QUAIL MANAGEMENT: ISSUES, CONCERNS, AND SOLUTIONS FOR PUBLIC AND PRIVATE LANDS— A SOUTHEASTERN PERSPECTIVE

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ABSTRACT

In the Southeastern United States, Breeding Bird Surveys that bobwhite populations have been declining at 3.8%/year over the last 3 decades. Declines have been attributed the cumulative effects of large-scale deterioration of quail habitat quality associated with advanced succession, intensive monoculture farming, and intensive timber management. Additional factors such as changing role of predation, expansion of red imported fire ants, and metapopulation processes may exacerbate declines. Declining bobwhite hunter participation, changing public values, and realignment of conservation emphases have diminished the emphasis on bobwhite management nationally. However, within the Southeast 3 states, Virginia, Georgia, and North Carolina, have developed targeted private lands initiatives to enhance local and regional bobwhite habitats and populations. Additional opportunities exist for enhancing regional populations through broad avian conservation initiatives such as the North American Bird Conservation Initiative and Partners in Flight. Potential benefits from these regional efforts will be accrued only if greater value and emphases are placed on conservation of early successional habitats. As anthropogenic activities and natural successional processes influence regional usable space for bobwhite in the Southeast, established paradigms regarding relationships among predation, harvest, habitat management, and population dynamics may no longer be germane. Restoration of local and regional bobwhite populations will require a much greater understanding of bobwhite population processes at a mechanistic level across local and regional spatial scales.

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POPULATION TRENDS

With few exceptions, northern bobwhite *(Colinus virginianus*) populations have declined over most of the range during the last 3 decades (Sauer et al. 2000). State agency harvest trends (Burger et al. 1999), Christmas Bird Counts (Brennan 1991), and North American Breeding Bird Surveys (BBS) all show similar declining trends. From 1966 through the present, the BBS conducted by the United States Geological Survey, Patuxent Environmental Science Center, provides the most consistent range-wide measure of bobwhite relative abundance and population trends. In the southeastern United States (United States Fish and Wildlife Service, Region 4), the BBS indicates a 3.8%/year decline from 1966–1999 (Sauer et al. 2000). The rate of decline is apparently increasing; BBS for the southeastern United States from 1966–1979 indicates a 1.7%/year decline, whereas those from 1980–1999 show a 5.3%/year decline (Sauer et al. 2000). During the period 1966–1979, 4 of 11 southeastern states exhibited significant declining trends, whereas from 1980–1999 11 of 11 states were declining (Table 1). Such a dramatic decline in a ubiquitously distributed species is of additional concern because of the loss of recreational opportunity and associated economic impacts on local economies (Burger et al. 1999). As bobwhite populations have declined, harvest of bobwhite in 10 southeastern states (Ala., Fla., Ga., Ky., La., Miss., N.C., S.C., Tenn., Va.) declined from an estimated 17.1 million birds in 1970 to 3.5 million in 1995. The rate of decline in hunter numbers from 1980–1995 (−6.9%/year, Burger et al. 1999) exceeds the rate of bobwhite population decline (−4.8%/year) during the same period (Sauer et al. 2000), reflecting a reduction in hunter participation. As northern bobwhite populations continue to decline this pattern will continue. Reductions in bobwhite hunter populations represents a loss of a key constituency group needed for habitat management advocacy.

Although declining bobwhite populations have been attributed to a variety of factors including coyotes, nest predators, fire ants, pesticides, and avian predators, the primary cause has been the cumulative effects of large-scale deterioration of bobwhite habitat quality associated with advanced succession (Roseberry et al. 1979, Fies et al. 1992), intensive monoculture farming (Vance 1976, Exum et al. 1982, Roseberry 1993), and intensive timber management (Brennan 1991). In the terms of Guthery (1997), this is a range-wide reduction in useable space. Specific factors that have contributed to population declines vary regionally. In agricultural systems, farming practices have changed from diverse rotational cropping of row crops, small grains, hay, and legumes to intensive monocultural production of cotton, corn, soybeans, and rice. In intensively cultivated regions, lack of suitable grassy cover for nesting, weedy areas for brood rearing, and woody fencerows for winter and escape cover has re-

Table 1. Northern bobwhite population trends in the southeastern United States as indexed by Breeding Bird Surveys, 1996–1999[a].

State	1966–1999			1966–1979			1980–1999		
	Trend	*P*	*n*	Trend	*P*	*n*	Trend	*P*	*n*
Alabama	−4.2	0.00	89	−1.2	0.10	42	−6.2	0.00	88
Arkansas	−3.2	0.00	33	0.5	0.49	29	−5.3	0.00	33
Florida	−3.4	0.00	74	−1.5	0.22	34	−4.4	0.00	70
Georgia	−4.3	0.00	67	−1.9	0.17	54	−5.4	0.00	66
Kentucky	−2.5	0.00	46	−3.6	0.00	38	−2.8	0.00	41
Louisiana	−4.8	0.00	49	−1.7	0.13	24	−4.8	0.00	43
Mississippi	−3.5	0.00	34	−0.9	0.42	27	−4.9	0.01	32
North Carolina	−4.5	0.00	65	−3.4	0.00	29	−6.5	0.00	58
South Carolina	−4.7	0.00	29	−2.8	0.00	20	−5.6	0.00	25
Tennessee	−3.6	0.00	44	−1.6	0.00	41	−5.5	0.00	44
Virginia	−4.1	0.00	55	−2.4	0.00	43	−5.6	0.00	48
Southeast Region[b]	−3.8	0.00	530	−1.7	0.00	338	−5.3	0.00	500

[a] Trend estimates from Sauer et al. (2000).

[b] U.S. Fish & Wildlife Service Region 4, includes: Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee.

duced the overall capability of the land to support bobwhite (Kabat and Thompson 1963). In forested regions of the southeast, reduction in extent and frequency of fire (Brennan et al. 1998), increasing forest coverage, loss of small agricultural fields to natural succession and reforestation, expansion of densely planted pine plantations, and increasing use of total vegetation control in clearcuts and regeneration stands have reduced availability of grassy and weedy areas required for nesting, foraging, and brood-rearing (Fies et al. 1992). Modern land use practices which strive to maximize food, fiber, and forest products have the net effect of simplifying the landscape. This reduction in landscape complexity, or heterogeneity, has simply reduced the proportion of the landscape in usable space for bobwhite (Guthery 1997), and the population size which a given location is able to support.

LAND USE PATTERNS

In the southeastern United States, bobwhite are inextricably linked to early successional ground cover communities, although in other regions, they might occupy mid- to late-successional habitats (Spears et al. 1993). These communities may occur as spatially static patches in annually disturbed systems such as agricultural landscapes or as spatially and temporally dynamic patches created by timber thinning, clear cutting, and site preparation in forested systems. In forested systems, early successional communities occur as ephemeral patches, coming into existence following timber harvest, persisting for a brief (2–5 years) period, then lost through natural succession. Early successional *ground cover* might occur, and be perpetually maintained, by intermediate disturbance (e.g., fire) in an otherwise climax forest ecosystem such as pine/grassland. Declining populations are not unique to bobwhite, but rather reflect the alteration of an entire ecosystem characterized by region-wide loss of early successional plant communities and associated fauna (Church et al. 1993). Factors contributing to declines in early successional species are complex and cumulative, attributable to the changing manner in which we as a society use our natural resources. Loss of early successional communities and reduction in landscape heterogeneity associated with large scale, intensive, and monocultural production of agricultural and forest products is likely the direct causes of region-wide population declines of these species.

