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Rollins, Dale and Carroll, John P., "Impacts of predation on northern bobwhite and scaled quail" (2001). *Papers in Natural Resources*. 651.

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#### SPECIAL COVERAGE

# Impacts of predation on northern bobwhite and scaled quail

by Dale Rollins and John P. Carroll

Abstract

Northern bobwhite (Colinus virginianus) and scaled quail (Callipepla squamata) populations have declined throughout most of their distribution, and these declines have become more dramatic in recent years. In this review, we examine the role of predation in quail management. Predation is the major source of nest loss and of mortality for young and adult quail. Mean nest success across studies reviewed was 28%. Estimates of annual survival rates have varied from 5 to 26% for radiotelemetry studies and from 15 to 30% based on age-ratio studies. Breeding season survival estimates ranged from 13 to 51% in telemetry studies reviewed. Brood survival is the least studied aspect of quail survival; estimates ranged from 13 to 47%. Mammalian predators most often implicated in nest predation include striped skunks (Mephitis mephitis), raccoons (Procyon lotor), opossums (Didelphis virginianus), foxes (Urocyon cinereoargenteus and Vulpes vulpes), coyotes (Canis latrans), and feral hogs (Sus scrofa). Accipiters (Accipiter spp.) and northern harriers (Circus cya*neus*) are the most common avian predators of quail. Less information is available to assess impact of predation on scaled quail, but observations from areas where bobwhites and scaled quail are sympatric suggested that scaled quail are less vulnerable to predation than bobwhites. Although quail have adapted to cope with high predation rates (e.g., renesting, large clutches), populations in some areas may be suppressed by predation. Changes in land use, management practices, and predator communities interact to depress quail populations over much of the bobwhite's range. Additional studies are needed to assess the role of predation and predation management in light of these landscape-level changes. A variation of the Integrated Pest Management philosophy used in crop production is proposed as an appropriate model to address predation management for quail.

**Key Words** avian recruitment, *Callipepla squamata, Colinus virginianus,* game birds, Integrated Pest Management, mesomammals, northern bobwhite, population regulation, predation, raptors, scaled quail

ecause of their relatively small size and the fact that they spend their entire lives on the ground, various species of quail (Odontophoridae) are extremely vulnerable to predation. However, prevailing paradigms in quail management suggest that predators are rarely a management concern and that predation should be managed only indirectly (e.g., habitat management; Errington 1934). Herein we review the evidence relative to the impacts of predation

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Wildlife Society Bulletin 2001, 29(1):39-51

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on northern bobwhite (*Colinus virginianus*, hereafter bobwhite) and scaled quail (*Callipepla squamata*) as models for North American species. For bobwhites, we focus our discussion primarily on the eastern and western peripheries of the range, i.e., the southeastern United States and Texas, respectively, because bobwhite abun-

We do not discount the current management paradigm of indirect predator control (i.e., habitat management).... However, the issue of predation as it relates to quail must be evaluated in a more contemporary context of an increasingly fragmented landscape...and temporal changes in predator populations.

2000). Bobwhite populations in the Rolling Plains and South Texas Plains ecoregions have remained relatively stable, but roadside counts in 2000 were the lowest since counts began for the Gulf Prairies and Marshes, Cross Timbers and Prairies, and Edwards Plateau ecoregions (Texas Parks and Wildlife 2000).

quail trends vary among ecoregions (Peterson and Perez

Scaled quail

Scaled quail range over most of the Chihuahuan desert, including portions of Arizona, Colorado, Kansas, New Mexico, Oklahoma, and Texas. Scaled quail populations have declined significantly (from -3.8%/yr from 1966 to 1991 to

dance typically declines along a west-to-east gradient. We also identify areas where additional research is needed and offer a more contemporary philosophy of predation management for quail, which is based on the philosophy of Integrated Pest Management.

#### Current status of bobwhite and scaled quail

#### **Bobwhites**

The decline of the bobwhite in the southeastern United States (U.S.) is well documented (reviewed by Brennan 1999). Bobwhite populations declined -2.8%/year from 1966 to 1999 (P < 0.01) across its range according to Breeding Bird Survey data (Sauer et al. 2000, Figure 1). The decline of bobwhites is correlated generally with dramatic changes in land use throughout the region over the last 80 years. The shift away from a landscape dominated by rather diverse and low-impact agriculture in the early twentieth century to landscapes dominated by hardwood forests and intensive pine silviculture in the latter twentieth century reduced habitability for bobwhites. In more recent times, dramatic changes in agricultural practices (e.g., clean farming, increased use of pesticides) also may have contributed to poorer quality or quantity of remaining habitats. In any event, a landscape that supported large and widespread populations of quail is now gone. Presently, bobwhite populations over most of the Southeast seem to be generally at much lesser levels and very fragmented (Brennan 1999).

