_{2c}). For components that changed over time (e.g., due to timber harvests, road construction, changes in anthropogenic food sources, forest aging), we created maps for every year 1981-1994; we created a single map for components that did not change with time (e.g., slope). We produced final HSI maps for the sanctuary for each year by combining component maps. We set the grain (cell size) of final images used for tests at 250 × 250-m "cells" to approximate median error for our telemetry locations of bears (260-m radius; Zimmerman and Powell 1995).

To determine the relative contribution of each HSI component to the final model, we conducted sensitivity and elasticity analyses (Caswell 1978, Stearns 1992). For each HSI component, we calculated a set of HSI estimates across the range of input values observed for that component, with values for all other components held constant. As an index of HSI sensitivity to variation in that component (i.e., absolute effects of input values of that component on final HSI estimation), we used

$$S = \frac{\sum_{i=1}^{n}\left(\mathrm{HSI}_i - \overline{\mathrm{HSI}}\right)}{n}.$$

As an index of HSI elasticity to variation in that component (i.e., proportional effects of input values of that component on final HSI estimation), we used

$$E = \frac{\sum_{i=1}^{n}\left(1 - \mathrm{HSI}_i / \overline{\mathrm{HSI}}\right)}{n}.$$

For both indices, HSI_i = the final HSI value calculated using observation i of the component across the observed range $i...n$ of that component. Neither index reflected the weight a given component received in the HSI; rather, S and E reflected how variability in the component could affect final HSI values, given the weighting assigned to it in the model. Therefore, equal values of S and E among components suggested a balanced model, whereas unequal values indicated that variation in model

Table 1. Components, sampling methods, and functions for a habitat suitability index (HSI) for black bears in the southern Appalachians, 1981–1994. Summarized from Zimmerman (1992) and Powell et al. (1997).

Model	Index	Sub-index[a]	Habitat feature modeled	Survey methodology	Function	Source(s)
HSI					$HSI = [(LRV_F + LRV_E + LRV_D) / 3] \times I_{LRV}$	
LRV_F[b]			Life requisite variable for food resources		$LRV_F = Fy / 7 + (Fsp / 7 + 2Fsu / 7 + 4Ff / 7) \times I_f$, for $Fy / 7 + (Fsp / 7 + 2Fsu / 7 + 4Ff / 7) \times I_f < 1.0$; $LRV_F = 1.0$, for $Fy / 7 + (Fsp / 7 + 2Fsu / 7 + 4Ff / 7) \times I_f \geq 1.0$	
	Fy		*Year-round foods*		$Fy = Fy_1 + Fy_2$, for $Fy_1 + Fy_2 \leq 1.0$; $Fy = 1.0$, for $Fy_1 + Fy_2 > 1.0$	
		Fy_1[b]	Abundance of colonial insects,	Ground survey	$Fy1 = 0.00082x + 0.1$, for $x \leq 1{,}100$; $Fy1 = 1.0$ for $x > 1100$, where: x = number of fallen logs / ha	Zimmerman (1992)
		Fy_2	Anthropogenic foods		$Fy_2 = (Fy_{2a} \times Fy_{2b} \times Fy_{2c}) / 3$	
		Fy_{2a}	Quality of anthropogenic food source	Aerial–ground survey	$Fy_{2a} = [(A+R) / 2]S$, where: A = food available (high=1.0, medium=0.6, low=0.1), R = risk of reprisal (high=1, medium=0.5, low=0.1), S= number of seasons available to bears (0 to 3) divided by 3	Zimmerman (1992)
		Fy_{2b}	Costs of traveling to anthropogenic food source	GIS	$Fy2b = 1.0$, for $x \leq 1.5$; $Fy2b = -0.667x + 2$, for $1.5 < x \leq 3.0$; $Fy2b = 0$, for $x > 3.0$, where: x = distance (km) to anthropogenic food source	Beeman (1975), Garshelis et al. (1983)
		Fy_{2c}	Access to escape cover ≥400 ha from anthropogenic food source	Topographic map	$Fy2c = 1.0$ for $x < 25$; $Fy2c = -0.0017x + 1.0425$, for $25 \leq x \leq 200$; $Fy2c = -0.0015x + 0.6$, for $200 < x < 400$; $Fy2c = 0$, for $x > 400$, where: x = distance (m) between anthropogenic food source and escape cover	McCollum (1973), US Fish and Wildlife Service (1982), Rogers and Allen (1987)
	Fsp		*Spring foods*		$Fsp = (2\ Fsp_1 + Fsp_2) / 3$	
		Fsp_1	Productivity of vegetation associated with moist habitats and availability of water after denning	GIS	$Fsp = 1.0$, for $x \leq 0.64$; $Fsp = 1.167x + 1.75$, for $0.64 < x < 1.5$; $Fsp = 0$, for $x \geq 1.5$, where: x = distance (km) to perennial water	Beeman and Pelton (1980), Carlock et al. (1983), Rogers and Allen (1987)
		Fsp_2	Productivity of spring vegetation	Ground survey	$Fsp_2 = 0.08x$, for $x < 12.5$; $Fsp_2 = 1.0$, for $x \geq 12.5$, where: x = percent cover of *Smilax* spp.	US Fish and Wildlife Service (1982)
	Fsu		*Summer foods*		$Fsu = Fsu_1 + Fsu_2$, for $Fsu_1 + Fsu_2 \leq 1.0$; $Fsu = 1.0$, for $Fsu_1 + Fsu_2 > 1.0$	
		Fsu_1	Productivity of berry species[c]	Ground survey	$Fsu_1 = (0.027 + 0.005n)x$, for $(0.027 + 0.005n)x < 1.0$; $Fsu_1 = 1.0$, for $(0.027 + 0.005n)x \geq 1.0$, where: n = number of berry genera present, x = percent cover in berry plants	Rogers and Allen (1987)
		Fsu_2	Productivity of squaw root (*Conopholis americana*), indexed by prevalence of red oak in overstory	CISC[d]	0.0 to 0.1, See Powell et al. (1997), USDA Forest Service (1982)	Baird and Riopel (1986), Zimmerman (1992)

