

Linking resources with demography to understand resource limitation for bears

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Summary

1. Identifying the resources that limit growth of animal populations is essential for effective conservation; however, resource limitation is difficult to quantify. Recent advances in geographical information systems (GIS) and resource modelling can be combined with demographic modelling to yield insights into resource limitation.

2. Using long-term data on a population of black bears *Ursus americanus*, we evaluated competing hypotheses about whether availability of hard mast (acorns and nuts) or soft mast (fleshy fruits) limited bears in the southern Appalachians, USA, during 1981–2002. The effects of clearcutting on habitat quality were also evaluated. Annual survival, recruitment and population growth rate were estimated using capture–recapture data from 101 females. The availability of hard mast, soft mast and clearcuts was estimated with a GIS, as each changed through time as a result of harvest and succession, and then availabilities were incorporated as covariates for each demographic parameter.

3. The model with the additive availability of hard mast and soft mast across the landscape predicted survival and population growth rate. Availability of young clearcuts predicted recruitment, but not population growth or survival.

4. Availability of hard mast stands across the landscape and availability of soft mast across the landscape were more important than hard mast production and availability of soft mast in young clearcuts, respectively.

5. *Synthesis and applications.* Our results indicate that older stands, which support high levels of hard mast and moderate levels of soft mast, should be maintained to sustain population growth of bears in the southern Appalachians. Simultaneously, the acreage of intermediate aged stands (10–25 years), which support very low levels of both hard mast and soft mast, should be minimized. The approach used in this study has broad application for wildlife management and conservation. State and federal wildlife agencies often possess long-term data on both resource availability and capture–recapture for wild populations. Combined, these two data types can be used to estimate survival, recruitment, population growth, elasticities of vital rates and the effects of resource availability on demographic parameters. Hence data that are traditionally used to understand population trends can be used to evaluate how and why demography changes over time.

Key-words: clearcuts, habitat quality, λ , recruitment, resource limitation, survival, *Ursus americanus*

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Introduction

Understanding resource limitation is critical to effective management and conservation of wild populations (Leopold 1933). A resource is limiting if changes in its availability quantifiably affect population growth (Messier 1991). Resource limitation can be examined by augmenting resource availability for an animal population and estimating the demographic response (Hubbs & Boonstra 1997; Hoodless, Ludiman & Robertson 1999; Hart, Milson, Fisher, Wilkins, Moreby, Murray & Robertson 2006); however, resource augmentation is not always logistically feasible and experimentation has limited spatial and temporal scope (Stephens, Freckleton, Watkinson & Sutherland 2003). An alternative method for examining resource limitation is to link estimates of demographic parameters (e.g. survival, reproduction and population growth) with estimates of resource availability over time (Pennycuik 1969; Skogland 1985; Messier 1991; Langvatn, Albon, Burkey & Clutton-Brock 1996; Mduma, Sinclair & Hilborn 1999).

If a resource is limiting, then an increase in the resource should result in a numerical response, i.e. the rate of increase in animal abundance as a result of enhanced survival, reproduction or both (Solomon 1949; May 1981). Although linking resource availability with survival and reproduction is important (Hudson, Dobson, Cattadori, Newborn, Haydon, Shaw, Benten & Grenfell 2002), resource availability should also be linked with population growth rate (λ ; Bayliss & Choquenot 2002; Hone & Sibly 2002; Sinclair & Krebs 2002; Sutherland & Norris 2002) because individual vital rates may not contribute equally to λ . Adult survival, for example, often contributes most to λ for populations of slow or *K*-selected species, whereas reproduction often contributes most to λ for populations of fast or *r*-selected species (Partridge & Harvey 1988).

Linking estimates of resource availability with individual vital rates (e.g. survival and reproduction) and knowing the contribution of vital rates to variation in λ (i.e. elasticity analyses) provides a way to help understand the magnitude of limitation among resources. If survival has the highest elasticity for a population, then a resource that affects survival should be limiting relative to resources that affect only reproduction. Alternatively, if reproduction has the highest elasticity for a population, then a resource that affects reproduction should be limiting relative to resources that affect only survival.

For this research, we linked estimates of resource availability with estimates of survival, reproduction and λ for a population of black bears in Pisgah Bear Sanctuary (PBS) in western North Carolina, USA, during 1981–2002. Previously, Brongo, Mitchell & Grand (2005) used capture–recapture data to estimate demography of PBS bears, and Brongo (2004) found that adult survival contributed most to variation in λ for PBS bears. Why demographic parameters changed

over time, however, was not evaluated. The goal of this study was to expand upon previous research by assessing the effects of temporal variation in resource availability on individual vital rates and on λ for PBS bears during 1981–2002.

Black bears require the following resources: food, den sites and escape cover. Of these, food is probably most critical to most bear populations (Rogers 1987; Powell, Zimmerman & Seaman 1997), so we focused on food resources. In the southern Appalachian Mountains, black bears eat herbaceous vegetation, squaw root *Conopholis americana*, soft mast (fleshy fruit), hard mast (acorns and nuts), insects and carrion (Beeman & Pelton 1977; Eagle & Pelton 1983). Of these foods, hard mast and soft mast have been shown to affect reproduction and survival of individuals in different bear populations. Hard mast productivity correlated positively with reproduction of individual bears in the southern Appalachian Mountains (Eiler, Wathen & Pelton 1989; Pelton 1989) and New Mexico (Costello, Jones, Inman, Thompson & Quigley 2003), whereas soft mast productivity correlated positively with reproduction of individual bears in Montana (Jonkel & Cowan 1971) and possibly in Arkansas (Clark & Smith 1994). The combined effect of hard mast and soft mast was important to survival and reproduction of individual bears in Minnesota (Rogers 1976, 1987) and Massachusetts (Elowe & Dodge 1989).

No study has linked estimates of hard mast and soft mast availability with estimates of bear λ . Moreover, all previous studies, except Rogers (1987), have lasted ≤ 10 years (mean duration 6 years), which may be too short to accurately estimate bear demography (Brongo *et al.* 2005) and the effects of resources on bear demography (Reynolds-Hogland & Mitchell 2007). Finally, no study has evaluated the relationships between bear demography and availability of hard mast and soft mast as each resource changes through time as a result of disturbance and succession. The goal of our research was to use long-term data (22 years) to link estimates of hard mast and soft mast with estimates of survival, reproduction and λ of bears in PBS to evaluate the following hypotheses: H1, only hard mast limited PBS bears; H2, only soft mast limited PBS bears; H3, both hard mast and soft mast limited PBS bears; H4, neither hard mast nor soft mast limited PBS bears (null model).