Although bobwhite densities are generally greater at the western periphery of their range (e.g., Texas), their abundance there has declined at a rate of -4.7/year since 1981 (Sauer et al. 2000). The Texas population's trend is essentially parallel to that of populations in the Southeast (Figure 1). Bobwhites occur over most of Texas, but

-8.2%/yr from 1982 to 1996) throughout their range, especially during the last 15 years (Brennan 1993; Church et al. 1993; Schemnitz 1993, 1994; Peterson and Perez 2000; Rollins 2000; Sauer et al. 2000). Scaled quail populations experienced a drastic, inexplicable decline about 1989 over much of their range in Oklahoma and north Texas (Rollins 2000). Populations in the Oklahoma panhandle declined 50% from 1956 to 1991 (Schemnitz 1993), and scaled quail essentially disappeared along the eastern periphery of its range, where they were common to abundant in 1987 (Rollins 2000). Data from the Breeding Bird Survey (Sauer et al. 2000) and the Texas Parks and Wildlife Department (2000) documented this demise (Figure 2). Relative to the Southeast, land-use changes have been less dramatic in scaled quail range, which is dominated largely by livestock grazing.

## Factors contributing to quail population declines

Aside from the possible impacts of predation and land-use changes, other factors may be involved in the



Figure 1. Northern bobwhite abundance in the southeastern U.S. (dotted line) and Texas (solid line) according to Breeding Bird Survey data, 1966–99 (Sauer et al. 2000).

decline of bobwhite and scaled quail populations. Other factors believed to be contributing to the decline of quail in the Southeast range from fire ants (Solenopsis spp.) to acid rain (Brennan 1999). However, there also is ample evidence that bobwhite populations in some areas of the Southeast are being maintained at high densities, especially in the plantation regions of southern Georgia and northern Florida. In these areas suitable landscapes have been maintained and quail are managed intensively (Burger et al. 1998).

This suggests that landscape changes are important at the regional scale, but that additional mechanisms may be operating at the local scale.

Presently there is much speculation about the role predators play in the long-term declines of quail populations at a local scale, despite habitat management (Hurst et al. 1996). There is little evidence to suggest that predators are suppressing bobwhite populations at a regional level. However, anecdotal observations of predator removal where habitat management is being practiced suggest that some predators may be suppressing local quail populations.

How predators interact with quail populations may be affected not only by the way landscape changes have impacted habitat, but likewise predator populations, communities, and search efficiencies. For example, recent changes in land use may have made quail more vulnerable to predation (Hurst et al. 1996, Rollins 1999a). Such changes may operate at landscape and local levels.

The causes of the scaled quail decline are unknown. Schemnitz (1993) speculated that land-use changes (e.g.,



Figure 2. Scaled quail abundance in Texas according to Breeding Bird Survey data (solid line), 1996-99 (Sauer et al. 2000) and Texas Parks and Wildlife Department roadside counts (dotted line), 1968-2000 (Texas Parks and Wildlife Department 2000).

Table 1. Nest success rates (%) and percentage of mortalities lost to predators of bobwhite nests at various locations.

Location	n	Nest success (%)	Method of monitoring	Lost to predators (%)	Reference
Illinois	863	34	Nest searching	37	Roseberry and Klimstra (1975)
Florida	601	36	Nest searching	64	Stoddard (1931)
Florida	51	45	Telemetry	89	DeVos and Mueller (1993)
Georgia	1,725	18	Nest searching		Simpson (1976)
Missouri	157	44	Telemetry	68	Burger et al. (1995 <i>b</i> )
North Carolina	35	34	Telemetry	73	Puckett et al. (1995)
Oklahoma	161	50	Telemetry	76	Peoples et al. (1996)
Tennessee	766	23	Nest search		Dimmick (1974)
Texas (north)	34	12	Nest search	88	Jackson (1947)
Texas (north)	81	46	Telemetry	91	Hernandez (1999)
Texas (south)	32	45	Nest search	84	Lehmann (1984)
Weighted mean		28			

Conservation Reserve Program) were responsible in the Oklahoma panhandle. Rollins (2000) provided anecdotal information suggesting that disease was the initial factor involved and that high nest depredation rates (>80%)may have kept populations suppressed. Bobwhites, which are sympatric with scaled quail over much of the Rolling Plains ecoregion, declined in about the same time period (1989-90), but have since rebounded and exhibited irruptive population changes typical of the species in this area (Jackson 1962, Peterson and Perez 2000, Sauer et al. 2000). Scaled quail remained absent or occurred at only remnant levels over much of their former range in Texas from 1989 to 1999.

