TIMBER HARVEST AND BLACK BEAR POPULATION DYNAMICS IN A SOUTHERN APPALACHIAN FOREST

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Abstract: Habitat capability models are frequently used in long-term land management planning to evaluate the effects of management alternatives on wildlife populations. We believe that the relationships between timber harvest operations and black bear (Ursus americanus) population dynamics in the southern Appalachians make habitat capability models alone inadequate to predict long-term population response to timber harvest. An explicit consideration of population dynamics is necessary. Most timber in the region is harvested by clear-cutting, which requires an extensive road system and subsequently increases the vulnerability of bears to hunters. We present a simple deterministic model in which habitat dynamics are linked to population dynamics in 2 ways. The 1st is through the classic notion of carrying capacity, the 2nd is through a vulnerability factor that depends on local road density, which is in turn a function of the amount of clear-cutting that has occurred. We simulate the dynamics of a bear population in an area of Pisgah National Forest under 3 management regimes that facilitate comparison of the effects of different rotation intervals on the population. We conclude that some timber harvest regimes may improve the biotic capability of bear habitat in terms of carrying capacity, but that these benefits may be easily outweighed by the concomitant increase in vulnerability to hunting. Under present conditions hunting is a stronger influence on the population than is biotic habitat quality.

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Timber production is a primary management objective on much of the national forest land in the southern Appalachian Mountains. National forests in the area also provide habitat for a heavily hunted black bear population. In this paper we examine the long-term interaction between timber production and bear population dynamics with a simple deterministic simulation model. The model grew out of attempts to predict the long-term effects of timber harvest on bears with simple habitat capability models and the subsequent conviction that population dynamics must be considered in conjunction with biotic habitat capability. Our model is comprised of 2 submodels, the 1st a habitat capability model, the 2nd a stock-recruitment population model. Neither is elaborate, and both make liberal use of simplifying assumptions. In building this model, we emphasized the identification of conceptual relationships in the system rather than precise mathematical formulations. We used what understanding we have of the system to abstract some essential relationships and incorporate them into the model. Simulation of the system under 3 management regimes allowed examination of the ecological implications of timber management for bears in the region. We view this work as an exploratory step in understanding bear habitat and population dynamics in the southern Appalachians.

Yossi Cohen, Dave Hanson, and Larry Jacobson helped develop the original habitat capability model. We benefited from discussions with them and Lauren Hillman but claim sole responsibility for any errors herein. The 1st draft of this manuscript was greatly improved by changes suggested by F. L. Bunnell, R. A. Powell, and another reviewer.

STUDY AREA

Our model is based on the observations of Brody (1984) in the Harmon Den and Twelve Mile Strip areas of Pisgah National Forest in western North Carolina. (In this paper “Harmon Den” refers to both areas.) The 11,400 ha of timber on the area are managed under an even-aged system, with clear-cutting the preferred method of harvest. In Harmon Den 50- to 70-year old stands dominate (Fig. 1), reflecting a period of heavy timber harvest in the early 1900s. The U.S. Dep. of Agric., Forest Service recognizes 25 distinct forest cover types on the area, but these fall into 3 general timber types: upland hardwoods (5,626 ha), dominated by mast-producing species such as oaks (Quercus spp.) and hickories (Carya spp.); cove hardwoods (4,379 ha), dominated by non-mast species such as yellow poplar (Liriodendron tulipifera); and softwoods (1,395 ha), dominated by white pine (Pinus alba). We consider each of these types independently in the model.

The bear-hunting season in western North Carolina extends for 9 weeks split into 2 fall seasons. The study area has historically supported a high annual kill, even though approximately 40% of the area is a state bear sanctuary. The Great Smoky Mountains National Park (GSMNP) lies immediately west of the study area, and undoubtedly many of the bears that are harvested in Harmon Den are immigrants from GSMNP. Telemetry data from Brody (1984) indicate that approximately 15% of the resident bear population is killed annually, legally or illegally. Over 95% of the bears taken by hunters in western North Carolina are taken with the aid of hounds (Carlock et al. 1983). Roads in bear habitat greatly increase the
efficiency of hunting, as large areas can be searched from a vehicle with a "strike dog" riding on the hood or bed. The overall road density in Harmon Den, including Forest Service, state, federal, and private roads, was 0.57 km/km² in 1984. Most new roads constructed in the area are built in conjunction with timber harvest operations.