(*Continued*)

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[a] Variables combined into a single index.

[b] LRV = Life Requisite Variable.

[c] Includes blueberries (*Vaccinium* spp.), huckleberries (*Gaylusaccia* spp.) and blackberries (*Rubus* spp.).

[d] Digitized Continuous Information of Stand Condition (CISC), United States Department of Agriculture Forest Service.

[e] Diameter breast height.

Table 1 (*continued*). Components, sampling methods, and functions for a habitat suitability index (HSI) for black bears in the southern Appalachians, 1981–1994. Summarized from Zimmerman (1992) and Powell et al. (1997).

Model	Index	Sub-index[a]	Habitat feature modeled	Survey methodology	Function	Source(s)
		Ff_{1b}	Age of stand	CISC	$Ff_{1b} = 0$, for $x < 20$; $Ff_{1b} = 0.025x - 0.5$, for $20 \le x \le 60$; $Ff_{1b} = 1.0$, for $60 \le x \le 100$; $Ff_{1b} = -0.004x + 1.4$, for $100 < x < 125$; $Ff_{1b} = 0.9$, for $x \ge 125$, where: x = age (years) of stand	Goodrum et al. (1971), Brody (1984)
		Ff_2	Productivity of grapes (*Vitis* spp.)	Ground survey	$Ff_2 = 0.005x$, for $x \le 200$; $Ff_2 = 1.0$, for $x > 200$, where: x = number of grape vines / ha	Collins (1983), Eiler et al. (1989), Zimmerman (1992)
		Ff_3	Effect of roads on access to hard mast	GIS	0.0 to 0.1, See Powell et al. (1997), USDA Forest Service (1982), where: x = distance (km) to nearest road, road type = temporary, improved dirt, or paved	Quigley (1982), Villarubia (1982), Collins (1983)
		I_f	Interspersion of food resources	GIS	$I_f = 1.0$, for $x \le 5$; $I_f = -0.07x + 1.35$, for $5 < x \le 19$; $I_f = 0$, for $x > 19$, where: x = distance (km)	Beeman (1975), Eubanks (1976), Garshelis and Pelton (1981)
LRV_E			Life requisite variable for escape resources		$LRV_E = (E_1 + 0.5E_2 + 0.25E_3) \times E_4$, for $(E_1 + 0.5E_2 + 0.25E_3) \times E_4 < 1.0$; $LRV_E = 1.0$, for $(E_1 + 0.5E_2 + 0.25E_3) \times E_4 \ge 1.0$	
		E_1	Accessibility via roads	GIS	$E_1 = 0$, for $x \le 4$; $E_1 = 1.11[\log_{10}(x \times 100)]-2.89$, for $4 < x < 32$; $E_1 = 1.0$, for $x \ge 32$, where: x = area (ha) of conterminous forest not bisected by roads	USDA Forest Service (1982)
		E_2	Density of understory	Ground survey	$E_2 = 0$, for $x \le 20$; $E_2 = -0.007x + (2.38 \times 10^{-4})x^2 + 0.06$, for $20 < x < 80$; $E_2 = 1.0$, for $x \ge 80$, where: x = percent closure of understory	Zimmerman (1992)
		E_3	Steepness of terrain	GIS	$E_3 = 0$, for $x < 15$; $E_3 = 0.0333x - 0.5$, for $15 \le x \le 45$; $E_3 = 1.0$, for $x > 45$, where: x = slope (degrees) of terrain	Zimmerman (1992)
		E_4	Distance from roads	GIS	$E_4 = 0$, for $x = 0$; $E_4 = 0.156x + 0.195x^2 = 0.25$, for $0 < x < 1.6$; $E_4 = 1.0$, for $x \ge 1.6$, where: x = distance (km) to nearest road	Collins (1983)
LRV_D			Life requisite variable for denning resources		$LRV_D = \{[(D_1 + D_2) / 2](D_3 + D_4)\}^{0.5}$, for $\{[(D_1 + D_2) / 2](D_3 + D_4)\}^{0.5} < 1.0$; $LRV_D = 1.0$, for $\{[(D_1 + D_2) / 2](D_3 + D_4)\}^{0.5} \ge 1.0$	
		D_1	Accessibility via roads	GIS	$D_1 = 0$, for $x \le 2$; $D_1 = (9.8 \times 10^{-2})x - 0.20$, for $2 < x < 12.25$; $D_1 = 1.0$, for $x \ge 12.25$, where: x = area (ha) of conterminous forest not bisected by roads	Beeman (1975), Eubanks (1976), Garshelis and Pelton (1981), Warburton (1984), Zimmerman (1992)