#### Predators of bobwhites

Predation is the primary source of mortality for bobwhites at all life stages. There are numerous studies, dating back to Stoddard (1931), documenting the impacts of predators on bobwhites, especially in the southeastern U.S.

#### *Nest depredation*

Rollins (1999a) estimated that only about 4 of 100 eggs result in a bobwhite eventually being added to the breeding population in Texas. Nest depredation on bobwhites has been studied in various locations using a range of techniques from anecdotal observations to video monitoring of radio-tagged hens. Estimates of predation rates on quail nests are typically high, and hatch success rates vary from 12 to 50% (weighted  $\bar{x}$ =28%, Table 1). Hatch rates of 36%, 18%, and 34% were reported from long-term studies in Florida, Illinois, and Georgia, respectively (Stoddard 1931, Klimstra and Roseberry 1975, Simpson 1976). Hatch rates in Texas ranged from 12 to 46% (Jackson 1947, Lehmann 1984, Hernandez 1999). Peoples

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et al. (1996) recorded a 50% hatch rate in western Oklahoma, with predators accounting for 81% of the losses. Accounting for predation on nests and adults, DeVos and Mueller (1993) suggested that 81% of nest losses were caused by some type of predation, with 52% of the losses attributed to mesomammals (i.e., medium-sized carnivores). Other locally important nest predators may include corvids (Slater 1996), rodents (Stoddard 1931), armadillos (*Dasypus novemcinctus*; E. Staller, Tall Timbers Research Station and University of Georgia, unpublished data), and various snakes (Stoddard 1931).

Bobwhites are persistent renesters, resulting in much greater percentages of hens actually producing chicks than would be suggested by low hatch rates (Burger et al. 1995*b*, Guthery 1995, Brennan 1999). Rollins (1999*a*) estimated that, given a hatch rate of 30%, no hen mortality, and 2 renesting attempts, 66% of hens would eventually hatch a clutch of eggs. However, number of successful clutches decreased to 49 and 33% when hen mortality was 20 and 40%, respectively.

Mesomammals are the most important group of nest predators. In Virginia, Fies and Puckett (2000), using simulated ground nests containing quail eggs, found that 41% of nest predators photographed by motion-sensing cameras were striped skunks (*Mephitis mephitis*), 37% were opossums (*Didelphis virginianus*), 8% were gray foxes (*Urocyon cinereoargenteus*), and 4% were raccoons (*Procyon lotor*). Hernandez et al. (1997) used similar equipment to study nest depredation in west Texas and reported that raccoons (82% of all nests destroyed) were the primary predator of simulated quail nests. Less common predators included striped skunks, bobcats (*Lynx rufus*), gray foxes, armadillos, and opossums.

Stoddard (1931) identified several species of snakes that were important nest predators. Snake depredation of bobwhite nests has been confirmed by recent camera-surveillance studies in Virginia (passive infrared still cameras, Fies and Puckett 2000) and in Georgia (continuous infrared video cameras; E. Staller, C. Sisson, W. Palmer, and J. Carroll, University of Georgia, Auburn University, and Tall Timbers Research Station, unpublished data). Often snakes are diagnosed as the cause of nest depredation when no eggshells are found. For example, Peoples et al. (1996) implicated snakes in 55% of the nest losses recorded in western Oklahoma. However, Hernandez et al. (1997) cautioned that snakes may be overly maligned as an egg predator when diagnoses are based on lack of eggshell evidence. Aside from depredating nests, rat snakes (Elaphus sp.) and rattlesnakes (Crotalus spp.) have been documented preying on bobwhites in Florida and bobwhite and scaled quail in Texas (Stoddard 1931; Carter 1995; D. Rollins, unpublished data; Figure 3).



Figure 3. Rattlesnakes, although not a major predator of quail, have been documented preying on radio-marked quail in Georgia and Texas. The bulge in this western diamondback rattlesnake represents the remains of a scaled quail wearing this telemeter.