Agricultural Landscapes

Throughout the southeastern United States, privately-owned, rural, agricultural and forested lands constitute 79% of the total land base and provide important wildlife habitats. The Southeastern landscape is forest dominated, in 1997 being comprised of 48.3% forest, 14.2% rowcrops, 11.4% pasture, 1% rangeland, 1% Conservation Reserve Program (CRP), and 3.5% other rural uses (United States Department of Agriculture 2000). Land use practices throughout the Southeast have changed dramatically during the previous 5 decades. These changes have included farm consolidation, replacement of native communities with exotic or offsite monocultures, and conversion of agricultural lands to urban uses and forest. Based on the United States Department of Agriculture–Natural Resources Conservation Service, Natural Resources Inventory (USDA-NRCS, NRI) survey of 12 Southeastern states (Ala., Ark., Fla., Ga, Ky., La., Miss., N.C., S.C., Tenn., Va., W.Va.), from 1982–1997, 4.7% of the rural land base (3.9% of total surface acres) was lost to urbanization or other uses (USDA-NRCS, NRI *http://www.nhq.nrcs.usda.gov/NRI/1997/*). Twenty percent of cropland (3.6 % of total landbase), 5.8% of pasture (0.7% total landbase), and 29% of range land (0.4% of total landbase) in these southeastern states were converted to other uses, while forested acres remained relatively stable (0.8% loss of forested acres, 0.4% of total landbase).

Simultaneously, more intensive management of remaining habitats has reduced the quality of these lands for wildlife. From 1950–1990 mean farm size doubled and the number of farms declined by nearly 60 percent. Specialized, high input, monocultural agriculture, increased field size, and elimination of idle areas have reduced the quality of agricultural lands for bobwhite. Introduction of exotic forage grasses, and increased grazing intensity have reduced the availability and quality of early successional habitats in agricultural landscapes. From 1982–1992, cattle numbers increased by more than 25% and cattle/100 acres increased by 34%. Much of the existing range and pasture has been planted to non-native forage grasses such as tall fescue, bermuda grass, and bahaia grass. Simultaneously, reduction in the use of fire has degraded the quality of remaining grasslands (Brennan et al. 1998).

Implementation of federal farm programs, such as the CRP, in the Southeast has had a significant effect on land use changes as well. Following CRP signup 22 almost 2.8 million acres were enrolled in CRP in 12 southeastern states (Ala., Ark., Fla., Ga, Ky., La., Miss., N.C., S.C., Tenn., Va., W.Va.). Conservation practices (CP) CP1 (cool-season grasses), CP2 (native warm-season grasses), CP3 (trees), CP4 (wildlife habitat), CP10 (existing grass), CP11 (existing trees), CP21 (filter strips), and CP22 (riparian buffers) collectively accounted for 97.6% of all enrolled acres. In contrast to the Midwest where grass establishment was the predominant conservation practice, tree planting (CP3 and CP11) was the most commonly selected CP in the Southeast, accounting for 61.9% of total enrolled acres. Current enrollment in tree planting practices is approximately equitably distributed between newly established stands (<15 years of age, 43.7%) and reenrolled stands (52.2% >10 years of age). The most commonly established tree species was loblolly pine, although a longleaf pine National Conservation Priority Area (CPA) was established beginning with signup 18. The longleaf pine CPA included parts of 9 southeastern states and provided special incentives (increased EBI and exemption from HEL requirements) for establishment of longleaf pine on eligible cropland. Through the 22nd signup, 168,541 acres of longleaf have been enrolled in this CPA. Grass cover practices account for 33.1% of current enrollment in the Southeast, and field border practices (CP21, CP22) account for 2.6% of enrolled acres. The distribution of enrollment between grass and tree practices differed substantially among southeastern states. Georgia and Florida enrolled almost exclusively trees (92.3%), whereas Kentucky, Tennessee, and West Virginia enrolled predominantly grasses (90.9, 85.9, 80.9%, respectively). As a result of strong involvement by state wildlife agencies, native warm-season grasses were more widely adopted in Virginia (9.5% of enrolled acres) and Kentucky (7.0% of enrolled acres), but < 1% were implemented in other states (e.g., Fla. 0.1%, Miss. 0.2%). Field border practices (CP21 and CP22) were extensively used in Kentucky (5.6% of enrolled acres), North Carolina (12.3% of enrolled acres), and South Carolina (11.1% of enrolled acres), but seldom used in Florida (0.1%), Georgia (0.3), or Louisiana (0.3%). Thus, CRP in the Southeast is quite different from that in other regions and tremendous variation exists among southeastern states as a result of differing land use and conservation goals and potentials. The net effect of the CRP in the Southeast was the conversion of agricultural lands to forest or forage grasses resulting in a long-term loss of potential habitat.

Forested Landscapes

Although forested acreage in the Southeast has been relatively stable during the past 2 decades, forest composition and quality have changed (Trani et al. 2001), reducing habitat quality for many wildlife populations. In general, there has been a conversion of longleaf pine to fast-growing slash and loblolly. The longleaf pine community once stretched from Texas to Virginia (Frost 1993) and was the dominant upland ecosystem across much of the southeastern coastal plain, covering more than 60% of uplands and 40% of the entire region (Noss et al. 1995). Today, less than 2% of the historic longleaf remains (Noss et al. 1995). Increasing human populations combined with increasing per capita consumption of paper products have contributed to a continuously expanding demand for pulpwood. Southern pulpwood production increased more than 4-fold from 1953–1993 and will likely continue to increase in the foreseeable future (Johnson 1996). In a 1995 survey of 7 Midsouth states (Ala., Ark., La., Miss., Okla., Tex., and Tenn.), most (67%) of 40,000,000 ha of timberland was in non-industrial private ownership (Rosson 1995). An increasing proportion of this timberland (16%) is artificially regenerated stands (plantations), mostly loblolly pine. Most (55%) plantation acreage in the Midsouth occurs on industrial forest lands with 39% on non-industrial private lands and 7% under public ownership (Rosson 1995). In the Coastal South, 32% of all timberland was in the seedling/sapling stage (Trani et al. 2001) but a substantial proportion (55%) of plantation acreage was in the seedling-sapling size-class. Thus, pine plantations will likely constitute an increasing component of the southern landscape and a significant proportion of early successional habitats. In the Gulf coastal plain, intensive plantation management has influenced both forest composition and age distribution (Trani et al. 2001). Use of genetically selected fast-growing seedlings and herbicidal competition control speed the time from planting to canopy closure, potentially reducing the window of early successional opportunity in reforested pine plantations.

Southern pine ecosystems are fire dependent. Fire has been one of the primary abiotic processes that has shaped the biota of the southern forest landscape (Brennan et al. 1998). The frequency and intensity of fire determines the composition and structure of pine forests in this region, particularly the degree of hardwood component in the mid- and understory. Presence and dominance of hardwood midstory canopy strongly influences herbaceous ground cover, and hence bobwhite habitat. Fire exclusion over the last 50 years, attributable to landscape fragmentation, intentional fire suppression, and declining application of prescribed fire (Brennan et al. 1998), has resulted in changes in forest ecosystems, including loss of herbaceous ground cover and expansion of forest land within former open habitats (White and Wilds 1998, Trani et al. 2001). The impact of fire exclusion on bobwhite habitat and populations in the Southeast cannot be overemphasized. Dramatic reductions in fire frequency in southern landscapes has resulted in decline and loss of numerous fire-adapted species, including northern bobwhite (Brennan et al. 1998). Fire exclusion in pyric southern pine systems is perhaps the greatest habitat problem facing bobwhite in the Southeast.