Information about resource limitation for black bears may be the key to effective conservation and management, a common goal of which is to manage population growth by manipulating habitat. For example, timber harvesting is often considered a management tool for maintaining bear habitat in the southern Appalachian Mountains because availability of soft mast can be relatively high in recently harvested stands (Noyce & Coy 1990; Perry, Thill, Peitz & Tappe 1999; Reynolds-Hogland & Mitchell 2006). Harvesting trees by clearcutting (i.e. removal of all trees within a stand), however, eliminates production of hard mast for

25–50 years, the time required for regenerating hardwoods to reach reproductive age in the southern Appalachians (Burns & Honkala 1990). Because clearcutting affects availability of soft mast and hard mast differently, the overall effect of clearcutting on habitat quality for a bear population will depend, in part, on whether hard mast, soft mast or both limit the population.

Another goal of this study was to evaluate the effect of clearcutting on habitat quality for black bears. Habitat quality is the capacity of an area to provide resources necessary for survival and reproduction relative to the capacity of other areas (Van Horne 1983). If clearcutting had a positive effect on habitat quality because it provided increased soft mast, we predicted that both availability of soft mast and availability of young clearcuts would help to explain bear reproduction, survival or population growth, and the relationships would be positive. If clearcutting did not have a positive effect on habitat quality because hard mast was removed, we predicted that availability of hard mast would help to explain bear reproduction, survival or population growth, but the availability of young clearcuts would not.

Methods and materials

STUDY SITE

The study was conducted in the PBS (35°17'N, 82°47'W) from 1981 to 2002. The PBS encompasses 235 km² and is nested within the Pisgah National Forest. From 1960 to 2002, 184 older stands (50+ years) were harvested (7688 acres); most (77%) were clearcut. The mean proportion of 50+-year-old stands ranged between 77% and 85% from 1981 to 2002 in PBS. Eighty-eight per cent of PBS contained oak and oak-hickory species, including northern red oak *Quercus rubrus*, southern red oak *Quercus falcata*, white oak *Quercus alba*, chestnut oak *Quercus prinus* and hickory *Carya* spp. Cove hardwoods (*Liriodendron tulipifera*, *Magnolia* spp. and *Betula* spp.) and pine-hemlock (*Pinus rigida*, *Pinus strobus*, *Pinus virginiana* and *Tsuga canadensis*) constituted approximately 4.5% and 3.0%, respectively, of PBS [continuous inventory stand condition (CISC); USDA Forest Service 2001].

The topography of PBS is mountainous, with altitudes ranging from 650 m to 1800 m. The region is considered a temperate rainforest, with annual rainfall approaching 250 cm year⁻¹ (Powell, Zimmerman & Seaman 1997).

TRAPPING BEARS

Bears were captured in PBS from May to mid-August during 1981–2002 (except for 1991 and 1992) using Aldrich foot snares, modified for safety (Johnson & Pelton 1980), or barrel traps. Captured bears were immobilized using a combination of approximately 200 mg ketamine hydrochloride (Fort Dodge Animal Health, Fort Dodge, IA) + 100 mg xylazine hydrochloride

(Phoenix Pharmaceutical Inc., St Joseph, MO) 90 kg⁻¹ body mass (Cook 1984), or telazol (Wyeth Holdings Corporation, Carolina, Puerto Rico) administered with a blow dart or jab stick. Immobilized bears were sexed, weighed, measured, tattooed and had two ear tags attached. All procedures complied with the requirements of the Institutional Animal Care and Use Committees for Auburn University (IACUC 0208-R-2410; Auburn, AL) and North Carolina State University (IACUC 96–011; Raleigh, NC).

MODELLING DEMOGRAPHIC PARAMETERS

Encounter histories, based on a 1-year time interval, were created for each female bear captured during 1981–2002. The temporal symmetry survival and recruitment model (Pradel 1996) in program MARK (White & Burnham 1999) was used to estimate annual apparent survival (the probability that the animal is alive and remains on the study area and hence is available for recapture; ϕ), annual recruitment (proportion of females added to the breeding population over a specified period of time; f) and annual recapture probability (p). Survival and its complement, seniority (the parameter used to estimate recruitment), were bounded between 0 and 1, so the logit link was used to develop models of survival and recruitment. Based on preliminary analyses, the fully time varying model (ϕ_t, f_t, p_t) did not perform well, so annual ϕ and f were estimated using model averaging in program MARK, based on seven models with different time intervals (2, 3, 4, 5, 7, 10 and 21 years; Brongro *et al.* 2005). For example, the 2-year model had 11 time intervals, each 2 years long. The objective was to balance increased precision associated with short time intervals while still capturing as many of the short-term dynamics as possible that were associated with longer time intervals. ϕ and f were constrained to be equal among years within time intervals, but they were allowed to vary among time intervals. Because we were not specifically interested in estimates of recapture rate, those estimates were allowed to vary annually (Cooch & White 2002). After model averaging, realized λ was calculated for each year as the sum of estimated annual ϕ and f .

Apparent survival does not account for immigration or emigration, but we assumed our study population was closed because female black bears rarely disperse (Elowe & Dodge 1989; Powell *et al.* 1997). Consequently, recruitment represented primarily the proportion of female cubs per female added to the population that survived to be old enough for capture. Because a goodness-of-fit test does not currently exist for the temporal symmetry parameterization (Cooch & White 2002), a bootstrap approach, based on the Cormack–Jolly–Seber model, was used to calculate \hat{c} -hat (Franklin, Anderson, Gutierrez & Burhnam 2004).