(*Continued*)

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[a] Variables combined into a single index.

[b] LRV = Life Requisite Variable.

[c] Includes blueberries (*Vaccinium* spp.), huckleberries (*Gaylusaccia* spp.) and blackberries (*Rubus* spp.).

[d] Digitized Continuous Information of Stand Condition (CISC), United States Department of Agriculture Forest Service.

[e] Diameter breast height.

Table 1 (*continued*). Components, sampling methods, and functions for a habitat suitability index (HSI) for black bears in the southern Appalachians, 1981–1994. Summarized from Zimmerman (1992) and Powell et al. (1997).

Model	Index	Sub-index[a]	Habitat feature modeled	Survey methodology	Function	Source(s)
		D_2	Availability of dense stands of rhododendron (*Rhododendron* sp). or mountain laurel (*Kalmia latifolia*) for ground dens	Aerial photographs	$D_2 = 0.0333x$, for $x < 30$; $D_2 = 1.0$, for $x \geq 30$, where: x = area (ha) in rhododendron or mountain laurel	Zimmerman (1992)
		D_3	Availability of cave and rock dens	GIS	$D_3 = \tan(x)$, for $x \leq 45$; $D_3 = 1.0$, for $x > 45$, where: x = slope (degrees) of terrain	Zimmerman (1992)
		D_4	Availability of tree cavity dens	Ground survey	$D_4 = 0.564(\log_{10}x) - 0.352$, for $x \leq 250$; $D_4 = 1.0$, for $x > 250$, where: x = number of trees $\geq$90 cm DBH[e] / ha	
I_{LRV}			Interspersion of all resources	GIS	$I_{LRV} = 1.0$, for $x \leq 5$; $I_{LRV} = -0.07x + 1.35$, for $5 < x \leq 19$; $I_{LRV} = 0$, for $x > 19$, where: x = distance (km)	

[a] Variables combined into a single index.

[b] LRV = Life Requisite Variable.

[c] Includes blueberries (*Vaccinium* spp.), huckleberries (*Gaylusaccia* spp.) and blackberries (*Rubus* spp.).

[d] Digitized Continuous Information of Stand Condition (CISC), United States Department of Agriculture Forest Service.

[e] Diameter breast height.

output was due primarily to a subset of model components (i.e., strong imbalance in S or E among components indicated that the model could be reduced to a subset of components without changing model predictions substantially). Whereas sensitivity and elasticity analyses could identify relative importance of model components given input data used to generate the model, they could not indicate anything about biological relevancy of the components, which must ultimately be tested with data on habitat use or demography collected from animals.

Trapping of bears, telemetry, and home range estimation

We captured bears from May through mid-August of 1981-1994 (except 1991 and 1992) using modified Aldrich foot snares (Johnson and Pelton 1980) or barrel traps. Every effort was made each year to capture all bears in the central portion of the study area, although trapping effort varied among years. We immobilized captured bears using a combination of Ketaset, Rompun, and carbocaine (approx. 200 mg ketamine hydrodrochloride + 100 mg xylazine hydrochloride/cc; Cook 1984) or Telazol administered with a jabstick or blowgun. We fitted immobilized bears with ear tags, then sexed, weighed, measured, and drew blood samples. We extracted a first premolar to estimate age. We fitted selected bears with motion-sensitive radiotransmitter collars (Telonics, Inc., Mesa, Ariz.; Lotek, Inc., Newmarket, Ont., Canada; 3M and Wildlink, both of St. Paul, Minn.). We captured and handled all bears in compliance with requirements of the Institutional Animal Care and Use Committees for North Carolina State University (IACUC# 96-011) and Auburn University (IACUC # 0208-R-2410). For our analyses, we considered bears to be adult at 3.5 years old; we classified females known to produce cubs at age 3 as adult at age 2.5.