THE MODEL

The habitat capability submodel calculates the annual carrying capacity for bears based on the amount of food available in the habitat. This model is linked to a population model through the carrying capacity. An additional link between the 2 submodels is effected by including a "vulnerability" term, giving the proportion of the population killed by hunters each year. Vulnerability is a function of road density, which is in turn a function of the amount of clear-cutting that has occurred.

Habitat Capability Submodel

We assume that the carrying capacity of the habitat depends on the amount of bear food available. Bee- man and Pelton (1980) and Eagle and Pelton (1983) described pronounced seasonal shifts in the diets of black bears in GSMNP. Summer foods consisted of grass, forbs, and berries, whereas fall foods were acorns and hickory nuts. Summer foods generally grow best in open sunlight and hence are most common in early successional stands. Fall foods are found in mature timber. It thus seemed appropriate to consider summer foods and fall foods separately in the model.

The model uses timber type and stand age as predictors of the amount of food available in a given stand. We used timber type and stand age as predictors not only because of their biological relationships to bear food production, but also because of their usefulness in formulating timber management plans. Using timber type and stand age as predictors of habitat quality in the model ensured that habitat capability would be tightly coupled with the timber harvest regime.

The core of the habitat capability submodel is a set of 6 functions relating stand age to food production in 2 seasons for each of the 3 timber types (Fig. 2). These relationships were set up so that food production varied from 0.0 to 1.0, with 1.0 being the amount of food produced on 1 ha of the best possible bear habitat in the southern Appalachians (an "ideal hectare").

The functional relationships in Figure 2 were drawn freehand. Each curve traces the habitat capability of a hectare of timber through succession, after being clear-cut at age 0. The summer curves are the same for all timber types, reflecting a surge of early successional plants and declining to a constant level under a mature forest canopy. The curve for fall food in upland hardwoods assumes advanced oak reproduction (Watt 1979), so that softwoods are essentially absent from the mature canopy. Acorn production peaks when trees are approximately 80 years old (U.S. Dep. Agric., For. Serv. 1971), and then declines as oaks senesce and late successional species take their place in the canopy. The curve for fall food in cove hardwoods reflects the presence of mast species as subdominant trees in the early yellow poplar canopy and the eventual replacement of yellow poplar by oaks later in succession. The curve for fall food in softwoods rises gradually to a steady level between 50 and 100 years and then increases, reflecting the presence of a few oaks that gradually come to dominate the canopy after 100 years.

To translate the habitat capability functions into a carrying capacity, the relative importance of fall and
timber harvest and bear population dynamics

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porating the influence of habitat quality on popula-
tion dynamics unless age-specific relationships among
habitat quality, survivorship, and reproduction are
known. As we were unable to estimate any age-spe-
cific effects of habitat quality but wanted to consider
habitat quality in the model, we used a much simpler
lumped parameter model of population growth based
on the discrete logistic equation:

\[ N_{t+1} = N_t \left(1 + r[1 - N_t/K]\right) \]  \hspace{1cm} (2)

where \( N \) is population size, \( K \) is carrying capacity,
and \( r \) is the intrinsic rate of increase. The intrinsic
rate of increase is an elusive parameter, not easily
estimated from field observations. We arrived at the-
oretical estimates of \( r \) by constructing life tables from
the vital rates in Table 1 and solving Lotka’s equation.

The difference between the higher estimate of \( r \) (0.27)
and the lower estimate (0.15) is due primarily to
differences in the theoretically maximum litter size
and age at 1st breeding. The logistic formulation is
an inappropriate model of bear population dynamics
in many respects, but the simple biological interpre-
tation of its parameters was consistent with the heu-
ristic nature of our approach and outweighed its
dynamic inadequacies.

The logistic equation can be extended to a stock
recruitment model that explicitly considers hunting
mortality with the addition of harvest parameters:

\[ N_{t+1} = N_t \left(1 + r[1 - N_t/K]\right) - qEN \]  \hspace{1cm} (3)

where \( r, N, \) and \( K \) are as in (2), \( E \) is hunting effort,
and \( q \) is the finite rate of harvest (Ricker 1975). In
our model we hold hunting effort constant so that
\( qE \) reduces to the single parameter \( Q \), the propor-
tion of bears killed in the hunt.