To evaluate whether the observed temporal variation in vital rates could be explained by resource availabilities that changed over time, annual estimates of resource

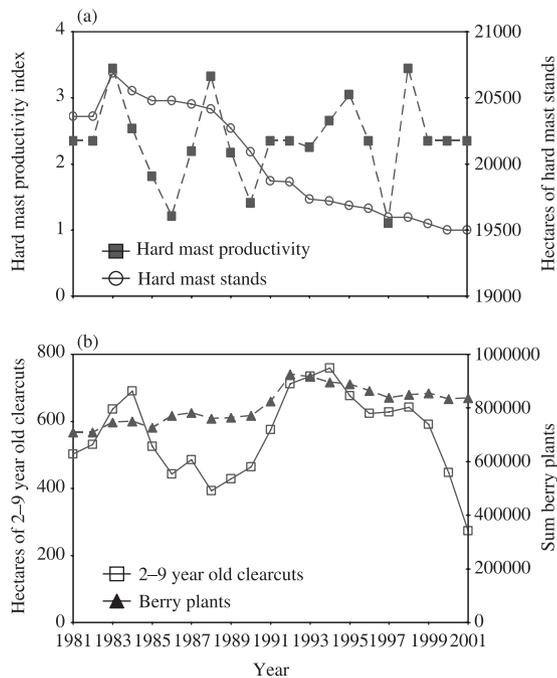


Fig. 1. Availability of hard mast and soft mast in Pisgah Bear Sanctuary, North Carolina, USA, 1981–2001. (a) Index of hard mast production for western North Carolina (data from North Carolina Wildlife Resources Commission) and availability of stands most likely to produce hard mast (hectares of stands with $\geq 70\%$ hard mast producing trees and ≥ 50 years old). (b) Availability of berry plants (sum cover of huckleberry, blueberry and raspberry plants) and availability of stands most likely to produce soft mast (hectares of 2–9-year-old clearcuts).

covariates were linked with annual estimates of each demographic parameter. All covariates were standardized so that effects among covariates would be relative. A suite of models was developed for predicting the log linear relationship between realized λ and annual availability of resource covariates (SAS Institution Inc. 2002). The intercept-only model was considered the null model. Akaike's information criterion, with an adjustment for small sample bias (AIC_c ; Akaike 1973; Anderson, Burnham & White 1994), was used to rank the models in terms of their ability to explain the data. Models with ΔAIC_c values < 2.0 were considered to have substantial support (Burnham & Anderson 2002). Akaike weights were evaluated for each model, and slope estimates were evaluated for model variables. A similar approach was used to develop and rank a suite of models for predicting the effects of resource covariates on both survival rates and recruitment rates, except that the linear relationships were evaluated.

COVARIATES: ANNUAL AVAILABILITY OF HARD MAST AND SOFT MAST

Annual variability in hard mast production was estimated using an index estimated annually by the North Carolina Wildlife Resources Commission (NCWRC, Raleigh, NC) for the Pisgah National Forest. NCWRC

measured mast production of northern red oak, southern red oak, white oak, hickory and beech (*Fagus* spp.) trees and calculated an index of production for each year (except 1981 and 1982) for each species and for all species combined (Warburton 1995). Because bears consume acorns and nuts from several hard mast species (Beeman & Pelton 1977), the annual index for all species combined was used (Fig. 1a).

Most previous studies that have evaluated the effect of hard mast on reproduction or survival of individual bears have done so by considering only annual variability in hard mast production (Rogers 1976, 1987; Eiler *et al.* 1989; Elowe & Dodge 1989; Pelton 1989; Costello *et al.* 2003) but availability of hard mast should also be a function of availability of stands that produce hard mast. The following criteria were used to model the distribution of stands most likely to produce hard mast in PBS. Stands had to: (i) have at least 70% hardwoods in which hard mast species were dominant (USDA Forest Service stand codes 51–57, 59 and 60; CISC database; USDA Forest Service 2001); (ii) be between 50 and 100 years old, because most oak and hickory species, which comprise approximately 85% of PBS stands, are maximally productive in the Southern Appalachians when they are that age (Burns & Honkala 1990). A geographic information system (GIS; ArcView 3.2 and Spatial Analyst 2.0) and the CISC database were used to calculate the area (ha) of these stands in PBS for each year from 1981 to 2001 (Fig. 1a). Because of the constraints of the CISC database, we did not map availability of hickory stands separately from availability of different oak stands (e.g. northern red oak and southern red oak). If bears prefer one mast species over the others, then our estimates of hard mast availability may not reflect what is both available to and preferred by bears.

Hard mast availability should be a function of both hard mast production and availability of stands that produce hard mast. Therefore the interaction between hard mast production and availability of hard mast stands was considered a covariate to each demographic parameter.

Annual availability of berry plants across the PBS landscape, as it changed as a result of clearcuts (the primary harvest technique used during 1900–2002 in PBS) and succession, was estimated based on field data. The genera producing the majority of berries during the summer months in PBS were raspberries and blackberries *Rubus* spp., huckleberries *Gaylussacia* spp. and blueberries *Vaccinium* spp. (Powell *et al.* 1997), which were important foods for black bears in the southern Appalachians (Beeman & Pelton 1977; Eagle & Pelton 1983). Therefore, availability of these genera was estimated. A suite of models for predicting percentage plant cover of *Gaylussacia*, *Vaccinium* and *Rubus* spp. plants, measured in 100 randomly selected clearcuts (harvested 0–122 years ago), was developed using stand age, slope, altitude, aspect, curvature of the land, plane of the curvature, profile of the curvature and distance to water (for methods see Reynolds-Hogland & Mitchell 2006).

The best approximating model (stand age, slope, altitude, stand age⁻¹, slope², stand age^{-1/2}, distance to water; AIC = 0, $r^2 = 0.47$) and a GIS were used to map the distribution of berry plants in PBS, at a 30-m resolution, for each year from 1981 to 2001. The annual availability of berry plants in PBS was estimated as the sum of berry plant cover within all 30-m cells. Although values were without units, they were useful for comparing availability of berry plants across years (Fig. 1b).

Annual variability in berry production was not estimated because sufficient data to estimate berry production were lacking for most of the years 1981–2001. Field data on berry production were collected in PBS (Powell *et al.* 1997) but only for 12 of the 21 years of our study. Based on analysis of the 12-year data set, berry production did not differ statistically among years (Proc GLM; $F_{11,85} = 0.67$, $r^2 = 0.09$, $P > 0.65$; M. Reynolds-Hogland, unpublished data).

To evaluate the effect of clearcutting on habitat quality, the distribution of clearcuts most likely to produce soft mast was estimated because the change in availability of these stands could have affected survival, recruitment or λ if soft mast limited PBS bears. Based on field data collected on *Gaylussacia*, *Vaccinium* and *Rubus* spp. within 100 randomly selected clearcuts (0–122 years old) in PBS, both cover in berry plants and berry production were highest in 2–9-year-old clearcuts (Reynolds-Hogland & Mitchell 2006). A GIS and the CISC database were used to calculate the area (ha) of 2–9-year-old clearcuts for each year from 1981 to 2001 (Fig. 1b).