#### Brood survival

Chick survival is the least understood aspect of quail mortality (DeVos and Mueller 1993, Hurst et al. 1996). Researchers have attempted to assess mortality of chicks after hatching, but logistical constraints have complicated such attempts (Carver et al. 1999). DeMaso et al. (1997) reported a survival rate of 36% from hatching to 39 days post-hatch in western Oklahoma. DeVos and Mueller (1993) estimated 29% survival to 1 month post-hatch. Roseberry and Klimstra (1984) reported chick survival rates of 25–47% in southern Illinois. In Iowa, Suchy and Munkel (2000) reported survival rates of 81% for chicks 21–56 days post-hatch. They reported a cause-specific mortality rate of 14% for mammalian predation and 6% for avian predation.

Fire ants also may impact chick survival (Allen et al. 1995, Mueller et al. 1999). Allen et al. (1995) found that bobwhite declines in southeastern Texas were correlated with a particular county's invasion by imported red fire ants (*S. invicta*). Mueller et al. (1999) reported that 38% of all chick mortality up to 21 days post-hatch was attributable to fire ants.

#### Post-brood survival

Adult survival also varies widely by season and causes. Taylor et al. (2000) found that breeding season survival over 4 years in Mississippi ranged from 17 to 51%. Predators accounted for most of the mortality. During this study, avian mortality showed characteristics of being density-dependent; however, mammalian predation continued to increase despite declining quail populations. Over 5 years on a plantation in Georgia where predators were actively controlled, Burger et al. (1998) found that breeding season survival was 41%. Mammalian (25%) and avian predators (20%) accounted for most of the mortality. Other studies documenting breeding season survival suggested generally lower survival rates, including 33% in Missouri (Burger et al. 1995a), 40% in Florida (Curtis et al. 1988), 34% in Mississippi (Taylor et al. 2000), and 33% in North Carolina (Curtis et al. 1988, Puckett et al. 1995). Carter (1995) monitored the fate of 131 radio-marked bobwhites in west Texas during 1994-95 and reported a February-July survival rate of 13%. Mammals were responsible for 56% of the kills, whereas raptors caused 25%. Burger et al. (1998) also suggested that nonbreeding season mortality of adults was attributed mainly to predation from mammals (25%)and avian predators (16%); overall adult survival averaged 49%. Pollock et al. (1989) reported annual survival rates of leg-banded bobwhites from 10 to 24% ( $\bar{x}$ =17%) over a 13-year period in a hunted population in Florida. Hunting accounted for 30% of the annual mortality, but cause-specific rates of natural mortality (e.g., predation) could not be determined.

### Predators of scaled quail

#### Nest depredation

Nest success for scaled quail is typically low (<25%, Wallmo 1957), and depredation has been cited as a major, if not primary, cause of nest failure. Nest predators common in scaled quail range include coyotes, striped skunks, gray foxes, corvids (Slater 1996), various snakes, and, increasingly, feral hogs (Tolleson et al. 1993). Jackson (1942) reported that 10 of 13 scaled quail nests failed in the Texas panhandle. In a more detailed report from the same area, Jackson (1947) reported that 30 of 34 bobwhite nests (88%) failed. He attributed the losses to coyotes (11 nests), snakes (6 nests), and small mammals (5 nests). Schemnitz (1961) reported that only 6 of 42 nests (14%) hatched. The primary cause of nest failure was human disturbance (e.g., farming practices and mowing), and predators were implicated in only 19% of the nest losses. Recent studies (Hernandez et al. 1997, Fies and Puckett 2000) suggested that the accuracy of assigning species-specific causes of quail nest depredation is tenuous at best.

#### Brood survival

We found no published reports on chick or brood survival for scaled quail. As scaled quail population "busts" are characterized by poor recruitment, information on chick survival and brood ecology is sorely needed.

#### Post-brood survival

None of the 3 major autoecological studies on scaled quail (Wallmo 1957, Schemnitz 1961, Campbell et al.

1973) cited predation as a management concern; in fact, predation was hardly mentioned as a source of mortality. Wallmo's (1957) only mention of predation was that which occurred at quail trapping sites; species involved were gray foxes, striped skunks, ringtails (*Bassaricus astutus*), raccoons, and Cooper's hawks (*Accipiter cooperii*). Schemnitz (1961) mentioned predation only in that 7 of 36 scaled quail nests (19%) were destroyed by predators. Campbell et al. (1973) calculated annual survival rates of scaled quail from band recoveries in southeastern New Mexico as 6% on hunted areas and 10% on nonhunted areas, but made no mention of what proximate mortality factors were involved other than hunting.