Table 1. Maximum values of black bear life history parameters assumed in
the model.*

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Low estimate</th>
<th>High estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age at 1st breeding</td>
<td>3.5 yrs</td>
<td>2.5 yrs</td>
</tr>
<tr>
<td>Cub survival rate</td>
<td>0.90</td>
<td>0.90</td>
</tr>
<tr>
<td>Juvenile survival rate</td>
<td>0.70</td>
<td>0.70</td>
</tr>
<tr>
<td>Adult survival rate</td>
<td>0.97</td>
<td>0.98</td>
</tr>
<tr>
<td>Litter size (2-yr interval)</td>
<td>3.0 cubs</td>
<td>4.0 cubs</td>
</tr>
<tr>
<td>Age of last reproduction</td>
<td>10 yrs</td>
<td>15 yrs</td>
</tr>
<tr>
<td>Estimate of ( r )</td>
<td>0.15</td>
<td>0.27</td>
</tr>
</tbody>
</table>

* Life tables constructed from these hypothetical data were used in numerical
solutions to Lotka’s equation to estimate intrinsic rate of increase. Two
estimates were made.
Linking Habitat Capability and Population Dynamics

The most obvious link between our 2 submodels is the carrying capacity term, which is calculated in (1) and fed into (3). The 2nd link between the submodels derives from our perception of the relationship between hunting mortality and timber management in this system.

As stated previously, we believe there is a strong relationship between road density and the vulnerability of bears to the hunt. Brody and Pelton (unpubl. data) found evidence that individual bears in Harmon Den avoid crossing roads when possible. If vulnerability is related to the ability to avoid roads, the effect of a marginal increase in road density when there are few roads in the habitat will be small, as bears will still find it relatively easy to avoid the roads. Similarly, the effect of a marginal change in road density at high road densities will be small because the habitat is already saturated with roads, and bears will find them impossible to avoid. The greatest effect of marginal changes in road density will occur at intermediate road densities, where bears are no longer able to easily avoid roads and still exploit the habitat efficiently. Such a relationship can be described by a sigmoid saturation function of the form:

$$Q = \frac{1}{1 + be^{-sd}}$$

where $Q$ is the proportion of bears vulnerable to the hunt, $d$ is overall road density, and $s$ and $b$ are fitted constants. By bounding $Q$ between 0.01 and 0.99 and substituting values from Brody (1984) of $Q = 0.15$ and $d = 0.57\text{km/km}^2$, $b$ was estimated at 99.0, and $s$ at 4.93 to give a general relationship for Harmon Den.

Our model, then, calculates $Q$ from (4) and substitutes for $qE$ in the numerical solution of (3). To relate (4) directly to timber harvest, a relationship between the area clear-cut and the construction of new roads in the habitat is necessary. A regression of the length of new permanent roads constructed against the area regenerated using data from recent timber sales in Harmon Den yielded the relationship:

$$y = 0.0031x + 0.0491$$

($r^2 = 0.72, P < 0.10$), where $y$ is kilometers of new road constructed, and $x$ is hectares regenerated. The slope of (5) then allowed us to estimate the road density for any amount of regeneration:

$$d_r = d_{t-o} + 0.0031x/114$$

Review of Model Assumptions

Before discussing the simulations, it will be useful to reiterate the simplifying assumptions upon which the model is based.

Habitat capability:

1. Capability dependent only on food supply.
2. Food production dependent only on timber type and stand age.
3. Relationships between food production, timber type and stand age as in Figure 2.

Population:

1. Discrete logistic growth.
2. Hunting effort constant; vulnerability dependent only on overall road density, as in (4).

For the simulations we describe next, we needed to make the following assumptions about timber management:

1. Regeneration after clear-cutting is the only management technique available.
2. Overall road density is a linear function of the area regenerated, as in (6).

SIMULATION

The model we have described could be used to predict the effects of any timber harvest regime on the local bear population. Because a large number of harvest regimes is possible, we needed a regime that was simple and easily manipulated to systematically evaluate the ecological implications of the model. A "fully regulated forest" has a uniform distribution of stand ages up to the rotation interval, thus providing a steady yield of timber of rotation age (Davis 1966). We chose to run our simulations under a timber harvest regime that would bring the present age distribution of the forest to the uniform distribution of a fully regulated forest as quickly as possible, by cutting the oldest stands first. It is admittedly unlikely that such a management regime would ever be employed in Harmon Den, as 51% of the area is classified as unsuitable for timber harvest because of steep
slopes or soil conditions, and actual timber harvest levels depend on market pressures and political climates. However, such a regime allowed direct comparison of the effects of different rotation intervals and had the added advantage of reaching an equilibrium condition at full regulation.

Initial conditions in all simulations were carrying capacity, 43.8 bears; road density, 0.57 km/km²; and population size, 22 bears. The initial carrying capacity and road density values were taken from the present state of the forest as previously discussed. The initial population size of 22 animals is within the range of population sizes consistent with capture data from Brody (1984). Setting the initial population size at half of the carrying capacity ensured that annual recruitment would begin at as high an absolute level as possible given the constraints of logistic growth.