PUBLIC PERCEPTIONS

Tom Dailey (*this volume*) thoroughly documents the changing characteristics and attitudes of our ''increasingly urbanized and nonconsumptive society.'' Despite trends in urbanization we see an ever increasing, but superficial sense of environmental awareness. With this new awareness comes increasing public expectations for resource stewardship. Changing public expectations are expressed through regulatory action, consumer pressure, and evolving priorities of legislation and governmental programs. Although conservation of natural systems and resources has broad public support, it seems that the public does not equally value all systems. Studies of public perception of forest landscapes indicate that, generally, aesthetic preference increases with forest stand age (summarized in Askins 2001). Furthermore, as Askins (2001) acknowledges, the history of extensive forest clearing in the eastern United States has resulted in tree planting and forest protection becoming synonymous with conservation. Although many of these forests have regenerated, public perceptions of conservation remain linked with a single-minded focus on climax forest systems. Thus a ''not so subtle'' conservation bias against early successional systems seems evident. Despite the fact that nearly 80% of the perilously endangered ecosystems in eastern North America are disturbance-maintained systems (Noss et al. 1995, Askin 2001, Thompson and DeGraaf 2001) conservation of early successional systems has not received high priority. Askins (2001) suggests that a barrier to sustaining and restoring these systems is a perception that they are uninteresting or unappealing and their maintenance often requires ''removing trees to favor vegetation associated with human disturbance.'' These perceptions of conservation, coupled with a misinformed attitude that simply ''letting nature take its course'' (Hunter et al. 2001) will restore or maintain ''natural'' systems have resulted in little conservation attention focused on disturbance-maintained systems. In the southeastern United States, bobwhite are inextricably linked to disturbance-maintained systems. Insofar as many natural disturbance processes have been permanently disrupted, human intervention with premeditated disturbance regimes (management) is essential for restoration and maintenance of the communities to which bobwhite are adapted. Even among natural resource professionals, creation of early successional systems through disturbance regimes deemed ''unnatural'' meets with substantial resistence. This is illustrated in opposition by many ornithologists to mechanical or herbicidal removal of hardwoods from fire excluded pine systems, even when accomplished for the purposes of red-cockaded woodpecker management. Within a recent special section in The Wildlife Society Bulletin, dedicated to maintenance of early successional systems, Hunter et al. (2001) acknowledged that direct management intervention *may* be justified, but ''restoration should not be at the expense of developing future old-growth conditions in many areas where mid-successional stands now dominate.'' Bobwhite are indeed associated with unpopular systems (Askins 2001).

Historical land use patterns accidently produced such abundant populations over broad areas. As Roseberry (1993) noted, bobwhite habitat can be affected by too much disturbance, or not enough disturbance. This is the paradox facing bobwhite populations in the Southeast. Essential plant communities, appropriately interspersed, have been lost in both agricultural and forested systems because of too much and not enough disturbance, respectively. Bobwhite are no longer an accidental by product of broadly applied land use regimes. In modern landscapes restoration of bobwhite populations requires premeditated creation and maintenance of essential habitats on a spatially broad extent. In modern southeastern landscapes, locally abundant populations can be produced, but only through intensive management over extensive areas. In the Southeast, this has produced a dichotomous situation in which bobwhite persist at low densities over large portions of the range with high density populations only occurring on primarily private land where wealthy landowners allocate substantial resources to produce huntable populations.

The common goal of species conservation is to maintain viable populations. In contrast, to be a viable game species, bobwhite must be reasonably abundant over large portions of the landscape (Roseberry 2000). Increasingly, within the professional conservation community, management objectives for bobwhite populations sufficiently abundant to produce moderate levels of sustainable harvest are viewed with disdain. Expanded funding bases, changing constituencies, broader conservation objectives, and ecosystem management philosophies have led conservation agencies in the Midwest to question the legitimacy of management regimes developed around production of sustainable harvest of a focal species (Dailey *this volume*). Although increasingly common in northeastern and midwestern states, and evident in conservation forums such as The Wildlife Society listserve, this emerging paradigm has largely not yet reached Southeastern Fish and Wildlife Agencies. Most southeastern fish and wildlife agencies are still funded primarily by license fees, and hunters and fishermen remain a key constituency. Although participation in bobwhite hunting has declined throughout the Southeast (Burger et al. 1999), northern bobwhite remain a high profile species for many resource management agencies. This is illustrated in several state level initiatives targeting bobwhite habitat management on private lands.

PROACTIVE INITIATIVES

To address creation and maintenance of bobwhite habitat, 3 Southeastern states (Va., Ga., and N.C.) have developed specific programs that provide technical and financial assistance to private landowners interested in enhancing bobwhite habitat. These programs differ in their spatial extent, level of support, and specific practices subsidized.

Virginia

In 1996, Virginia Department of Game and Inland Fisheries (VDGIF) developed the Virginia Bobwhite Quail Plan. This plan identified specific changes that have occurred in pasture, rowcrop, and forest management practices that have contributed to declining bobwhite populations. These problems included: a) increased reliance on cool season forages for livestock forages; b) decreased use of prescribed burning; c) increased acreage of dense pine plantations; d) trends toward "cleaner" farming; e) lack of consideration for wildlife in USDA farm programs; f) unrealized opportunities to improve utility right-of-ways for bobwhites; g) lack of areas which demonstrate good quail habitat; h) lack of knowledge on availability of quail habitat and effects of landscape changes; i) lack of understanding of predation impacts on quail in fragmented habitats; j) impacts of changing pine forestry practices; k) impacts of pesticides on quail; and l) impacts of releasing pen-reared quail on wild quail populations (Capel et al. 1996). The Virginia plan developed specific strategies to address each of these problems. This plan included components to establish demonstration sites, provide technical assistance, and cost share to facilitate implementation of bobwhite habitat management. Five years after the initial implementation of this plan, VDGIF has documented a number of tangible products produced through the program. In an effort to increase information transfer VDGIF has produced 5 excellent technical bulletins addressing bobwhite habitat requirements, pine management, brood habitat management, and wildlife plantings and hosted 59 workshops attended by >3000 people. The Virginia Bobwhite Plan targeted habitat enhancement on private lands in 9 counties in the Piedmont and Tidewater regions. To implement this plan, VDGIF hired a dedicated biologist and reallocated substantial time of a second biologist to program delivery. This plan provided cost share funding for adding field borders to agricultural fields, idling land, converting fescue to native warm-season grasses, and adding wildlife plants to field buffers. These practices and cost shares were delivered through the Best Management Practices Program of the Department of Conservation and Recreation and Soil & Water Conservation Districts. A total of $272,000 was invested in cost shared agricultural practices in 3 of the 5 years and an additional $90,000 in prescribed burning cost share in 4 of 5 years. During 1996–2001, the Virginia Bobwhite Plan established 103 demonstration areas and cost shared 3,510 acres of habitat improvement on more than 400 landowners. The Virginia Bobwhite Plan did not provide for a specific evaluation of the efficacy of habitat management practices in increasing local bobwhite populations.