### Relative vulnerability of sympatric bobwhite and scaled quail

Bobwhite and scaled quail occur sympatrically in portions of Texas, and some studies have mentioned the relative vulnerability of these species to predators. Jackson (1947) suggested that predation was the proximate cause of a catastrophic decline in bobwhites in northwest Texas during winter 1943. Bobwhites and scaled quail were sympatric on Jackson's study site, and scaled quail accounted for about 65% of the total quail during 1941–43. Total quail density (bobwhite + scaled quail) was high (estimated at 1.6 birds/ha). Jackson (1947: 514) detailed how bobwhite populations on his study area crashed "with explosive suddenness and all but remnants were lost to predation" between 7 and 15 January 1943. He conducted transects to estimate amount of mortality that had occurred and concluded that "everywhere the ground was littered with evidence that predation had been recent and terrific" (Jackson 1947: 514). Northern harriers (Circus cyaneus), red-tailed hawks (Buteo *jamaicensis*), and Cooper's hawks were the raptors involved, but Jackson concluded that northern harriers were the only raptor species abundant enough in that area to have killed so many quail. Four of 18 northern harriers examined had consumed bobwhites. Jackson reported that evidence of predation on scaled quail was "light" and that scaled quail were apparently less vulnerable to avian predation than were bobwhites.

P. S. Carter (Angelo State University, unpublished data) radio-marked 27 scaled quail in west-central Texas (Irion County) and reported higher survival (70%) from February to July than for sympatric bobwhites (18%, n= 54). In Carter's study (for both species of quail) 60% of mortalities were attributed to mammalian predators. He documented 9 scaled quail mortalities, 5 from mammals, and 2 from unknown raptors. One scaled quail was killed by a great horned owl (*Bubo virginianus*) and one

by a western diamondback rattlesnake (C. atrox).

These data support Jackson's (1947) observation that scaled quail may be less vulnerable to predation than bobwhites and Lehman's (1984: 225) opinion that "blue (i.e., scaled) quail seem somewhat more intelligent than bobwhites" in sympatric ranges.

It seems plausible that earlier investigations of scaled quail (Wallmo 1957, Schemnitz 1961, Campbell et al. 1973) either were unaware of or dismissed the incidence of predation because they lacked the technology to study it (i.e., radiotelemetry). Rollins (2000) divided the knowledge about scaled quail ecology into 2 distinct eras: before telemetry and after telemetry. More comprehensive studies involving radio-marked scaled quail are needed to assess cause-specific mortality patterns.

#### Role of predation in quail irruptions

Bobwhite and scaled quail exhibit irruptive population growth in Texas (Jackson 1962, Lehmann 1984). Population "busts" are believed to be a result of normal attrition but below-normal reproduction (Wallmo 1957). Such busts tend to be characterized by drought conditions (Wallmo 1957, Campbell et al. 1973, Giuliano and Lutz 1993), but scaled quail appear to be more productive during drought years than are sympatric bobwhites (Schemnitz 1964, Lehmann 1984, Rollins 2000). Irruptions appear to be related indirectly to rainfall, possibly through some plant-related stimulus (e.g., nutrition). Various investigators have proposed vitamin A deficiencies (Nestler 1946, Lehman 1953), phytoestrogens (Cain et al. 1987), and water deprivation (Koerth and Guthery 1991) as possible explanations for reproductive failures in quail in the southwestern U.S.

An alternate hypothesis is that precipitation increases nesting cover across the landscape, i.e., "usable space" (Guthery 1997: 294), and subsequently increases nesting success by complicating the predators' search efficiency (Rollins 1999*a*). Quail irruptions in the Rolling Plains ecoregion of Texas are characterized by landscapes dominated by common broomweed (*Xanthocephalum dracunculoides*, Jackson 1962, Rollins 1999*b*). Dense canopies of common broomweed effectively "insulate" quail from predators (avian and mammalian) and hence increase "usable space."

Predator search efficiency may decline as abundance of suitable nest sites or habitat heterogeneity increases across the landscape (Bowman and Harris 1980). It is more difficult for predators to locate ground nests in areas supporting abundant bunchgrasses compared to areas with few bunchgrasses (Jackson 1947). Lehmann (1984) noted greater nest survival in areas where the nest was situated in cover that was uniform with the surroundings.