First we subjected only the habitat capability model to the simulation regime to see how carrying capacities of each timber type would change through time under different rotation intervals. We ran 200-year simulations, using rotation intervals from 40 to 200 years. The transient responses (Fig. 3) indicated that habitat capability would increase temporarily under some rotation intervals, but for all intervals the equilibrium carrying capacity was lower than the initial carrying capacity (Fig. 4).

The rotation intervals that maximized equilibrium carrying capacities were 140 years, 130 years, and 200 years for upland hardwoods, cove hardwoods, and softwoods, respectively. The total carrying capacity at full regulation under this harvest schedule was 39.6 bears. Harvest on such a schedule would require 81 ha/year to be regenerated, increasing road density by 0.0022 km/km²/yr. We simulated bear population dynamics for 200 years under this regime, using the stock recruitment model. With \( r = 0.15 \), the population dropped steadily to 5.5 with about 1 bear/year being killed by hunters after 200 years. With \( r = 0.27 \) the population dropped to an equilibrium level at 16.7 bears, with 2.6 being killed by hunters annually (Fig. 5a).

By incorporating a subroutine based on timber volume tables in Forbes (1955), we were able to compute the rotation intervals that would maximize the total volume of timber harvested over the 200-year projection. These intervals were 70 years, 90 years, and 40 years for upland hardwoods, cove hardwoods, and softwoods, respectively. The equilibrium carrying capacity for bears under this regime was 36.1, not very different from the value for the rotation intervals that maximized habitat capability. This regime, however, required 164 ha of timber to be cut each year, increasing road density by about 0.0046 km/km² each year. Simulation indicated that under this harvest schedule the bear population would be hunted to extinction in 120 years if \( r = 0.18 \), and in just over 200 years if \( r = 0.27 \) (Fig. 5b).

In examining the results of these simulations it became apparent that deaths from hunting affected population dynamics more than carrying capacity. In the next simulations, therefore, we attempted to re-
duce the number of deaths from hunting. Allowing no timber harvest for the 200-year simulation would result in no more roads being built and keeping vulnerability constant at the initial rate of 0.15. Simulating with a no-timber-harvest regime resulted in an equilibrium carrying capacity of 38.5, intermediate between the 2 previous regimes. The bear population decreased under this simulation also but to levels closer to carrying capacity than in either of the other simulations. With $r = 0.15$ the population level was 7.8 after 200 years, with 1.1 bears being killed annually. With $r = 0.27$ an equilibrium level of 18.2 bears was attained, with 2.7 being killed annually (Figure 5c).

**DISCUSSION**

**Habitat Capability**

It is likely that the actual timber harvest regime over the next 200 years will be intermediate between the no-cut scheme and full regulation schemes in our model. Whether the area is managed for bear production, timber production, or simply left alone, our model predicts a steady state habitat capability about 15% below that of the present level. The habitat capability submodel is simply a bookkeeping device—it grows the forest, cuts timber according to the designated schedule, and sums the values of the habitat capability functions. If the habitat capability functions are at all accurate, a long-term decline in habitat capability is unavoidable.

The decline is an inevitable result of the present nonuniform stand age distribution. Of the timber in the study area, 61% is now 50–70 years old, just entering the age of peak mast production. Once this timber has passed through the age of peak production, overall production will decline because only the 19% of the forest presently less than 50 years old will replace it. Imbalances in the age structure of the forest result in long-term cycles of habitat capability, and presently the habitat capability is nearing the crest of a cycle.

**Population Dynamics**

All 6 simulations predict drastic declines in the bear population from the initial level. With $r = 0.15$, the population went extinct under any timber management regime, as reproduction failed to balance
Relationship Between Timber Harvest and Population Dynamics

We can dismiss none of the 6 simulation outcomes as entirely impossible; all of them are consistent with what data we have, with what experience we have had, with our perceptions, and with the perceptions of other biologists considering the situation. Despite inaccuracies in the model we believe it is useful for its intended task, that is, examining the relationship between timber harvest and bear population dynamics.