Georgia

In 1999, the Georgia Department of Natural Resources implemented the Georgia Bobwhite Quail Initiative (BQI). The BQI is a comprehensive program that provides technical assistance and cost share to enhance bobwhite habitat on private lands in Georgia. The BQI is primarily directed at providing nesting and brood rearing habitats in 3 focus areas comprised of 20 counties in central Georgia. Within focus areas, Wildlife Resource Division (WRD) biologists provide cooperators with detailed technical assistance on bobwhite habitat management. Cooperators may receive incentive payments for establishment and maintenance of specific types of early successional habitats. Habitat management plans are developed for all interested landowners and incentive payments are allocated on a competitive basis. To be eligible for incentive payments potential coopeorator's property must be located in 1 of the focus counties, must be at least 50 contiguous acres, must include commercial rowcrop agriculture, must be enrolled in the CRP longleaf Pine Conservation Priority Area, or in the Piedmont Physiographic Province and must be a pine forest not currently under intensive management for quail. Habitat management plans are competitively ranked for funding and plans containing multiple habitat practices receive higher rankings and increased chances for funding. Incentive contracts are for 3 years and are renewable annually based on cooperator performance. Specific cost-shared practices include herbaceous field borders, hedgerows, fallow patches and center pivot corners, pine forest openings, linear practices, prescribed burning in thinned pine forests, and conservation tillage. Funding is distributed annually contingent upon successful implementation of habitat practices and approval by WRD biologists. Funds are delivered through the local Soil and Water Conservation Commissions. During 1999 and 2000, WRD biologists provided technical assistance for 98 cooperators managing 203,466 acres. Cooperators enrolled 2,716 acres in cost-shared practices at a total cost of $258,775 in incentive payments. Prescribed burning, field borders, and center pivot corners were the most commonly adopted practices. To deliver this program, Georgia Department of Natural Resources-WRD hired 6 wildlife biologists with exclusive responsibilities associated with the BQI. The Wildlife Resources Division is evaluating the efficacy of the BQI through a cooperative research project with University of Georgia. The goals of this project are to monitor baseline populations before and after initiation of BQI practices and compare treated and untreated farms. Fall covey density is being used as a response variable in an observational study that compares bobwhite abundance on lands enrolled in the BQI and neighboring farms not enrolled in the program. Both grid census methods and single-observer point counts are being used to index fall abundance. All fields enrolled in the BQI will be monitored with one of these monitoring protocols. Initial results indicate a positive bobwhite response on 75% of BQI enrolled properties (R. Thackston, Georgia Department of Natural Resources, personal communication).

North Carolina

The North Carolina Wildlife Resources Commission has developed a new private lands initiative named CURE (Cooperative Upland habitat Restoration and Enhancement) to create and maintain early successional upland habitats for the benefit of northern bobwhite and associated early successional species. This program is targeted at those areas in North Carolina where existing land use and other habitat conditions provide the greatest potential for successful habitat restoration and enhancement. Funding and technical assistance will be concentrated in focal areas where combinations of agricultural, pasture, woodland, and shrubland exist in proportions that indicate overall suitability as small game habitat. Suitable habitat was identified from a habitat suitability model based on resampled and reclassified 1993–95 LANDSAT TM data. Three focal areas have been identified, 2 in the coastal plain and 1 in the Piedmont region. Within these focal areas, technical assistance and incentives will be available for landowners or landowner cooperatives that wish to implement habitat management on at least 5000 acres for a minimum of 5 years. Once enrolled in a cooperative, landowners will be eligible for technical assistance for management plan development and financial assistance for land rental, vegetation control and management, forest management, and fencing. North Carolina Wildlife Resources Commission proposes to allocate 7.5 full-time positions at a cost of nearly $500,000/year to program delivery. Additionally, $150,000/year will be allocated for practice cost-sharing. Bobwhite response to management regimes will be evaluated annually with a 50% sample of all potential habitat within participating landowner cooperatives using the fall covey call index.

Regional Initiatives

In addition to state-level initiatives, bobwhite populations could benefit from several regional and national initiatives. A Southeast Quail Technical Committee has been formed under the auspices of the directors of the Southeastern Association of Fish and Wildlife Agencies and charged with developing a national plan for restoration of bobwhite populations within the context of the North American Bird Conservation Initiative (NABCI). Ralph Dimmick is spearheading development of this plan, called the Northern Bobwhite Conservation Initiative (NBCI), with assistance from biologists around the region. The NBCI has set ambitious goals of stabilizing population declines within 5 years and restoring regional populations to 1980 levels within 20 years. Under the NABCI, the Southeastern Coastal Plain is designated as Bird Conservation Region (BCR) 27. This region comprises 39% of the land area of 10 southeastern states and provides perhaps the greatest opportunity for bobwhite restoration in the Southeast. Bobwhite is a priority species within BCR 27. Strategies identified in the NBCI were developed under the assumption that the availability of grasslands suitable for nesting and brood rearing limit bobwhite populations in agricultural and forest lands within BCR 27. The NBCI provides specific habitat acreage goals for each BCR and landscape type (crop, pasture, forest lands, etc). Under this plan, population objectives would be achieved primarily through conversion of crops to native grasslands, implementation of field borders and riparian corridors, conversion of exotic cool-season pastures to native warm-season grasses, reestablishment of longleaf, and enhancement of forest ground cover through prescribed burning, thinning, and improved site preparation.

In addition to the NABCI, Partners in Flight (PIF) has developed regional bird conservation plans (BCP). The 2 primary PIF physiographic regions in the southeastern United States are the East Gulf Coastal Plain (EGCP) and the South Atlantic Coastal Plain (SACP). Under the PIF conservation prioritization process, bobwhite are listed as a category I (highest priority) species in the EGCP and occur in 4 of the 7 priority habitat associations (longleaf pine/slash pine, loblolly pine/shortleaf pine, early successional habitats, grasslands and pastures). In the SACP region, bobwhite are listed as category IIa species (moderate priority) and occur in 3 of 8 priority habitat associations (early successional shrub-scrub, grasslands and associated habitats, and southern pine). Many of the primary habitat objectives proposed in the both the SACP and EGCP BCP would benefit regional bobwhite populations. Specific examples from the SACP include: retain and restore 1.3 million acres of native warm season grass habitats and associated long leaf pine, provide at least 300,000 acres of 5-year idle lands, 300,000 acres of annual communities, and 600,000 acres of 10–20-year idle lands, and increase long leaf pine acreage from 1.5 to 2.2 million acres, and improve herbaceous ground cover conditions favoring native grass communities. The SACP BCP specifically identifies the northern bobwhite as an extremely important species helping to drive habitat restoration efforts in this region. Many of the suggested habitat objectives for grassland and shrub-scrub are specifically to restore bobwhite populations in accordance with the NBCI, but will benefit other vulnerable grassland species.

As conservation funding bases expand and constituencies diversify, ecosystem management will increasingly be the philosophical framework under which public conservation programs are developed and delivered. As such, bobwhite conservation efforts framed in the context of restoration of early successional communities, disturbance-maintained systems, and pine grasslands will have the greatest probability of being widely adopted and implemented. Efforts such as the NABCI, NBCI, and PIF-BCP provide a vehicle for regional restoration of bobwhite and associated species. However, maximum benefits from regional conservation planning will only be accrued through collaboration among quail ecologists, avian ecologists, and conservation biologists. We must be plugged in to broader conservation initiatives.