From April or May each year until bears denned (late November to mid-December), we estimated locations using telemetry receivers (Telonics Inc., Mesa, Ariz.) and truck-mounted or hand-held antennas. We estimated locations by triangulating compass bearings taken from a minimum of 3 separate locations within 15 minutes (Zimmerman and Powell 1995). When practicable, we located each bear every 2 hours for 8 consecutive hours. We repeated sampling every 32 hours to standardize bias from autocorrelation within 8-hr sampling periods and to eliminate bias between periods (Swihart and Slade 1985, Powell 1987).

Each observer collecting telemetry data also regularly estimated locations of "test" collars to document telemetry error (Zimmerman and Powell 1995; M. S. Mitchell, unpublished data). Zimmerman and Powell (1995) evaluated telemetry error using test collar data and found that median error was 261 m ($n = 371$), 95% of estimates were <766 m from the true location, angle error was significantly leptokurtotic around 0, and error did not differ among observers ($P > 0.05$).

We estimated home ranges from locations using a fixed-kernel estimator with bandwidth determined by cross validation (program KERNELHR; Seaman et al. 1998). We used a grid size of 250 m for kernel estimation to match resolution of our telemetry and habitat maps. A minimum of 20 locations was required for home range estimates (Noel 1993, Seaman and Powell 1996), and home ranges were defined as the area containing 95% of the estimated utility distribution.

HSI and habitat selection by bears

With more data we repeated Powell et al.'s (1997) tests of the ability of HSI and HSI_2 to predict bear selection of habitat (second-order habitat selection, Johnson 1980) at population and individual scales, and to predict how many bear home ranges would include patches based on their HSI values. For each bear each year, we used the kernel density assigned to each cell of its 95% kernel home range to index the value of that cell to that bear (Powell 2000). For maps of HSI and HSI_2 for each year, we rounded all HSI and HSI_2 values to the nearest 0.05 and calculated percent availability of cells for each of 20 HSI classes within the sanctuary. Combining home range and habitat data for each year, we used Ivlev's electivity index (Ivlev 1961, Powell et al. 1997) to calculate a habitat selection index, P, for space use by each bear based on classes of HSI and HSI_2:

$$P = \frac{\text{\% use of Class } HSI_i - \text{\% availability of Class } HSI_i}{\text{\% use of Class } HSI_i + \text{\% availability of Class } HSI_i}.$$

P standardized the use of habitat classes by their availability so that selective use by animals could be discerned. Values for P ranged from -1 (avoidance) to 1 (strong selection). Any index of habitat selection is sensitive to how habitat availability is defined, and no objective biologically based means of defining availability exist. Because we were interested in the bear population living within Pisgah Bear Sanctuary, we used all habitat types contained within the sanctuary to define availability. Nothing precluded bears from using all habitat classes within the sanctuary. The sanctuary was large enough to comprise all HSI classes, and interspersion of HSI classes throughout the sanctuary was high. Further, the distribution of HSI classes was representative of the full range of habitat classes a bear could encounter in the southern Appalachians. We concluded therefore that this definition of availability minimized the likelihood of bias in our analyses of habitat selection (McClean et al. 1998).

For all habitat selection analyses, we used individual bears as the experimental units. We used linear regression to evaluate the ability of HSI and HSI_2 to predict values of P at two levels of resolution: the bear population and individual bears. To discern habitat selection at the population scale, we averaged values of P for each HSI and HSI_2 class over all bears within each year prior to regression analysis (Proc GLM, SAS Institute 1990). To discern habitat selection on an individual scale, we regressed values of P for individuals against HSI and HSI_2 classes (Proc GLM, SAS Institute 1990). Because bear behavior can vary with sex and maturity (i.e., juvenile or adult), we included these as explanatory variables in the analysis of individual habitat selection. We blocked observations in the final analysis by sex or maturity if either explained a significant (Type III sums of squares $P < 0.05$) amount of variability in the data. To determine whether HSI and HSI_2 predicted the number of bear home ranges that included a given habitat patch, we regressed number of home ranges including each cell against HSI classes assigned to cells (Proc GLM, SAS Institute 1990).

Results

Estimating HSI values and model analysis

We created HSI and HSI_2 maps for Pisgah Bear Sanctuary for each year between and including 1981 to 1994 (e.g., Figure 2*b*). Our maps captured considerably more detail than those prepared for the first evaluation of the HSI (e.g., Figure 2*a*; Powell et al. 1997). The increase in detail was due to our ability to map stands harvested for timber and to map HSI components explicitly using GIS data not available when the HSI was first tested (e.g., digital elevation models and digitized overstory data), thus requiring Powell et al. (1997) to interpolate all 20 components between isolated sampling points.