Because quail population "busts" are usually associated with drought conditions in the southwestern U.S. and often confounded by overgrazing, suitable nesting cover is often limited in dry years. Slater et al. (2001) found that nest success of simulated quail nests in 8 counties in west Texas was greater on sites that provided >760 potential nests sites/ha, a number similar to Guthery's (1986) recommendation of >500 suitable nest clumps/ha for bobwhites in Texas. Carter (1995) found that sympatric bobwhites and scaled quail frequently used prickly pear (Opuntia spp.) for nesting sites. Subsequently, Slater et al. (2001) documented that nests situated in prickly pear survived at about twice the rate of more conventional nest sites (i.e., bunchgrasses). Thus, prickly pear appears to provide some measure of protection against nest predators, especially when traditional nest sites are limited by overgrazing or drought (Hernandez 1999).

### Temporal changes in predator populations and communities

Our review of published research suggests that bobwhite and scaled quail populations have changed at local and regional scales. What about their predators? Comparing earlier studies (e.g., Stoddard 1931) to more contemporary studies suggests that changes have occurred within populations and communities of various predators that are often implicated in the decline of quail populations. Such temporal changes in predator populations may be important, especially in light of landscape changes that may make quail more vulnerable to predation (Rollins 1999*a*).

#### Mesomammal trends

There is general consensus that mesomammal populations (e.g., raccoons) have increased over the last 20 years in the Southeast. Rollins (1999a) identified a number of mechanisms that may be contributing to greater mesomammal populations or otherwise accentuating predation on quail and their nests. These mechanisms include 1) demise of the fur market in the mid-1980s, 2) increased supplemental feeding of deer (Odocoileus spp.), 3) increasingly fragmented habitats, and 4) a proliferation of farm ponds on the landscape. Other authors have speculated on the impacts of various of these factors on recruitment in galliformes (Palmer et al. 1993, Hurst et al. 1996). Raccoons, a primary nest predator in Texas (Hernandez et al. 1997), probably benefit by an increasingly popular practice of providing supplemental feed to deer in Texas. As many as 12 raccoons have been photographed at a single free-choice protein feeder (D.

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Figure 4. The increasing popularity of supplemental feeding for whitetailed deer may be influencing raccoon populations in Texas.

Rollins, unpublished data; Figure 4). Cooper and Ginnett (2000) found that simulated ground nests (e.g., chicken eggs) had lesser survival rates in 2 of 3 years on sites where deer feeders were present.

Another example of temporal changes in a predator community is suggested by comparing 2 studies conducted in north-central Texas (Wise and Parker counties). Jackson (1952) removed potential quail predators (n=574) from a 1,200-ha study site in Wise County, Texas, over a 13-month period (1948-49), but dismissed the predator removal as having no impact on quail abundance. Of particular note, only 11 raccoons (2.0% of the predators removed) were trapped during his study. Fifty years later, E. Lyons (Angelo State University, unpublished data) removed 21-40 raccoons from 2 study sites (each 260 ha) during only 30-day trapping efforts in an adjacent county (Parker) during 1999 and 2000, respectively. In other words, Lyons removed about 3 times more raccoons than Jackson did on study sites only 20% the size of Jackson's sites and with only 10% of the trapping effort.

In Mississippi, hunter harvest data from 1980 to 1996 suggested that red foxes (*Vulpes vulpes*), gray foxes, and bobcats remained stable but that coyote (*Canis latrans*) populations increased 7-fold (Lovell et al. 1998). The relationship between coyotes and quail is unclear. Lehmann (1984) identified coyotes as perhaps the most common mammalian predator of bobwhites in south Texas, but Guthery (1995) concluded that controlling coyotes likely would not increase quail productivity given the quail's ability to renest. Interestingly, the greatest bobwhite populations are found typically in the Rolling Plains and Rio Grande Plains ecoregions, and these are the same areas of Texas that typically harbor the greatest densities of coyotes. Similarly, the Edwards Plateau ecoregion, located between the Rolling and Rio Grande Plains, typically has the least quail abundance of these 3 ecoregions. The fact that the Edwards Plateau has the lowest coyote densities in Texas (because of a history of sheep and goat ranching in this area [Nunley 1985]) suggests that coyote suppression may "release" mesomammals like raccoons, gray foxes, and feral cats. Additional studies are needed to document this relationship, however, as edaphic factors also differ among these 3 ecoregions.