CHANGING PARADIGMS

As anthropogenic activities and natural successional processes influence regional usable space for bobwhite in the Southeast, established paradigms regarding relationships among predation, harvest, habitat management, and population dynamics may no longer be germane (Robel 1993, Roseberry 1993, Hurst et al. 1994). On both public and private lands throughout the Southeast, bobwhite populations, and the biologists who would manage them, face a myriad of circumstances that challenge prevailing paradigms.

Predation

Among the most controversial challenges is the poorly understood interactions between predator communities and bobwhite populations in modern landscapes. Under the influence of Errington's teaching and in an effort to maintain a public focus on habitat management, several generations of biologists have confidently promoted the enduring paradigm that ''predation has no effect on bobwhite populations.'' However, the role of predation in limiting avian populations has received substantial attention in recent years (Hurst et al. 1996, Rollins and Carroll 2001, Jimenez and Conover 2001, Nelson 2001). Increasingly, the ecological community is recognizing that, contrary to historical paradigms, predation may limit recruitment and abundance of some species in modern landscapes (Cote and Sutherland 1995). Rollins and Carroll (2001) suggest that *how* predators interact with quail populations may be affected by changes in habitat, predator populations, predator community composition, and search efficiency. In modern landscapes, declining bobwhite populations may face increasing predator populations in a habitat matrix that increasingly favors the predator. Populations of some mesomammal nest predators are apparently increasing throughout the Midwest and Southeastern United States (Lovell et al. 1998, Hubbard et al. 1999). Similarly, primary avian predators of adults may be increasing. During the period 1980–1999, BBS indicates increasing population trends for sharp-shinned hawk (18.1%/year), Cooper's hawk (13.8%/year), and red-tailed hawk (2.1%/year) (Sauer et al. 2000). In this changing context, previous assumptions about the impacts of predation on bobwhite demographics needs to be reevaluated (Hurst et al. 1994, Rollins and Carroll 2001).

Most published studies on bobwhite demographics have simply quantified the presumptive causes and rates of mortality of adults, chicks, and eggs. In recent years, a few researchers have begun to study the patterns and processes of predation and bobwhite populations in the South. Researchers have employed motion-sensitive cameras (Fies and Puckett 2000) and infrared video cameras (Staller 2001, Staller et al. 2001) to document patterns and rates of nest depredation by specific nest predators. An interesting outcome of this camera research is a renewed appreciation for the role of snakes in nest depredation. Stoddard (1931) recognized that certain snakes, including rat snakes, coachwhips, and king snakes were important nest predators. So much so, that he advocated control methods that today would be considered ethically repugnant and illegal. The general hunting public and wildlife managers tend to focus on the more visible mammalian predators such as skunk, raccoon, and opossum; however, these camera studies demonstrate that snakes are typically the most frequent nest predator (40–50% of depredations) and other species such as armadillos, that were previously ignored, might be as important as raccoons and other mesomammals (Staller 2001, Staller et al. *this volume*). Despite this progress, there needs to be a greater collective effort to understand the process of predation as it relates to habitat use and demographic parameters of bobwhites.

The term ''predator context'' has been used to describe the predator community at a given location in time and space (B. Palmer, Tall Timbers Research Station, personal communication). Just like weather and vegetation, predator communities change in space and time, we have just failed to measure these changes. Failure to characterize the predator context in which demographic studies have been conducted has limited our ability to understand habitat quality and population processes (Leopold and Hurst 1994). Relevant questions that have not been asked include ''How does the abundance and composition of a predator community affect bobwhite demographics (survival, reproductive success, and population growth), population processes, and population trajectories?'' and ''How do weather, vegetation, and landscape structure alter the nature of these relationships?'' That is, we need to understand the process of predation, rather than considering predation in terms of individual events or simply cause-specific mortality rates (Leopold and Hurst 1994). Research in progress on the relations of indices of predator abundance and bobwhite demographics across multiple sites throughout the Southeast is demonstrating correlations among demographic parameters and predator abundance (B. Palmer, Tall Timbers Research Station and L. W. Burger, Mississippi State University, unpublished data). If predators affect the demographic processes that lead to higher or lower densities of bobwhite then how can we judge habitat ''quality'' without understanding predator context.

Van Horne (1983) suggested that habitat quality is best understood through the demographic measures of success (e.g., rates of survival and reproduction). Guthery (1997) framed habitat quality in a binary context (usable space) where a specific point in space and time is either usable or not. Usable space is cover that provides essential resources compatible with the behavioral, physical, and physiological adaptations of bobwhite (Guthery et al. 2000). The usable space hypothesis states that bobwhite abundance on an area is proportional to functional space-time available on that area. Guthery (1997) argued that, after controlling for the frequency and severity of catastrophic weather events, a general constant of proportionality might describe the relationship between abundance and usable space-time throughout the range. It follows from this that habitat quality, and therefore mean fitness, are the same whereever populations persist (Guthery et al. 2000). Guthery (1997) referred to this as ''operational constancy.''

Southeastern state resource management agencies are coming under increasing pressure from stakeholders to liberalize wildlife codes to facilitate increased opportunities for predator management. These calls for enhanced flexibility in predation management go contrary to prevailing public sentiment that increasing harvestable surplus is not a legitimate justification for lethal control of predators. Renewed emphasis on predation management as a viable, even essential, tool for bobwhite management is based on the premise that reductions in predator abundance or efficacy would enhance demographic parameters such as nest success and survival. But Guthery et al. (2000) suggest that for bobwhite, because of this operational constancy in mean demographics, it is not feasible to increase ''demographic capacity'' or stabilize populations with management practices designed to increase survival or production (Guthery et al. 2000). This is in contrast to empirical observations by Cote and Sutherland (1997) and Tapper et al. (1996) that, for gray partridge and other ground nesting birds, selective reduction in abundance of important nest predators can increase nest success, recruitment, fall densities, and in some cases breeding densities. Predator removal, or habitat modification that alters use of the landscape by predators, changes the predator context. What is not yet understood is how predator context affects usable space and demographic capacity in a landscape. By analogy, Forrester et al. (1998) clearly demonstrate that, in the arid southwest, operative temperature alters the distribution of usable space for bobwhite during portions of the year. Vegetation mitigates the effects of ambient temperature and solar radiation, influencing the distribution of habitable (standard operative temperature within the thermal neutral zone or at least below the upper critical temperature) in the landscape. A given distribution of vegetation produces a different distribution of usable space under different thermal and radiant conditions. Similarly, predator context might alter the distribution of habitat space. Research has not adequately addressed how the abundance and types of predators affect the suitability of a given location to quail. In the context of usable space, the quantity of usable space through time might vary in relation to extant predator community. More specifically, a point in space (i.e., foraging location) that is usable in the absence of a particular predator, may be unusable in the presence of abundant populations of that predator. Throughout the ecological literature it has been demonstrated for numerous other species that optimal foraging strategies and habitat use differ in the presence and absence of efficient predators. Thus, we cannot understand habitat use and optimal habitat composition in the absence of information on the abundance and composition of the predator community.