It appears that a long-term stable food supply will necessarily be lower than the present level. Such stability could be accomplished in several ways. One would be to cease all timber harvest operations and let the forest return to the aboriginal uneven-aged structure characterized by gap-phase dynamics (Shugart 1984). Several centuries would have to pass before succession erased the shadow of the current age distribution. A 2nd way to achieve a long-term stable food supply would be a regular timber harvest regime that ensured a relatively constant supply of timber in the most productive age classes. Yet another alternative would be to influence food supply through management independent of timber harvest, such as thinning mast species competitors or artificial plantings of bear food plants. In any event, our analysis indicates that timber production and an adequate biotic potential of the habitat for bears are not incompatible, and in fact a carefully implemented timber harvest regime may ensure a steady supply of bear food above that of an unmanaged level. The model does, however, underline the fact that forest habitat dynamics operate under longer time frames than population dynamics. Management decisions that influence the forest habitat must be made with those long time frames in mind.

It is evident that hunting is a stronger influence on the dynamics of the local population than is habitat capability, especially when the population is well below carrying capacity. The most useful aspect of our model is the illumination of the trade-off between potential stability in food resources and an increase in vulnerability to the hunt as a result of higher road densities that accompany timber harvest. In all the simulations, habitat capability was similar, but vulnerability under the timber harvest regime that maximized timber production rose to 24% after 150 years, whereas vulnerability under the management regime that maximized bear habitat capability was only 17%.

deaths from hunting. With $r = 0.27$, the population went virtually extinct under the management regime that maximizes timber production; the high road densities required under this regime ensured that 26% of the population would be harvested annually after 200 years, so that less than 1 bear remained in the population at the end of the simulation. Equilibrium population sizes were attained only in the simulations with $r = 0.27$ under the maximal carrying capacity and no timber harvest regimes. Even though the equilibrium carrying capacity under the maximal carrying capacity regime was higher than it was under the no timber harvest regime, the equilibrium population size was lower because vulnerability increased as a result of timber harvest. In both cases, however, these equilibrium population levels were less than half of the carrying capacity and so were unstable (Ricker 1975). Only the deterministic nature of the model prevented extinction in these simulations.

An obvious question can be raised about the applicability of the logistic aspect of the population model. The density dependence of the logistic equation implies intraspecific competition for resources and, as stated earlier, in building a population model that considered food resources, such a formulation seemed appropriate. Considerable evidence indicates density dependence in bear populations, but most investigators believe it is sociobiologically based (e.g., Bunnell and Tait 1981, McCullough 1981, Stringham 1983). Rogers (1977) states that resource competition is the evolutionary origin of sociobiological density dependence, but this link may be irrelevant in the time frame of our model. Bunnell and Tait (1981) believe that reproductive response to food resources is density independent.

Immigration is an aspect of population dynamics that depends on habitat quality, but we we failed to consider it in the model. Telemetry studies in the southern Appalachians document frequent long-distance movements by bears, and often these movements are thought to be related to the spatial distribution of food resources (e.g., Garshelis and Pelton 1981). Harmon Den is almost certainly not a large enough area to consider the population closed, as our model does. As stated earlier, many of the bears killed in Harmon Den are probably immigrants from GSMNP. It is possible that the drastic decline in population size seen in the 1st 3 simulations would indeed occur in the actual population without additional recruitment from GSMNP.
after 150 years. Potential biotic increases in habitat quality resulting from timber harvest may easily be outweighed by the potential effects on population dynamics.

Theoretically it is possible to continue to harvest timber without the linear increase in road density presumed in the model. Permanent roads can be closed (by locked gate) once harvest operations are complete. We implicitly assume in the model that the ratio of open to closed roads will remain constant through time. Despite local public pressure to the contrary, current Forest Service policy requires that all new roads be closed from inception. This would “stretch out” the vulnerability saturation function somewhat, but given current hunting (and, especially, poaching) pressure, a gated road still leaves bears much more vulnerable than no road at all. Attention to the spatial arrangement of roads in relation to bear food resources and clear-cuts might weaken the relationship between timber harvest and vulnerability.

Finally, our model has implications for the way we use bear habitat capability models in long-range forest planning. In early habitat capability models the biotic potential of the habitat was calculated and the assumption made that the bear population would reach that potential. Forest managers have realized that road density affects bear populations; thus road density recently has been considered a factor in determining habitat quality (e.g., U.S. Dep. Agric., For. Serv. 1984). We maintain that the effects of roads on bear populations are fundamentally different than the effects of biotic habitat capability and are more properly considered as factors in population dynamics than in habitat quality per se. We believe that habitat capability models, no matter how complex, cannot predict the status of bear populations by themselves. Population dynamics must be explicitly considered in evaluating the long-term effects of habitat manipulation on bears.

LITERATURE CITED