Sensitivity and elasticity analyses suggested that no component or set of components exerted inordinate influence over the HSI, although components did vary in proportional effects. Sensitivity and elasticity were highest for number of fallen logs (Fy_1), anthropogenic food source (Fy_{2a}), distance between anthropogenic food source and escape cover (Fy_{2c}), distance to nearest road (E_4), and area covered in rhododendron (*Rhododendron* spp.) or mountain laurel (*Kalmia latifolia*; D_2). Variation in all other components had approximately equal effects on final HSI calculations (Table 2).

HSI and habitat selection by bears

We used 127 annual home ranges (38 belonging to adult males, 32 to juvenile males, 55 to adult females, 2 to juvenile females; mean locations per annual home range = 121.5±72.28 [SD]) observed for 81 collared bears (mean number of annual home ranges per bear = 1.56±0.95) in the sanctuary from 1981-1994 to analyze relationships between habitat use and HSI and HSI_2. HSI explained nearly half the variability in habitat selection (*P*), for the bear population ($r^2 = 0.45$, $F_{1,\ 181} = 145.67$, $P = 0.0001$, Figure 3*a*). Neither sex, maturity, nor multiple home ranges from individual bears affected the relationship between habitat use and habitat suitability indices ($P > 0.05$), and blocking was not required. Similar to original analyses (Powell et al. 1997), we found that the relationship between HSI_2 and habitat selection by bears was much stronger on a population scale than for HSI ($r^2 = 0.90$, $F_{1,\ 159} = 1476.53$, $P = 0.0001$, Figure 3*b*). Unlike original analyses, we found both HSI ($r^2 = 0.14$, $F_{1,\ 1617} = 269.18$, $P = 0.0001$, Figure 3*c*) and HSI_2 ($r^2 = 0.62$, $F_{1,\ 1430} = 2327.18$, $P = 0.0001$, Figure 3*d*) predicted habitat selection by individual bears, although not as strongly as at the population scale. The number of home ranges incorporating any given cell correlated positively with both HSI ($F_{1,\ 179} = 15.75$, $P = 0.0001$) and HSI_2 ($F_{1,\ 159} = 13.41$, $P = 0.0003$).

Discussion

Roloff and Kernohan (1999) set out 7 criteria for assessing reliability of habitat models: evaluation of model components, assessment of variability in input data, use of valid comparative tests, use of appropriate spatial scale for testing, evaluation of models across entire range of habitat quality, use of a valid population index for testing, and use of animal data collected over sufficient duration to provide robust tests. We addressed each to the extent practicable in our evaluation of the HSI for the Pisgah Bear Sanctuary.

Roloff and Kernohan (1999) recommended evaluating each of 4 modeling components: assumptions, input variables, relationships between input variables and output, and accuracy of output. Thomasma et al. (1991) stated that 3 underlying assumptions applied to most testing of HSI models: 1) the study site must be within the current range of the animal for which the model was developed, 2) individual animals had unobstructed access to the total area, and 3) the population of animals was unharvested. In our test, assumption 1 was clearly

Table 2. Sensitivity and elasticity of a habitat suitability index for black bears in the Southern Appalachians calculated from data collected in the Pisgah Bear Sanctuary, North Carolina, 1983–1994.

		Sensitivity		Elasticity	
Component	Habitat characteristic sampled	Mean	SD	Mean	SD
Fy_1	Number of fallen logs/ha	−0.044	0.064	−0.087	0.013
Fy_{2a}	Anthropogenic food source	−0.048	0.000	−0.096	0.000
Fy_{2b}	Distance to anthropogenic food source	0.008	0.005	0.015	0.010
Fy_{2c}	Distance between anthropogenic food source and escape cover	−0.048	0.000	−0.096	0.001
Fsp_1	Distance to perennial water	0.004	0.010	0.006	0.018
Fsp_2	Percent cover of *Smilax* spp.	0.004	0.005	0.007	0.009
Fsu_1	Percent cover in berry species	0.016	0.016	0.029	0.030
Fsu_2	Presence of oak species	0.016	0.016	0.029	0.028
Ff_{1a}	Forest cover type	0.004	0.000	0.007	0.000
Ff_{1b}	Age of stand	0.004	0.000	0.007	0.000
Ff_2	Number of grape vines/ha	0.004	0.000	0.007	0.000
Ff_3	Distance to nearest road	0.004	0.000	0.007	0.000
E_1	Area of conterminous forest not bisected by roads	0.004	0.049	0.007	0.089
E_2	Percent closure of understory	0.002	0.042	0.004	0.077
E_3	Slope of terrain	0.011	0.014	0.021	0.026
E_4	Distance to nearest road	−0.084	0.082	−0.154	0.149
D_1	Area of conterminous forest not bisected by roads	0.018	0.043	0.032	0.078
D_2	Area in rhododendron or mountain laurel	0.047	0.023	0.086	0.043
D_3	Slope of terrain	0.006	0.037	0.011	0.068
D_4	Number of trees ≥90 cm DBH[a]/ha	0.006	0.037	0.011	0.068

[a] Diameter breast height.