Beyond simply affecting quantity of usable space, the predator context may influence the nature of density-dependent demographic processes. Guthery et al. (2000) suggested that the reason it is not feasible to ''. . . increase demographic capacity or stabilize populations with management that increases production or survival'' is that ''. . . density-dependent processes would mediate against a survival-production approach to augmentation of demographic capacity.'' However, working on gray partridge, Potts (1986) suggested that predator management (altering the predator context) altered the nature of the density dependent relationship between partridge density and mortality rates. Rollins and Carroll (2001) suggested that predator removal might suppress the predator-mediated density-dependent mortality of adults and nests leading to higher rates of recruitment at a given density than would be predicted by the density-dependent reproduction relationship (Roseberry and Klmstra 1984). Thus, if altering the predator context alters the functional nature of the density-dependent relationship, a survival-production approach to enhancement of demographic capacity might work. Further theoretical and empirical research is needed to understand relationships among predator context, usable space, and demographic capacity. Integration of predator monitoring into ongoing demographic studies of bobwhite would provide a first step in this direction. A large, replicated, manipulative, multi-institutional study in Georgia is currently investigating relationships among predator density and bobwhite demographics (B. Palmer, Tall Timbers Research Station; personal communication; J. Carroll, University of Georgia; personal communication; C. Sisson, Auburn University, personal communication). Empirical and theoretical work directed at understanding relationships among vegetation structure, landscape structure, and vulnerability to avian and mammalian predators would provide additional insight. Approaches such as Guthery's ''cone of vulnerability'' and the multi-resolution methodology in Stockett et al. (2001) illustrate promising avenues of investigation.

Management responses to mitigate the effects of predation on prey species include modifying the predator community, providing alternative prey, habitat modification, and manipulation of patch and landscape characteristics (Jimenez and Conover 2001). Although direct manipulation of predator communities has been shown to enhance productivity of some prey species (Cote and Sutherland 1997) public acceptance depends on the specific objectives of removal efforts (Messmer et al. 1999). Rollins and Carroll (2001) suggested an integrated pest management (IPM) approach to predation management involving establishment of ''economic thresholds'' of predation damage and application of non-lethal and lethal means of predation management. They suggested that non-lethal means (e.g., habitat manipulation) are the first line of defense. Fleske and Klaas (1991) and Herkert (1994) suggest that abundance and composition of a local predator community might be manipulated by removing den sites and nesting and perching structures. For example, if the availability of suitable den sites in prairie and agricultural landscapes limits raccoon distribution and abundance (Stains 1956) or the distribution of foraging activity and space use (Mech et al. 1966, Rabinowitz and Pelton 1986), identification and selective removal of these features might provide a non-lethal means of managing predation in an IPM context. Similarly, if the abundance of midstory and mature hardwoods in a pine ecosystem influences predator abundance or efficiency, thinning or hardwood removal might enhance bobwhite survival or reproductive success. The efficacy of these non-lethal strategies should be experimentally investigated. Ongoing research projects in Florida (B. Palmer, Tall Timbers Research Station, personal communnication) and Georgia (C. Sisson, Auburn University, personal communication) are investigating the effects of hardwood removal in a pine ecosystem on predator abundance and bobwhite demographics. Current research on Ames Plantation in Tennessee is investigation effects of manipulating landscape structure and composition on bobwhite demographics. All 3 of these studies show initial demographic increases in response to altering habitat structure.

Bobwhites occupy a wide variety of habitats across their range. By far most of these ecosystems have been dramatically altered by humans with resulting changes to abiotic (soils, weather, water) and biotic (disease, predators, vegetation) factors. Each of these factors has been identified as important in population regulation of game birds. The issue of predation and bobwhite populations is emotionally and politically charged. An unsavory history of predator extirpation associated with game bird management and recent incidents of illegal and unethical predator control on some southeastern quail plantations has cast a dark cloud on any discussion of predation management. Dailey (*this volume*) suggests that predator control puts quail conservation on a ‘‘slippery slope’’ and that the perception of quail enthusiasts as being indifferent to ecological values of other fauna could hamper regional conservation initiatives beneficial to bobwhite, and ultimately ‘‘doom’’ the sport. However, sensitivity to public perceptions and acceptance of broader conservation objectives, while laudable, should not be an excuse for failure to conduct the best possible research to understand the ecological processes at work in modern landscapes.

Fire Ants

Although bobwhite population declines are most often attributed to habitat loss, Allen et al. (1995) implicated the red imported fire ant (RIFA, *Solenopsis invicta)* as an additional factor that might contribute to declining bobwhite populations in the southeastern United States. Some studies have de-emphasized effects of fire ants on bobwhite populations (Johnson 1961, Komerak 1980, Brennan 1993). Brennan (1993) argues that only habitat availability limits bobwhite populations in the Southeast and RIFA are relatively unimportant. Brennan (1993) cites high density populations on managed properties as evidence that bobwhite throughout the southeast respond to intensive habitat management and can be maintained even in the presence of RIFA. Yet Allen et al. (1995), Pederson et al. (1996), Giuliano et al. (1996) and Mueller et al. (1999) provide substantial experimental evidence that RIFA can negatively affect bobwhite populations under some circumstances. Effects of RIFA on bobwhite and other native animals are greatest in the presence of polygyne colonies (Porter and Savignano 1990, Lofgren 1986, and Allen et al. 1995). Polygyne colonies have multiple fertile queens, exhibit less territoriality, and consequently occur in very dense concentrations (300–2000 mounds/ha; Glancey and Lofgren 1988, Porter et al. 1988, and Lofgren and Williams 1984).

Red imported fire ants can affect bobwhite populations through direct and indirect effects on chicks. Allen et al. (1995) proposed 3 mechanisms by which RIFA may affect bobwhite populations: 1) depredation on pipping chicks, 2) indirect effects on invertebrate food resources of chicks, and 3) direct effects (pathological and mortality) of RIFA stings. Red imported fire ants can directly affect bobwhite populations through predation on pipping chicks (Johnson 1961). Johnson (1961) reported that fire ants may cause 6–12% mortality of pipping chicks. In a study of 440 bobwhite nests in Georgia (L. W. Burger, Mississippi State University, unpublished data), RIFA were responsible for 9.6% of all nest failures. Fire ants destroyed nests by attacking pipping chicks, constructing mounds over the nest cup, and invading the nest during incubation, causing abandonment. Loss to RIFA varied annually from 0 to 14.3% of all nest failures. Exposure to RIFA can reduce survival and weight gain of chicks (Giuliano et al. 1996). Giuliano et al. (1996) reported that exposure to RIFA stings reduced survival and body mass of 4-day-old bobwhite chicks. Moreover, RIFA may alter time and energy budgets of chicks, affecting weight gain and survival (Pederson et al. 1996). Red imported fire ants may reduce foraging efficiency of bobwhite chicks by simplifying invertebrate communities through competition and predation (Fillman and Sterling 1983, Porter et al. 1988, and Porter and Savignano 1990). In a manipulative field experiment, Mueller et al. (1999) demonstrated that RIFA abundance in the vicinity of the nest influenced survival of free-ranging, wild bobwhite chicks to 21 days.