If both hard mast and soft mast limited PBS bears, their additive or interactive effects may have been important to demography. Therefore the additive and interactive effects between availability of hard mast stands and availability of berry plants were considered covariates. Similarly, the additive and interactive effects between availability of hard mast stands and availability of young clearcuts were considered covariates. The interactive effects of hard mast production and soft mast production were not evaluated because sufficient data on berry production were lacking.

Table 1. Ranking of models of apparent survival, each with different covariates of hard mast and soft mast, for the female population of black bears in Pisgah Bear Sanctuary, North Carolina, USA, during 1981–2002. Sample size was $n = 21$ years

Model	ΔAIC_c	AIC _c weights	Model likelihood
Hard mast stands × berry plants	0.00	0.47	1.00
Berry plants	0.05	0.46	0.98
Hard mast stands + berry plants	5.03	0.04	0.08
Hard mast stands	7.74	0.01	0.02
Null	7.76	0.01	0.02
Availability of young clearcuts × hard mast stands	8.19	0.01	0.02
Availability of young clearcuts	8.85	0.01	0.01
Availability of young clearcuts + hard mast stands	9.46	0.00	0.01
Hard mast production	10.09	0.00	0.01
Hard mast stands × hard mast production	12.79	0.00	0.00

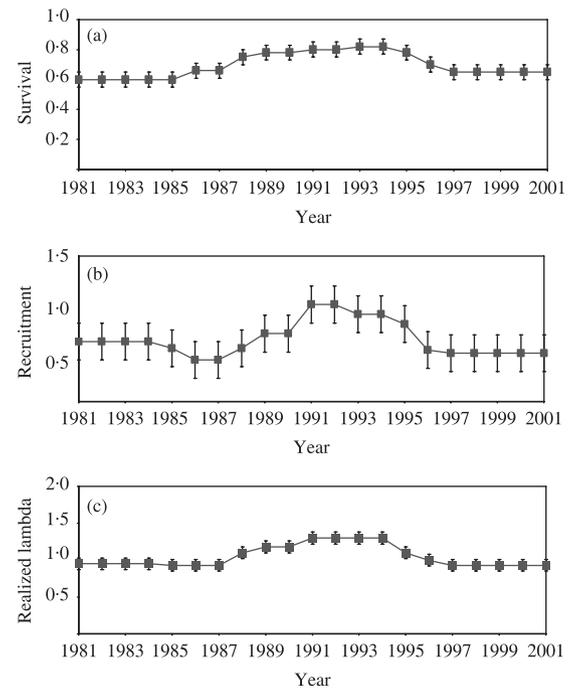


Fig. 2. Estimates of (a) survival, (b) recruitment and (c) realized population growth rate, calculated as the weighted average of all models, with SE bars, for the population of black bears in the Pisgah Bear Sanctuary, North Carolina, USA, 1981–2002 (Brongo, Mitchell & Grand 2005).

Results

SURVIVAL

During 1981–2002, we captured 101 tagged females 194 times. We used 500 simulations to test goodness-of-fit. The estimate of \hat{c} was 1.3, which when adjusted did not change the rankings of the survival models, each of which was based on different time intervals (Brongo *et al.* 2005). Annual estimates of survival based on model averaging indicated that survival was low at the beginning of the study, increased in the middle years, and then decreased near the end of the study (Fig. 2a; Brongo *et al.* 2005). Survival for year t represented the probability of surviving from year t to year $t + 1$.

When resource covariates were used to develop a suite of models to explain survival, two models had ΔAIC_c values < 2.0 (Table 1). The top-ranked model incorporated the interaction between hard mast stands and berry plants across the landscape as a covariate. The second-ranked model included berry plants across the landscape as a covariate. As strength of evidence for model selection, the AIC_c weights for the top two models were 0.47 and 0.46, respectively, indicating that the top two models were 11.75 times more likely to be selected over the null model (AIC_c weight = 0.04). The slope estimates for the top two models were positive and significant (i.e. zero was not in the 95% confidence interval; Table 2).

Table 2. Estimates of slope (with 95% confidence intervals; CL) for model variables in top models of apparent survival and recruitment in order of rank, for the female population of black bears in Pisgah Black Bear Sanctuary, North Carolina, USA, during 1981–2002

Model*	Slope†	Slope lower CL	Slope upper CL
Survival			
Hard mast stands × berry plants			
Hard mast stands	0.09	0.05	0.14
Berry plants	0.05	0.01	0.09
Interaction term	0.08	0.01	0.15
Berry plants	0.05	0.02	0.08
Recruitment			
Availability of young clearcuts			
Hard mast stands + berry plants	0.09	0.03	0.15
Hard mast stands	0.10	0.01	0.20
Berry plants	0.16	0.06	0.26

*Only models with $\Delta AIC_c < 2.0$ are shown.

†Models with additive or interaction terms have more than one slope estimate.

RECRUITMENT

Annual estimates of recruitment based on model averaging indicated that recruitment was low at the beginning of the study, decreased and then increased in the middle years, and then decreased again near the end of the study (Fig. 2b; Brongro *et al.* 2005).

Table 3. Ranking of models of recruitment, each with different covariates of hard mast and soft mast, for the female population of black bears in Pisgah Bear Sanctuary, North Carolina, USA, during 1981–2002. Sample size was $n = 21$ years

Model	ΔAIC_c	AICc weights	Model likelihood
Availability of young clearcuts	0.00	0.49	1.00
Hard mast stands + berry plants	2.00	0.18	0.37
Berry plants	2.37	0.15	0.31
Hard mast stands × berry plants	4.83	0.04	0.09
Availability of young clearcuts + hard mast stands	4.83	0.04	0.09
Availability of young clearcuts × hard mast stands	6.37	0.02	0.04
Hard mast stands	6.38	0.02	0.04
Null	6.60	0.02	0.04
Hard mast production	6.74	0.01	0.03
Hard mast stands × hard mast production	12.09	0.00	0.00

Table 4. Ranking of models of population growth rate, each with different covariates of hard mast and soft mast, for the female population of black bears in Pisgah Bear Sanctuary, North Carolina, USA, during 1981–2002. Sample size was $n = 21$ years