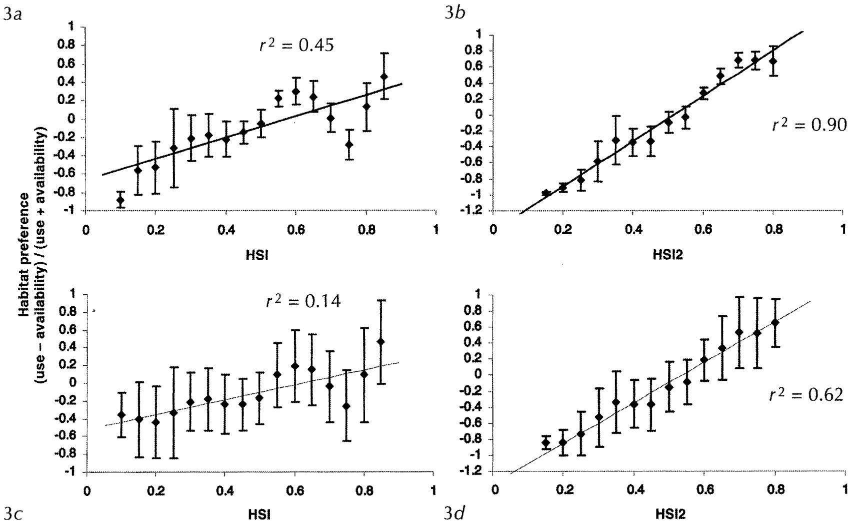

Figure 3. Relationships between habitat use and 2 habitat suitability indices, HSI and HSI_2, for black bears in the Pisgah Bear Sanctuary, Pisgah National Forest, North Carolina. Each figure depicts habitat selection ([use – availability] / [use + availability]) calculated using data from 127 home ranges of black bears living in the Sanctuary from 1981 to 1994. Figures 2*a* and 2*b* depict population-level (average use of habitat classes for bears in each year) selection for classes of HSI and HSI_2, respectively. Figures 2*c* and 2*d* depict individual-level selection (use of habitat classes estimated for each individual bear) for HSI and HSI_2, respectively.

justified. Violation of assumption 2 was unlikely because Pisgah National Forest represented one of the largest blocks of contiguous bear habitat in North Carolina, presenting few obstacles to bear access to habitat. Although we were studying a protected population, several of the 81 collared bears we tracked were known to be poached within the sanctuary ($n=6$) or legally killed by hunters outside the sanctuary ($n=6$) while we were tracking them. Strictly speaking, assumption 3 was therefore violated; however, this assumption can be relaxed for the HSI we evaluated. Thomasma et al. (1991) tested an HSI that did not include effects of human trappers on fisher (*Martes pennanti*) habitat. As such, an evaluation of their HSI on a harvested population would be biased if trapping influenced habitat choices of fishers. The third assumption could therefore be more broadly interpreted to mean that conditions modeled by an HSI must accurately reflect existing conditions for the population used to test the HSI. Because several components of our HSI explicitly modeled effects of exposure to human-caused mortality on bear habitat (e.g., Fy_{2a}, Fy_{2c}, Ff_3, LRV_E, D_1), it was a reasonable model for a population where individuals are occasionally killed by people. We conclude that our test satisfies the intent of assumption 3, and any violation in a strict sense is unlikely to bias our findings.

Because most HSI components were modeled directly from empirical studies, the only assumption we made about the biological validity of the components was that studies on which the components were based were not spurious. We did not directly test this assumption beyond the critical evaluation of those studies during HSI development. Beyond replicating the studies on which the HSI was based in our study area, which would be unrealistic, it is not clear to us how this assumption could be more rigorously evaluated. We assessed the relative effects of individual components on model output with sensitivity and elasticity analyses and demonstrated that HSI output was sensitive to variation in all model components, although not disproportionately to any single component. Strongly disproportional effects among components would indicate the need for discarding those with little effect on model calculations. Considering only relationships between input variables and model output, our results suggested that most components were important to model output and did not indicate that a significantly more parsimonious version of the HSI would make predictions similar to the complete HSI. Finally, we were able to thoroughly assess accuracy of model predictions through tests using independent data on habitat use and home range distribution.