Biologists, operating under the assumption that bobwhite populations are limited by habitat, frequently prescribe management practices that create early successional plant communities through disturbance (discing and prescribed fire). However, land management practices that disturb soil and vegetation and create early successional habitats, might actually increase RIFA abundance and associated negative effects (Allen et al. 1998). Red imported fire ants prefer the open and semi-open vegetation structure characteristic of early successional plant communities (Porter and Tschinkel 1987). Disturbance promotes RIFA colonization in 2 ways: 1) by opening canopy or dense herbaceous layers allowing light penetration, and 2) by removal of competitive native ant species. Native ants generally do not colonize as rapidly or exhibit the rapid population growth of the RIFA (Tschinkel 1993, Allen et al. 1998). Williamson et al. (*this volume*) demonstrate that management practices commonly prescribed to enhance bobwhite habitat (discing and fire) can have the unintended consequence of increasing RIFA abundance or activity in areas of high infestation, creating a management conundrum. Maintenance of early successional habitats is essential for bobwhite, yet in areas of high RIFA infestations, these practices can be expected to increase local abundance of RIFA, which could result in associated negative impacts on bobwhite population performance (Allen et al. 1995, Giuliano et al. 1996, Mueller et al. 1999).

Consistent with Brennan's (1993) argument, high density bobwhite populations can clearly be maintained in the presence of RIFA populations. However, actual population consequences of RIFA to bobwhite in the southeastern United States are unknown, but potentially significant. Range expansion and population growth of RIFA may exacerbate bobwhite population declines. Ironically, the very management practices we would prescribe to enhance bobwhite habitat may increase local RIFA populations. To this point, most of the RIFA/bobwhite research has been conducted in Texas. Throughout the remainder of the Southeast, the crucial experiments have not been conducted to quantify the magnitude and mechanisms by which expanding RIFA populations might affect bobwhite population processes. Additional research is needed to experimentally document the effects of RIFA on bobwhite demographics throughout the Southeast.

Harvest

The effect of harvest on bobwhite populations is an issue of prominent theoretical and applied interest to the natural resource profession and society. Bobwhite populations are a renewable resource that provide nutritional, economic, recreational, and aesthetic benefits (Burger et al. 1999). Compensatory mortality and density dependent reproduction have been proposed as mechanisms that buffer harvest mortality. Traditional harvest management for small game species, like bobwhite, assumes that more animals are produced than can survive. It is presumed that, up to a point, this "doomed surplus" can be harvested without affecting standing densities (Errington 1934). Relative stability of hunted bobwhite populations and small differences in breeding densities between hunted and unhunted populations have been cited as evidence that hunting minimally affects abundance (Errington and Hamerstrom 1935, Marsden and Baskett 1958, Baumgartner 1944, Vance and Ellis 1972). However, despite decades of research, theoretical and empirical aspects of harvest theory remains poorly understood for bobwhite (Roseberry and Klimstra 1984, Robertson and Rosenberg 1988) and fundamental hypotheses regarding mechanisms of compensation remain untested (Caughley 1985).

For bobwhite populations to persist under sustained harvest, corresponding reductions in natural mortality or increases in reproductive rate must occur to compensate for harvest losses (Kautz 1990). Various models have been proposed to describe the relationships among harvest, mortality, reproduction, and density. At one extreme is the completely compensatory model, whereby harvest less than some threshold level does not increase seasonal or annual mortality of the harvested population (Anderson and Burnham 1976, Kautz 1990). The other extreme is the completely additive model which suggests that any level of harvest mortality is in addition to natural mortality and reduces annual survival correspondingly (Anderson and Burnham 1976, Kautz 1990). Intermediate to these extremes is the partial compensation model, whereby harvest at any level reduces the breeding density below its unharvested level; however, remaining individuals have enhanced survival and reproductive success and the population achieves a potential rate of increase greater than that of an unharvested population (Caughley 1985). It is this annual increase, or growth increment, that is harvested (Roseberry and Klimstra 1984, Caughley 1985, Robertson and Rosenberg 1988). The complete compensation and partial compensation models assume that reductions in natural mortality and increases in fecundity occur through density-dependent mechanisms. The completely additive model assumes that survival and reproductive success are independent of density.

For bobwhite, the complete-compensation harvest model is unrealistic and provides an inadequate basis for scientific harvest management of game bird populations (Roseberry and Klimstra 1984, Potts 1986, Pollock et al. 1989). A prediction of this model is that harvested populations will experience similar fall-spring mortality rates as unharvested populations. Guthery et al. (2000), citing 7 published and unpublished studies of hunted and unhunted populations, conclude that empirical evidence does not support this prediction because harvested populations generally experience fall-spring mortality rates nearly double that of unhunted populations. Studies in Illinois (Roseberry and Klimstra 1984) and Florida (Pollock et al. 1989) suggest that, for bobwhite, harvest mortality falls closer to the additive than compensatory end of the continuum. Furthermore, the timing of harvest influences the degree of additivity (Roseberry and Klimstra 1984, Pollock et al. 1989). For harvest mortality to be compensated for by a density-dependent reduction in natural mortality, the harvest must precede the period of highest natural mortality. The later in the season the harvest occurs, the less opportunity for compensation and the greater the additive nature of harvest mortality (Roseberry and Klimstra 1984).

The only mechanisms by which harvest mortality may be compensated for are density-dependent mortality, density-dependent reproduction and/or density-dependent emigration/immigration (Potts 1986, Robertson and Rosenberg 1988, Kautz 1990).

The extent to which hunting mortality is compensated for by a reduction in natural mortality is central to an understanding of the effects of harvest on populations (Roseberry and Klimstra 1984, Caughley 1985). Because the relationships among survival, breeding density, and reproduction are complex, estimates of annual survival alone may be misleading (Burger et al. 1998). As noted by Roseberry and Klimstra (1984), the relationship between hunting and natural mortality prior to the breeding season is the central issue. Therefore, the seasonal timing and nature of mortality is critical to evaluating the potential additive nature of harvest mortality. However, additive harvest mortality during the fall-spring period does not preclude compensation through density-dependent reproduction (Guthery et al. 2000). Density dependent reproduction might occur through variation in any 1 or a combination of the components of reproductive success (Burger et al. 1995).

Although experimental studies of the effects of harvest on bobwhite populations have not been conducted, Guthery et al. (2000) modeled bobwhite population viability for northern and southern populations subject to harvest and weather catastrophes (winter and summer). Given the set of assumptions underlying their model, in the absence of harvest the demographic capacity required for 95% probability of persistence for 100 years was approximately 100 for summer catastrophes, 500 for winter catastrophes and 800 for both summer and winter catastrophes. Demographic capacity required for population sustainability under summer catastrophes and harvest (assuming harvest completely additive) was 140 at 10% harvest, 450 at 20% harvest, and 700 at 30% harvest. They reported that a demographic capacity in excess of 10,000 would be required to sustain populations under a 40% harvest and summer catastrophes. Populations subject to winter catastrophes required a demographic capacity of 80 at 10% harvest, 100 at 20% harvest, and 400 at 30 or 40% harvest. Populations were unsustainable at 50% harvest rate. An important outcome of this model is that southern populations are less vulnerable to extinction under no harvest, but northern populations are less vulnerable to extinction in the presence of harvest (Guthery et al. 2000). Furthermore, southern populations required larger demographic capacities for persistence at all harvest rates. They demonstrate that northern and southern populations respond differently to harvest and these differences should be considered in developing appropriate harvest regimes across latitudinal gradients (Guthery et al. 2000). The strength of this modeling exercise is that it realistically incorporates known demographic processes such as density dependence and allows testing of the effects of various extraneous events such as weather catastrophes and harvest. Furthermore, it demonstrates the effect of demographic capacity on population persistence and when coupled with estimates of density or usable space (Guthery 1997) provides an approach for biologists to estimate minimum size landscapes required for self-sustaining populations. The clear relationships among demographic capacity, harvest rate, and population persistence point out the difficulties in developing sustainable harvest regimes for bobwhite populations inhabiting fragmented landscapes. Populations inhabiting small or isolated habitat fragments (such as those throughout much of the Southeast) will be more vulnerable to extinction and harvest may increase probability of extinction (Guthery et al. 2000).