Model	ΔAIC_c	AICc weights	Model likelihood
Hard mast stands + berry plants	0.00	0.41	1.00
Berry plants	0.50	0.31	0.77
Hard mast stands × berry plants	1.91	0.15	0.38
Availability of young clearcuts	3.85	0.06	0.15
Null	5.64	0.02	0.06
Availability of young clearcuts + hard mast stands	6.54	0.01	0.03
Hard mast stands	7.34	0.01	0.03
Availability of young clearcuts × hard mast stands	7.49	0.01	0.02
Hard mast production	8.31	0.01	0.02
Hard mast stands × hard mast production	12.64	0.00	0.00

Table 5. Estimates of slope (with 95% confidence intervals; CL) for model variables in top models of population growth rate in order of rank, for the female population of black bears in Pisgah Black Bear Sanctuary, North Carolina, USA, during 1981–2002

Model*	Slope†	Slope lower CL	Slope upper CL
Hard mast stands + berry plants			
Hard mast stands	0.09	0.01	0.17
Berry plants	0.17	0.07	0.27
Berry plants	0.09	0.03	0.15
Hard mast stands × berry plants			
Hard mast stands	0.11	0.03	0.19
Berry plants	0.18	0.08	0.28
Interaction term	0.08	−0.07	0.23

*Only models with $\Delta AIC_c < 2.0$ are shown.

†Models with additive or interaction terms have more than one slope estimate.

When resource covariates were used to develop a suite of models to explain recruitment, two models had ΔAIC_c values < 2.0 . The top-ranked model incorporated availability of soft mast in clearcuts (Table 3). The second-ranked model included the additive availability of hard mast stands and berry plants across the landscape. The null model ranked low and had low model weight. Slope estimates for all components of the top two models were positive and significant (Table 2). As strength of evidence for model selection, the AIC_c weight for the top model was 0.49, indicating it was 2.7 times more likely to be selected over the second-ranked model and 24 times more likely to be selected over the null model (AIC_c weight = 0.02). All models with only hard mast covariates ranked relatively low and had low AIC_c weights.

POPULATION GROWTH

Annual estimates of λ based on model-averaged survival and recruitment rates indicated that λ was low at the beginning of the study, increased in the middle years, and then decreased near the end of the study (Fig. 2c; Brongro *et al.* 2005).

When resource covariates were used to develop a suite of models to explain λ , three models had ΔAIC_c values < 2.0 (Table 4). The top-ranked model incorporated the additive availability of hard mast stands and availability of berry plants across the landscape, the second-ranked model included availability of berry plants across the landscape and the third-ranked model included the interaction between availability of hard mast stands and availability of berry plants across the landscape. As strength of evidence for model selection, the top model (AIC_c weight = 0.41) was 1.32 times more likely to be selected than the second-ranked model and 20 times more likely to be selected over the null model. Slope estimates for all components of the top two models were positive and significant (Table 5). The interaction term in the third-ranked model was not significant (Table 5).

Discussion

Understanding how and why the demography of wild animals changes over time is critical to effective conservation and management of wild populations. (Hudson *et al.* 2002; Sutherland & Norris 2002). Although it is generally agreed that food supply usually determines population growth rate for most vertebrate populations (Sinclair & Krebs 2002), it is unclear how particular foods affect the demography for many species. Until we understand which food resources are and are not limiting to wild animals, management efforts are likely to be ineffective.

Comprehensive understanding of resource limitation requires estimating population growth (Bayliss & Choquenot 2002; Hone & Sibly 2002; Sinclair & Krebs 2002; Sutherland & Norris 2002), which can be calculated as either a function of animal abundance or a function of survival and reproduction. Estimating animal abundance is rife with problems (Krebs 2002), however, and collecting reproduction data on wild animals can be time and cost prohibitive. If capture–recapture data are available, the Pradel model in program MARK provides a way to estimate both survival and recruitment when reproduction data are lacking (Pradel 1996). Subsequently, estimates of survival and recruitment can be used to calculate realized λ , without estimating animal abundance. Each demographic parameter can then be linked with estimates of resource availability to yield insights into resource limitation.

This approach has broad application for wildlife management, the goal of which is often to manipulate population growth by managing habitat. Both state and federal wildlife agencies typically collect data documenting species presence, many data sets include capture–recapture information and many studies are long-term. Traditionally, these data have been used in a limited fashion to understand population trends, but such analyses can be expanded to estimate survival, recruitment, population growth and elasticities of vital rates. Because wildlife agencies often also collect data on wildlife habitats and resources, they have the data necessary to evaluate resource limitation. Even when data on annual production of resources are lacking, recent advances in GIS and resource modelling make it possible to estimate temporal and spatial changes in resource availability over time so that estimates of demography may be linked with estimates of resource availability. Results from such analyses can help streamline conservation efforts to increase endangered species or maintain game species.

When we linked resource availability with demographic parameters for black bears, the data supported the hypothesis that both hard mast and soft mast limited PBS bears during 1981–2002. The model with the additive availability of hard mast stands and berry plants across the landscape ranked highest for λ . Moreover, the model with the interaction between hard mast stands and berry plants across the landscape ranked

high for survival. These results indicate that conservation efforts to maintain or increase λ for bears in the southern Appalachians should focus on maintaining the availability of both hard mast and soft mast. This objective may be achieved by increasing or maintaining the acreage of oak stands >70 years old, which can support high levels of hard mast (Burns & Honkala 1990) and intermediate levels of soft mast (Reynolds-Hogland & Mitchell 2006). Another way to maximize both hard mast and soft mast is to minimize the acreage of stands between 10 and 25 years old, which support very low levels of both soft mast (Reynolds-Hogland & Mitchell 2006) and hard mast (Burns & Honkala 1990).

Other studies that have linked food availability with demography of mammals have also found that variability in foods predicted vital rates. Grass production predicted wildebeest *Connochaetes taurinus* survival and reproduction (Mduma *et al.* 1999), lichen cover predicted reindeer *Rangifer tarandus* survival and reproduction (Skogland 1985) and climate (a surrogate for food availability) predicted red deer *Cervus elaphus* reproduction (Langvatn *et al.* 1996). These studies evaluated the influence of density-dependent processes, which we could not assess because we were unable to estimate population density accurately. We could, however, determine that PBS bears were unlikely to be near carrying capacity (K) because they did not demonstrate territorial behaviour (Powell *et al.* 1997). Because density-dependent influences for populations of large mammals should be strongest when populations are high or near K (Sinclair & Krebs 2002), and PBS bears were probably not near K, the results we found regarding the effects of resources on demography were probably little influenced by density dependence. Nevertheless, future research on bears should strive to combine the effects of extrinsic factors (e.g. resource limitation) on demography with the effects of intrinsic factors (e.g. density dependence).