Roloff and Kernohan (1999) identified 2 sources of error in input data that should be assessed: sampling error in assigning values to mapped units and mapping error in depicting mapped units. We did not assess either source of error analytically, in part because of the impracticality of doing so for an HSI as complex as ours. The ground-truthing required to verify assigned values and mapped boundaries would have been daunting for 20 independently modeled HSI components mapped on a 235 km^2 landscape. Nonetheless, the potential for error to bias our observations or to contribute to unexplained variability in P is unknown. We can speculate, however, on the strength of this potential. Only the forest overstory data contained in the USDAFS Continuous Information of Stand Condition (CISC) database consisted of vegetation classes, and because only 4 HSI components were generated using CISC, we were comfortable relying on ground-truthing standards and mapping precision set by the USDAFS. Similarly, we were comfortable with standards set by the United States Geological Survey for Digital Elevation Models and topographical maps from which 9 HSI components were derived. Error might have been more of a factor, however, for the 7 components for which we had no GIS data and mapped using field data (with potential sampling error) through landform modeling or interpolation (with potential for mapping error). This presented a potential concern because the HSI, though not strongly influenced by any component, was relatively sensitive to 2 components mapped using landform modeling and interpolation (Fy_1 and D_2,Table 2). We cannot be certain how sampling or mapping error associated with these components affected the HSI, although as 2 of 20 largely independent components, we expect that their effects were proportionally small. We believe the large number of mainly independent components that were combined to generate the HSI likely mitigated effects of sampling error in any one component.

For all HSI components, we expect that the potential effects of mapping error were in part a function of extent and grain of the maps we generated. Because extent of the landscape we mapped was large relative to the scale at which bears used habitat (235 km^2 compared to an average home range size of 43.3 ± 27.9 km^2; Powell et al. 1997) and because of the large number of home ranges we assessed, the likelihood of isolated mapping errors resulting in consistent bias across habitat classes and bears sampled was probably small. The aggregation of spatial data we used to convert HSI component maps generated at a fine grain (30 × 30 m) to final coarse-grained maps of HSI used for analyses (250 × 250 m) would have reduced effects of sampling error through averaging but also would have increased mapping error for spatial information distributed on a grain finer than 250 × 250 m. We chose the coarser grain for our analyses, however, to match the grain of habitat mapping with our confidence level in bear locations based on telemetry error. Assessing habitat selection at a finer grain would risk spurious findings resulting from telemetry error. Therefore, habitat information depicted at grains finer than 250 × 250 m was essentially irrelevant to our analyses. Grain at which habitat was mapped also corresponded to the biological resolution of questions being asked. We were not seeking to predict fine-scale behaviors of bears corresponding to a fine-grained depiction of habitat (e.g., foraging in a particular berry patch). By addressing habitat selection within annual home ranges, however, we targeted a level of resolution in bear behavior that we deemed appropriate to the confidence we had in our telemetry locations. Our analysis was unlikely to be strongly affected by a coarse-grained depiction of habitat.

Finally, because we modeled the HSI as a continuous surface of pixels, not as polygons representing habitat classes, developing a measure of error such as a confidence interval (Bender et al. 1996) on a pixel-by-pixel basis, particularly for a model as complex as our HSI, became problematic. Although it is conceptually appealing, we do not know of tools to accomplish this.

Our large sample size of animals ($n=127$) using habitat across nearly the full range of the HSI easily satisfied Roloff and Kernohan's (1999) criterion for validity of comparative tests (Johnson 1981), and the 12 years over which our data were collected satisfied their duration criterion. Because our sample size was large and contained a reasonable cross-section of sex and maturity classes (only juvenile females were underrepresented), we have confidence that our findings on habitat selection were representative for all bears living in Pisgah. Our confidence in how HSI could predict the number of home ranges incorporating a patch based on its HSI value, however, is more qualified. These findings were based on the untested assumption that our average annual sample size (approx. 10 bears/yr) was sufficient to ensure no bias from uncollared bears whose home ranges were uncounted in patches we analyzed. Without estimates of bear density that we could compare to number of collared bears each year, we could not be certain this assumption was unviolated; our conclusions on how HSI predicted number of home ranges that included a given patch are therefore tentative.

Because we evaluated the HSI at both the population (an aggregation of home ranges) and individual levels (a large number of home ranges with variable home range sizes), we addressed applicability on multiple spatial scales appropriate to the biological resolution of our questions (e.g., second-order habitat selection, Johnson 1980), satisfying Roloff and Kernohan's (1999) criterion of appropriate spatial scaling. Their requirement for evaluation of an HSI across its entire range of values was nearly satisfied since HSI values for areas of the Pisgah Bear Sanctuary used by bears ranged from 0.1 to 0.85.