#### Other mammals

When Stoddard (1931) undertook his studies on plantations in southern Georgia, striped and spotted skunks (*Spirogale putorius*) were important predators of quail nests. However, recent video data from several hundred nests on plantations in the same region found no evidence of predation by either species (E. Staller, C. Sisson, W. Palmer, and J. Carroll, University of Georgia, Auburn University, and Tall Timbers Research Station, unpublished data). This video surveillance of nests also confirmed armadillos as a predator of bobwhite nests, substantiating the findings of Hernandez et al. (1997) in Texas. During Stoddard's era, there were no armadillos in that region, but today they are ubiquitous.

Finally, the distribution and abundance of feral hogs (*Sus scrofa*) has increased over much of the Southeast and Texas (Tolleson et al. 1993). Feral hogs were implicated in 9 and 24% of the simulated nest losses in Shackelford and Foard counties (respectively) in Texas. However, the impact of feral swine depredation on quail nests is unclear. Similar to coyotes, those areas of Texas with the greatest feral hog abundance (e.g., Rolling Plains, Rio Grande Plains) also support the greatest quail populations.

#### Status of avian predators

Among common avian predators of bobwhites, population increases of >2.0%/year have been observed using the Breeding Bird Survey (1966–99) over large areas of



Figure 5. Cooper's hawk (solid line) and sharp-shinned hawk (dotted line) abundance in the U.S. according to Breeding Bird Survey data, 1966–99 (Sauer et al. 2000).

the U.S. (Sauer et al. 2000). Trends for accipiters, e.g., the Cooper's hawk (6.7%/year, n=359, P<0.01) and sharp-shinned hawk (A. striatus, 2.8%/year, n=233, P= 0.03), have increased steadily over the last 30 years (Figure 5). Factors responsible for the increase of various avian predators of quail are unknown, but could include the dissipation of organochlorine insecticides, increased law enforcement, and educational efforts on raptor conservation. Accipiters are generally considered the most efficient predator of quail, and Stoddard (1931: 212) characterized Cooper's hawks as "the outstanding natural enemy of the bobwhite." Other raptors, such as the great horned owl, have not increased over the whole southeastern region (0.5%/year, n=136, P=0.82), but in some states, such as Georgia, they have increased (5.5%/year, n=23, P=0.002). Errington (1934) considered great horned owls an important predator of bobwhites in Wisconsin. Greater roadrunners (Geococcyx californianus) are implicated often as a serious predator of quail nests and chicks in Texas. However, recent research in south Texas (C. Ruthven, Texas Parks and Wildlife Department, personal communication) found quail remains (2 chicks) in only 1 of 120 roadrunner stomachs. Nevertheless, roadrunner abundance in the Chihuahuan Desert has increased 3.6%/year over the last 30 years (n=32, P=0.19, Figure 6).

### *Effects of predator reduction on quail populations*

Empirical evidence of the impact (or lack thereof) of predator removal on quail abundance is limited. Beasom (1974) studied the effects of intensive predator control on bobwhites and wild turkeys (*Meleagris gallopavo*) in the eastern Rio Grande Plains of Texas. He removed 188 coyotes, 120 bobcats, 65 raccoons, 46 striped skunks, and 38 other mammalian predators from a 23-km<sup>2</sup> study area over a 2-year period. He observed moderate gains in bobwhite abundance and strong increases in turkey pro-



Figure 6. Greater roadrunner abundance in the Chihuahuan desert according to Breeding Bird Survey data, 1966–99 (Sauer et al. 2000).

duction. Guthery and Beasom (1977) conducted a similar study of intensive removal of mammalian predators (e.g., coyotes, striped skunks) from a 15-km<sup>2</sup> study area in the western Rio Grande Plains of Texas, but could not demonstrate a treatment effect on either bobwhite or scaled quail populations. Their conclusion was that if predator removal was effective at all, the effect would be demonstrated by allowing quail populations on "poorer" areas to be similar to better habitats.

Burger et al. (1998) measured bobwhite mortality and predation rates on intensively managed plantations in Georgia and found that 35% of mortalities were a result of predation by mammals, even with intensive mesomammal control. However, there were no comparative data where predators were not controlled.