Our results regarding the effects of clearcutting on the demography of PBS bears were mixed and therefore are best understood within the context of life history. For the bears in our study, Brongo (2004) found that adult survival was the vital rate with the greatest potential to contribute to future changes in λ . Hence resources that affect bear survival are more likely to be limiting compared with resources that affect only bear reproduction. The availability of young clearcuts predicted recruitment of PBS bears but not survival or λ (Tables 1, 3 and 4). This finding is probably the result of the fact that young clearcuts can support relatively high availability of soft mast (Noyce & Coy 1990; Perry *et al.* 1999; Reynolds-Hogland & Mitchell 2006) but they provide no hard mast. Even the additive availability of young clearcuts and hard mast stands across the landscape, however, had very low predictive power, indicating that the availability of soft mast across the landscape was more important than was the availability of soft mast in only young clearcuts. Clearly, young clearcuts contribute to the overall availability of soft

mast on the landscape, but correlation analyses revealed that young clearcuts explained only 25% of the variability in berry plants across the landscape ($F_{1,20} = 6.40$, $r^2 = 0.25$, $P = 0.02$). Changes in the availability of berry plants across the landscape were also the result of succession, as intermediate aged stands, where soft mast availability is very low (Noyce & Coy 1990; Reynolds-Hogland & Mitchell 2006), age into older stands, where soft mast availability is intermediate (Noyce & Coy 1990; Reynolds-Hogland & Mitchell 2006).

No other study has evaluated the effects of clearcuts on habitat quality for bears using bear survival, recruitment or λ . Instead, previous studies have examined habitat selection for clearcuts by bears to infer the effects of clearcuts on habitat quality for bears. The results have been conflicting: bears have been shown to both select (Jonkel & Cowan 1971; Costello & Sage 1994; Samson & Hout 1998) and avoid (Clark, Clapp, Smith & Ederington 1994; Unsworth, Beecham & Irby 1989; Mitchell & Powell 2003) young clearcuts. Because habitat use may not have demographic consequences for animal populations (Sutherland 1998; Gill, Norris & Sutherland 2001; Morrison 2001), future studies evaluating the effects of disturbances on bear habitat should use direct measures of fitness. Studies that evaluate habitat use instead should address explicitly the assumed linkage between habitat selection and fitness before inferring effects of habitat change.

We found that models with only hard mast covariates ranked low for all demographic parameters. Our results corroborate findings regarding bear reproduction by Clark & Smith (1994) and Kasbohm, Vaughn & Kraus (1996) but conflict with results of Eiler *et al.* (1989), Costello *et al.* (2003) and Pelton (1989). Most previous studies (Eiler *et al.* 1989; Pelton 1989; Clark & Smith 1994; Kasbohm *et al.* 1996) have not examined the effect of hard mast on bear reproduction relative to the effect of hard mast + soft mast. Had they considered the multiple hypotheses that we evaluated, they may have found that the combined availability of hard mast and soft mast was a better predictor of reproduction compared with the availability of hard mast alone.

Hard mast production did not predict any demographic parameter, which may have occurred if complete crop failures were uncommon in PBS. Beck (1977) and Beck & Olson (1968) examined acorn productivity in the southern Appalachian Mountains from 1962 to 1973 and found production of white oaks peaked about every 4 years while production of red oaks peaked about every 5 years. Hence complete crop failures were unlikely because large crops of acorns from white oaks compensated for small crops from red oaks and vice versa. During our study, white oaks produced small crops during 1989 that were offset by large crops during 1989 from red oaks (NCWRC). Similarly, red oaks produced small crops during 1987 and 2003 that were offset by large crops from beech and hickory during 1987 and 2003 as well as moderate crops from white oak.

That availability of hard mast stands predicted survival, recruitment and λ (when combined with availability of soft mast) yet hard mast productivity did not highlight the importance of estimating resource availability in terms of not only production but also availability across landscapes. Had we estimated only hard mast production, which is the traditional approach, we would have failed to detect an effect of hard mast on bear demography.

Our results provide interesting insights into resource limitation. For a resource to limit λ , positive changes in its availability must affect λ (Messier 1991), which typically happens only when a resource is in relatively short supply (Ricklefs 1993). If supply of resource i is greater than demand for resource i , changes in its availability are unlikely to affect λ . Because changes in availability of hard mast stands and berry plants predicted λ and their slopes were positive, their availabilities in PBS from 1981 to 2001 were probably in short supply for bears. Alternatively, changes in availability of 2–9-year-old clearcuts did not predict λ , so this resource was probably not in short supply. From 1981 to 2001, the proportion of PBS that comprised 2–9-year-old clearcuts was small (mean 2%, SD 0.05%) compared with the proportion of PBS that comprised stands most likely to produce hard mast (mean 82%, SD 2%). Yet 2–9-year-old clearcuts were probably not in short supply whereas hard mast stands probably were. Such counterintuitive results not only provide insights regarding the resource limitation of PBS bears, but also demonstrate the folly of assuming a resource that occurs in relatively small amounts is necessarily limiting.

We did not include estimates of annual berry productivity, which may have affected our ability to fit models that included estimates of soft mast. Although berry production in PBS did not differ statistically among the 12 years for which we had berry production data (M. Reynolds-Hogland, unpublished data), biological differences in annual berry productivity may have existed that we were unable to detect. If so, and if annual variability in berry production influenced bear demography, then our results regarding the predictability of soft mast were biased low. In addition, we used availability of hard mast stands to represent hard mast, but other bear resources (e.g. den sites and escape cover) may also have been available in hard mast stands. The positive relationship that we found between availability of hard mast stands and bear demography could therefore indicate the importance of hard mast stands beyond their capacity to provide food. Because we did not use controls nor did we replicate our study, sufficient causation could not be established and results may have been biased given that the time series data were autocorrelated (Bjornstad & Grenfell 2001).