Roloff and Kernohan (1999) listed reproductive rate, fecundity, survival, and mortality as appropriate surrogates for fitness in evaluating an HSI. Realistically, data such as those are difficult to collect for a large carnivore such as bears (and for many other animals as well), even in a long-term study such as ours. Fitness, however, can also be inferred indirectly from behavior of animals using the logic that natural selection favors animals that select habitat characteristics which enhance their fitness. Strong theoretical foundations for this approach are based in foraging ecology (optimality) and in empirical research showing that natural selection has molded foraging decisions, patch selection, and time of patch occupation to maximize fitness (or indices of fitness; Pyke et al. 1977, Stephens and Krebs 1986). In fact, this foundation underlies all studies of habitat selection. Although this approach can suffer from significant drawbacks because key assumptions must be made about both behavior of animals and what animals select (Garshelis 2000, Mitchell and Powell 2002), it may be the only viable option for studies unable to collect data on more direct surrogates for fitness. Caution is also warranted if competition or social antagonism among study animals can bias the findings because all animals do not have equal access to all resources. Both traits are common among carnivores, with intrasexual territoriality prevalent among solitary carnivores (Powell 1979). In an analysis of home range overlap, however, Powell (1987) documented broadly overlapping home ranges among adult female bears in Pisgah, with no exclusive use of any part of their home ranges. In a comparison of Pisgah bears to bears living in Minnesota (and known to be territorial; Rogers 1977, 1987), Powell et al. (1997) used an energetic model of territoriality (Carpenter and MacMillen 1976) to predict that Minnesota bears should be territorial whereas southern Appalachians bears should not. Powell et al. (1997) tested this prediction by comparing home range overlap (Lloyd 1967) between Pisgah and Minnesota bears, finding that overlap was significantly higher for Pisgah bears. These findings were consistent with other work on southern Appalachian bears (Garshelis and Pelton 1981). Bears in Pisgah do not appear to be territorial; therefore, we believe the habitat selection patterns we observed were reasonable reflections of fitness-based foraging decisions made without strong influence from social interactions.

Our tests supported Powell et al.'s (1997) conclusion that the HSI captured habitat characteristics important to black bears in the southern Appalachians. Therefore, the HSI could be used by researchers and managers to make meaningful predictions about the behavior of bears and how bears might be distributed on a landscape. No habitat model, however, can capture the relationship between an animal and habitat perfectly because social behavior, reproduction, and other activities also affect use of space, so room exists for improving the HSI. The number of variables in the HSI is high, raising questions about parsimony and ease of use by managers. Strictly from the perspective of how input variables shape HSI calculations, future improvements of the HSI could focus on those components we observed to have the greatest sensitivities and elasticities, although this would not necessarily improve biological meaning of the model. Removing the life requisite variable for escape (LRV_E) from the model to create HSI_2 improved our ability to predict bear behavior, however, suggesting that a more parsimonious model could have more biological meaning, at least in the Pisgah Bear Sanctuary. We do not know whether the greater predictive power for HSI_2 was because LRV_E inaccurately modeled escape resources, whether discarding LRV_E eliminated possible redundancy (area of conterminous forest and slope of terrain are in LRV_D and LRV_E; Table 1), or whether escape resources simply were not limiting to the relatively protected population of bears in the Pisgah Bear Sanctuary. Discerning these factors could be the subject for future work. Further, interrelationships among variables, establishing meaningful confidence limits on an HSI expressed as a continuous surface, and relationships between the HSI and more direct measures of fitness need to be explored. Nonetheless, the primary value of the HSI is that it represents an a priori model of the ecology of black bears that was evaluated and shown to relate strongly to observable characteristics of a bear population. Further refinement of the HSI, also performed in a hypothetico-deductive approach, would therefore refine our understanding of bears.

Beyond the ability to make robust predictions about bear habitat use and its heuristic value for achieving more insights, perhaps the most novel attribute of this HSI is that it is expressed as a continuous surface. Such a depiction makes sense when one considers that the diverse habitat elements a bear requires are distributed in space generally independently of one another. Although a common practice in HSI development is to assign values to vegetation classes thought to contain essential resources, no logical or biological linkage exists between any vegetation class and variables such as percent berry cover, distance to anthropogenic food sources, or number of downed logs. No single habitat classification scheme based on vegetation classes will satisfactorily capture the distribution of these key resources. We suggest that habitat classifications developed by humans which are convenient to land-cover maps often overly abstract important biological information. Further, beyond questions of biological merit, the ability of vegetation classes to model habitat relationships accurately is scale-dependent, whereas modeling resources more directly is not (Mitchell and Powell 2002). We suspect that violation of the assumption that simplistic habitat classes contain critical resources and such a depiction is appropriate to the scale of empirical evaluation probably underlies the poor reputation HSI models have for making robust predictions. We do not necessarily recommend that all habitat models must be complex and exhaustively comprehensive to have validity. However, given that any habitat model such as an HSI directly or indirectly attempts to capture the fitness relationship between an animal and its habitat, we suggest that habitat models will be most robust biologically when they model the distribution of critical resources directly, instead of through abstractions convenient to human classification schemes (Mitchell and Powell 2002).

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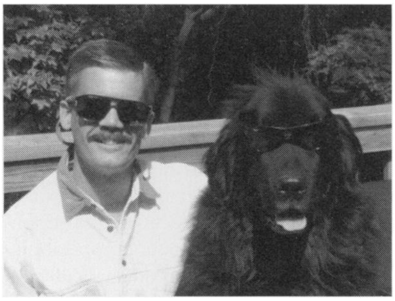

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