In recent decades, numerous Southeastern state resource management agencies, charged with setting and enforcing harvest regulations, have struggled with establishing a harvest framework that permits maximum recreational opportunity while at the same time minimizing additive harvest mortality in already declining populations. The principle approach has been to shorten season length by reducing late season (Feb) hunting opportunities. In outheastern states, warm temperatures and activity of venomous snakes limit hunting opportunity in November and December. Thus, January and February have traditionally provided most of the bobwhite hunting opportunity. Reductions in February hunting opportunities, although they might be biologically defensible, run contrary to long-term southern hunting tradition and may contribute to further attrition of bobwhite hunting enthusiasts (Burger et al. 1999). State agency biologists and conservation commissions find themselves in a quandary as they attempt to balance opportunity with sustainability. However, these decisions on harvest framework are more often made on the basis of tradition, economics, or political ramifications as opposed to biological sustainability. As our profession faces the 21st century there is an increasing need to understand the mechanics of bobwhite harvest management to support both harvest recommendations and management practices with defensible population performance data (Murphy and Noon 1991, Nudds and Morrison 1991, Burger et al. 1994). Experimental approaches such as those advocated by Burger et al. (1994) and modeling approaches demonstrated by Guthery et al. (2000) provide tools to acquire information needed for science-based management.

Metapopulation Processes

As early successional patches become more isolated and more ephemeral in duration, previously panmictic populations may become disjunct and local populations formerly interconnected by some level of gene flow may become isolated. In the face of diminishing habitat quantity and widely distributed habitat patches, isolated bobwhite populations may be more vulnerable to demographic and regional stochastic processes (random, regionally correlated catastrophic events such as weather) that increase the probability of local population extinctions, reduce recolonization rates, and contribute to regional population declines (Roseberry 1993). In an essay entitled ‘‘Bobwhite and the New Biology,’’ Roseberry (1993) recognized that ‘‘The viability of local populations depends not only on their own attributes, but also on certain spatial and temporal characteristics of neighboring patches and resident populations (i.e., the metapopoulation).’’ As early as 1984, Roseberry and Klimstra (1984) questioned whether populations that occupy remnant patches of remaining habitat might be at greater risk because of their isolation. Roseberry (1993) recognized that the structure of landscapes and the movements of individuals among populations likely influenced local and regional population stability. They called for quail biologists to incorporate elements of landscape ecology into their thinking and plan and implement management regimes at a broader spatial scale. Yet nearly a decade later, relatively few real advances in modeling bobwhite population processes at landscape scales have occurred (although see Guthery et al. 2000).

In modern landscapes, regional persistence of bobwhite populations are surely subject to metapopulation processes. A metapopulation is a regional set of local populations persisting in a balance between local extinction and recolonization (Levins 1969, 1970). When a regional population functions as a metapopulation, regional persistence depends critically upon parameters affecting extinction and colonization rates, rates and patterns of interpatch migration, and propagule establishment probabilities. Does metapopulation theory ''fit'' bobwhites? Early successional species in general may fit the metapopulation model because early successional communities are ephemeral by nature and often exist in a dynamic mosaic landscape (Harrison 1991). In these systems, habitat dynamics drive the dynamics of early successional wildlife species. Through natural plant succession, every population is subject to extinction and the competing processes of disturbance and succession govern colonization and extinction. If a species does not perfectly track its shifting habitat, it will show metapoplation attributes, such as absence from suitable habitats and vulnerability to regional collapse (Harrison 1991). Although metapopulation theory is well developed and has been applied to the conservation of numerous other species (Hanski and Gilpin 1991), as yet, the relevance of metapopulation principles to regional bobwhite population dynamics has not been investigated. This is, in part, because some of the critical parameters required to model metapopulation processes (e.g., dispersal rates and distances, colonization and extinction rates) have not been estimated for bobwhite (although see Fies et al. *this volume*).

During the first half of the 20th century, the southeastern landscape was characterized by a heterogeneous mosaic containing ubiquitously distributed and interconnected patches of early successional habitats. In such a landscape context (or in modern landscape with vast contiguous habitat), the metapopulation nature of bobwhite populations would not be apparent. In modern landscapes, the metapopulation nature of regional bobwhite populations may be more apparent. Some predictions that follow from the theory include: 1) as early successional patches are lost through changing management practices or fire exclusion, remnant patches become increasingly smaller and more isolated leading to reduced colonization and increased risk of regional decline; 2) regionally correlated, stochastic environmental events (drought, global warming, increasing regional predator populations, etc.) increase the risk of metapopulation extinction; 3) bobwhite may be missing from systems of small or isolated, but otherwise suitable habitat, and 4) vulnerability to regional collapse. Site-specific habitat management has been and will continue to remain the core strategy for bobwhite recovery efforts. However, it has been recognized that the success of a local management program is scale-dependent. That is, a given level of management intensity is more efficacious when conducted on a larger scale.

Guthery et al. (2000) demonstrate that viability (probability of population persistence) of a local population increases with increasing demographic capacity and that minimum viable population size varies under different types of environmental catastrophes. They illustrate application of their model to determine minimum quantity of usable space required for local population persistence. However, their model does not incorporate interactions among local populations (immigration/emigration). To address regional population persistence, biologists and managers must address the problem from a regional or landscape perspective and recognize that the viability of local populations is affected not only by local demographics, but also by interactions with surrounding populations (Fies et al. *this volume*). To adequately understand these regional processes, we must employ more sophisticated, spatially explicit population models. Application of these models requires robust quantitative characterization of the distribution of habitat patches across the landscape. Habitat models, both theoretical (Guthery 1997) and empirical (Roseberry and Sudkamp 1998, Schairer et al. 1999), have been developed to characterize habitat quality at various spatial scales and these models may provide a starting point for development of spatially explicit population models. Spatially explicit population models link habitat models with population models that incorporate habitat specific population parameter estimates. To incorporate stochasticity, we must have empirical estimates of key population parameters and the probability distributions from which they are drawn and know how these demographic parameters vary among habitat patches or in relation to relative habitat quality. Additionally, we must better understand bobwhite dispersal, colonization, and extinction processes. Despite the substantial progress in modeling habitat quality and population viability illustrated in Guthery (1997) and Guthery et al. (2000), we have yet to integrate habitat, population, and movement/dispersal models in comprehensive, spatially explicit population models that characterize regional population processes.

CONCLUSION

As human populations, per capita consumption of resources, and technological capabilities in agriculture and forestry continue to expand, the regional availability of suitable habitats and subsequently bobwhite populations will continue to decline. Changing demographic patterns and public values and declining hunter participation will contribute to a declining constituency that values bobwhite and the habitats to which they are adapted. State level initiatives may be successful in enhancing local populations; however, regional conservation efforts may provide the greatest opportunities for restoration. These efforts will benefit regional bobwhite populations only if early successional habitats are valued by the public and conservation community. Management of remnant bobwhite populations in modern, highly fragmented and simplified landscapes will require a new and more comprehensive understanding of the effects of predation, harvest, and landscape structure on population processes. Acquisition of this knowledge will not just require more research, but a different kind of research, one more rigorous, creative, quantitative, and mechanistic.

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