Finally, estimates of λ are necessarily a function of survival, reproduction, emigration and immigration. Therefore these demographic estimates are not independent. One way to address lack of independence is

to develop a model using one data set (e.g. DNA data) and then test the model using another data set (e.g. capture–recapture data). We did not have multiple data sets, so our results should be tested using data independent from the capture–recapture data we used.

CONCLUSION

Linking resource availability with individual vital rates and λ can yield information about resource limitation for wild populations. Moreover, this approach can be used to understand the effects of disturbance (e.g. clearcuts and roads) on population demography. When combined with information on elasticities of vital rates, this approach can be a powerful tool for wildlife conservation and management.

Our results for bears in the southern Appalachians suggest that older stands, which support high levels of hard mast and moderate levels of soft mast, should be maintained to sustain population growth of bears in the southern Appalachians. Simultaneously, the acreage of intermediate aged stands, which support very low levels of both hard mast and soft mast, should be minimized.

A long-term, landscape-level approach should be used to manage bear habitat. Soft mast in older stands may represent a relatively reliable resource for bears and managers who use clearcuts as a tool to manipulate bear habitat, therefore should balance the short-term temporary increases of soft mast with the subsequent reductions in overall availability of soft mast across the landscape as young clearcuts age. From a methodological point of view, we recommend that studies that evaluate resource limitation do so by including estimates of both resource productivity and resource availability across the landscape.

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References

- Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. *Proceedings of the 2nd International Symposium on Information Theory* (eds B. Petrov & F. Cazakil), Akademiai Kiado, Budapest, Hungary.
- Anderson, D.R., Burnham, K.P. & White, G.C. (1994) AIC model selection in overdispersed capture–recapture data. *Ecology*, **75**, 1780–1793.
- Bayliss, P. & Choquenot, D. (2002) The numerical response: rate of increase and food limitation in herbivores and predators. *Philosophical Transactions of the Royal Society of London B*, **357**, 1233–1248.
- Beck, D.E. (1977) *Twelve-year Acorn Yield in Southern Appalachian Oaks*. Research Note SE-244. USDA Forest Service, Southeast Forest Experiment Station, Asheville, NC.
- Beck, D.E. & Olson, D.F. Jr (1968) *Seed Production in Southern Appalachian Oak Stands*. Research Note SE-91. USDA Forest Service, Southeast Forest Experiment Station, Asheville, NC.
- Beeman, L.E. & Pelton, M.R. (1977) Seasonal foods and feeding ecology of black bears in the Smoky Mountains. *International Conference on Bear Research and Management*, **4**, 141–147.
- Bjornstad, O.N. & Grenfell, B.T. (2001) Noisy clockwork: time series analysis of population fluctuations in animals. *Science*, **293**, 638–643.
- Brongo, L.L. (2004) *Demography of black bears in the Pisgah Bear Sanctuary*. MS Thesis. Auburn University, Auburn, AL.
- Brongo, L.L., Mitchell, M.S. & Grand, J.B. (2005) Long-term analysis of a population of black bears with access to a refuge. *Journal of Mammalogy*, **86**, 1029–1035.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference*. Springer-Verlag Inc., New York, NY.
- Burns, R.M. & Honkala, B.H. (1990) *Silvics of North America*. US Department of Agriculture, Forest Service, Washington, DC.
- Clark, J.D. & Smith, K.G. (1994) A demographic comparison of two black bear populations in the interior highlands of Arkansas. *Wildlife Society Bulletin*, **22**, 593–603.
- Clark, J.D., Clapp, E.L., Smith, K.G. & Ederington, B. (1994) Black bear habitat use in relation to food availability in the interior highlands of Arkansas. *International Conference of Bear Research and Management*, **9**, 309–318.
- Cooch, E. & White, G.C. (2002) *Using mark: A Gentle Introduction*, 3rd edn. Cornell and Colorado Cooperative Fish and Wildlife Research Units, Ithaca, NY.
- Cook, B. (1984) Chemical immobilization of black bears in Great Smokey Mountains National Park. *Proceedings of the Eastern Workshop on Black Bear Research and Management*, **7**, 79–81.
- Costello, C.M. & Sage, R.W. (1994) Predicting black bear habitat selection from food abundance under three forest management systems. *International Conference on Bear Research and Management*, **9**, 375–387.
- Costello, C.M., Jones, D.E., Inman, R.M., Inman, K.H., Thompson, B.C. & Quigley, H.B. (2003) Relationship of variable mast production to American black bear reproductive parameters in New Mexico. *Ursus*, **14**, 1–16.
- Eagle, T.C. & Pelton, M.R. (1983) Seasonal nutrition of black bears in the Great Smoky Mountains National Park. *International Conference on Bear Research and Management*, **5**, 94–101.
- Eiler, J.H., Wathen, W.G. & Pelton, M.R. (1989) Reproduction in black bears in the southern Appalachian Mountains. *Journal of Wildlife Management*, **53**, 353–360.
- Elowe, K.D. & Dodge, W.E. (1989) Factors affecting black bear reproductive success and cub survival. *Journal of Wildlife Management*, **53**, 962–968.

- Franklin, A.B., Anderson, D.R., Gutierrez, R.J. & Burhnam, K.P. (2004) Population dynamics of the California spotted owl: a metaanalysis. *Ornithological Monograph*, **54**, 1–555.
- Gill, J.A., Norris, K. & Sutherland, W.J. (2001) Why behavioral responses may not reflect the population consequences of human disturbance. *Biological Conservation*, **97**, 265–268.
- Hart, J.D., Milson, T.P., Fisher, G., Wilkins, V., Moreby, S.J., Murray, A.W.A. & Robertson, P.A. (2006) The relationship between yellowhammer breeding performance, arthropod abundance, and insecticide applications on arable farmlands. *Journal of Applied Ecology*, **43**, 81–91.
- Hone, J. & Sibly, R.M. (2002) Demographic, mechanistic, and density-dependent determinants of population growth rate: a case study in an avian predator. *Philosophical Transactions of the Royal Society of London B*, **357**, 1171–1177.
- Hoodless, A.N., Draycott, R.A.H., Ludiman, M.N. & Roberston, P.A. (1999) Effects of supplementary feeding on territoriality, breeding success, and survival of pheasants. *Journal of Applied Ecology*, **36**, 147–156.
- Hubbs, A.H. & Boonstra, R. (1997) Population limitation in arctic ground squirrels: effects of food and predation. *Journal of Animal Ecology*, **66**, 527–541.
- Hudson, P.J., Dobson, A.P., Cattadori, I.M., Newborn, D., Haydon, D.T., Shaw, D.J., Benton, T.G. & Grenfell, D.T. (2002) Trophic interactions and population growth rates: describing patterns and identifying mechanisms. *Philosophical Transactions of the Royal Society of London B*, **357**, 1259–1271.
- Johnson, K.G. & Pelton, M.R. (1980) Prebaiting and snaring techniques for black bears. *Wildlife Society Bulletin*, **8**, 46–54.
- Jonkel, C.J. & Cowan, I.M. (1971) *The Black Bear in the Spruce-Fir Forest*. Wildlife Monograph, **27**, 1–57.
- Kasbohm, J.W., Vaughan, M.R. & Kraus, J.G. (1996) Effects of gypsy moth infestation on black bear reproduction and survival. *Journal of Wildlife Management*, **60**, 408–416.
- Krebs, C.J. (2002) Two complementary paradigms for analyzing population dynamics. *Philosophical Transactions of the Royal Society of London B*, **357**, 1211–1219.
- Langvatn, R., Albon, S.D., Burkey, T. & Clutton-Brock, T.H. (1996) Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. *Journal of Animal Ecology*, **65**, 653–670.
- Leopold, A. (1933) *Game Management*. C. Scribner's Sons, New York, NY.
- May, R. (1981) Models for two interacting populations. *Theoretical Ecology* (ed. R. May), pp. 78–104. Sinauer, Sunderland, MA.
- Mduma, S.A.R., Sinclair, A.R.E. & Hilborn, R. (1999) Food regulates the Serengeti wildebeest: a 40-year record. *Journal of Animal Ecology*, **68**, 1101–1122.
- Messier, F. (1991) The significance of limiting and regulating factors on the demography of moose and white-tailed deer. *Journal of Animal Ecology*, **60**, 377–393.
- Mitchell, M.S. & Powell, R.A. (2003) Response of black bears to forest management in the southern Appalachian Mountains. *Journal of Wildlife Management*, **67**, 692–705.
- Morrison, M.L. (2001) A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. *Journal of Wildlife Management*, **65**, 613–623.
- Noyce, K.V. & Coy, P.L. (1990) Abundance and productivity of bear food species in different forest types of northcentral Minnesota. *International Conference on Bear Research and Management*, **8**, 169–181.
- Partridge, L. & Harvey, P.H. (1988) The ecological context of life history evolution. *Science*, **241**, 1449–1455.
- Pelton, M.R. (1989) The impacts of oak mast on black bears in the Southern Appalachians. *Proceedings Workshop on Southern Appalachian Mast Management* (ed. C.E. McGee). University of Tennessee, USA.
- Pennycuik, L. (1969) A computer model of the Oxford great tit population. *Journal of Theoretical Biology*, **22**, 381–400.
- Perry, R.W., Thill, R.E., Peitz, D.G. & Tappe, P.A. (1999) Effects of different silvicultural systems on initial soft mast production. *Wildlife Society Bulletin*, **27**, 915–923.
- Powell, R.A., Zimmerman, J.A. & Seaman, D.E. (1997) *Ecology and Behavior of North American Black Bears: Home Ranges, Habitat and Social Organization*. Chapman & Hall Publishers, London, UK.
- Pradel, R. (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics*, **52**, 703–709.
- Reynolds-Hogland, M.J. & Mitchell, M.S. (2006) Spatio-temporal availability of soft mast in clearcuts in the southern Appalachians. *Forest Ecology and Management*, **237**, 103–114.
- Reynolds-Hogland, M.J. & Mitchell, M.S. (2007) Three axes of ecological studies: matching process and time in landscape ecology. *Temporal Dimensions of Landscape Ecology: Wildlife Responses to Variable Resources* (eds J.A. Bissonette & I. Storch), pp. 174–194. Springer, New York, NY.
- Ricklefs, R.E. (1993) *The Economy of Nature: A Textbook in Basic Ecology*, 3rd edn. W. H. Freeman, New York, NY.
- Rogers, L.L. (1976) Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. *Transactions of the North American Wildlife and Natural Resources Conference*, **41**, 432–438.
- Rogers, L.L. (1987) *Effects of Food Supply and Kinship on Social Behavior, Movements, and Population Growth of Black Bears in Northeastern Minnesota*. Wildlife Monographs, **97**, 1–64.
- Samson, C. & Hout, J. (1998) Movements of female black bears in relation to landscape vegetation type in southern Quebec. *Journal of Wildlife Management*, **62**, 718–727.
- SAS Institute Inc. (2000) *SAS/STAT User's Guide*. SAS Institute Inc., Cary, NC.
- Sinclair, A.R.E. & Krebs, C.J. (2002) Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society of London B*, **357**, 1221–1231.
- Skogland, T. (1985) The effects of density-dependent resource limitations on the demography of wild reindeer. *Journal of Animal Ecology*, **54**, 359–374.
- Solomon, M.E. (1949) The natural control of animal populations. *Journal of Animal Ecology*, **18**, 1–35.
- Stephens, P.A., Freckleton, R.P., Watkinson, A.R. & Sutherland, W.J. (2003) Predicting the response of farmland bird populations to changing food supplies. *Journal of Applied Ecology*, **40**, 970–983.
- Sutherland, W.J. (1998) The effect of local change in habitat quality on populations of migratory species. *Journal of Applied Ecology*, **35**, 418–421.
- Sutherland, W.J. & Norris, K. (2002) Behavioral models of population growth rates: implications for conservation and prediction. *Philosophical Transactions of the Royal Society of London B*, **357**, 1273–1284.
- United States Department of Agriculture Forest Service (2001) Continuous inventory stand condition for Pisgah National Forest, Asheville, North Carolina, USA.
- Unsworth, J.W., Beecham, J.J. & Irby, L.R. (1989) Female black bear habitat use in west-central Idaho. *Journal of Wildlife Management*, **53**, 668–672.
- Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*, **47**, 893–901.
- Warburton, G.S. (1995) *Study B1: Status of Black Bear in North Carolina*. Annual Performance Report 47. Federal Aid in Wildlife Restoration, North Carolina. Resources Commission, Raleigh, NC.
- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46** (Supplement), 120–138.