If an effect is to be realized from reducing predators, it will most likely result from reducing potential mesomammals involved in nest depredation (Rollins 1999*a*). However, reducing the populations of mammalian nest predators is labor intensive, costly, and will not necessarily result in an increase in quail abundance. Frost (1999) removed approximately 1 mesomammal per 5 ha (mostly raccoons) from 260-ha study areas over a 30-day period just prior to the 1998–99 nesting seasons in Tom Green County, Texas. Survival of radio-marked bobwhites and fate of simulated quail nests were similar on trapped and nontrapped sites. Scent stations indicated that at this scale and level of trapping (75 trap nights/ha), mesomammal abundance was not reduced even in the short term.

#### Discussion

Although predation is usually the primary source of mortality for quail at all stages of their life cycle, predator control has historically been dismissed as a management recommendation for quail. Errington's (1934) long-term studies of bobwhites and predators in the upper Midwest suggested that habitat, not predators, limited bobwhites. His concept-i.e., manage habitat, not predators-has been pervasive in the quail management literature since that time. We do not discount the current management paradigm of indirect predator control (i.e., habitat management) and especially as the "first line of defense." However, the issue of predation as it relates to quail must be evaluated in a more contemporary context of an increasingly fragmented landscape (Robel 1993) and temporal changes in predator populations. In light of these changes, and the current rate of declines observed in quail in some regions, we concur with Hurst et al. (1996) that the issue of predator control relative to avian recruitment in Galliformes should be revisited.

If we compare the prevailing thoughts of predation on

quail with those for a species for which predation and habitat management have been studied more thoroughly (e.g., gray partridge [Perdix perdix]), we find some interesting parallels and contradictions. Potts (1986) modeled the population dynamics of gray partridge using a variety of data sources in the United Kingdom. Potts (1986) presented evidence of density-dependent relationships for survival of gray partridge for major components of their life history, including nesting, hunting, and over-winter survival, as also was suggested by Roseberry and Klimstra (1984) for bobwhites. However, Potts (1986) also demonstrated that some aspects of the life history of gray partridge survival were impacted by density-independent factors, chick survival being the most important factor not related to bird densities. He suggested that predator control was very important in determining the relative importance of density-dependent mortality, especially nest mortality, in gray partridge and that the relative shape of mortality curves with predator control resulted in lower mortality rates at greater partridge densities. Potts' (1986) data suggested there was still densitydependent mortality in partridge nesting even with predator control, but that this relationship was much weaker. Tapper et al. (1996) went on to demonstrate the suppressive effect of nest predators on gray partridge productivity, recruitment, and populations with a 6-year predator removal experiment.

Burger et al. (1998) suggested that annual mortality rates were not a good measure to develop an understanding of the population dynamics of bobwhites. They point out that the annual survival rates they measured were only slightly greater than those for other studies in the Southeast, yet bobwhite densities on their study were much greater than other studies in the region. Burger et al. (1998) suggested that predator removal changed the dynamics of mortality within seasons in support of Potts' (1986) theory. We believe that Burger et al. (1998) are demonstrating that suppression of predator-mediated, density-dependent mortality produces greater recruitment rates. This results in continued high levels of productivity because the density-dependent mortality of nests also is suppressed by predator control, thereby providing at least a possible solution to the annual mortality conundrum presented by Guthery (1997).

### Predator control in simple versus complex environments

Among those studies demonstrating a positive impact of predator control in one form or another on game bird populations, most have occurred in simpler ecosystems and with simpler predator and prey communities than those found in the Southeast (Sargeant et al. 1995, Tapper et al. 1996, Redpath and Thirgood 1997, Kauhala et al. 2000). How these results translate to more complex ecosystems remains to be seen. More diverse (i.e., complex) systems in the Southeast are characterized by competing risks; accordingly, a reduction in one predator's abundance does not necessarily ensure a greater hatch or recruitment rate (Guthery 1995).



First, the predator-prey community on farmland in the United Kingdom is much simpler than those found in the Southeast. Much of the range of bobwhite and scaled quail harbors greater numbers and diversity of predator and prey species. Thus, there are more complex interactions and possible outcomes as we begin to alter the community. Second, management of gray partridge is occurring in a very intensively managed agricultural landscape. In effect, the argument becomes one in which a desire to have larger numbers of gray partridge helps to mitigate the intensive land management for production agriculture. This can positively impact land management for not only the desired game bird but also for other species, including the predators. Predator management helps enhance habitat management, thereby making the system more tenable for those wanting to hunt gray partridge.

The situation in the Southeast is one characterized by a much greater variety of ecosystems managed at different intensities. If predator management to enhance quail populations is done simply to increase the number of quail shot by hunters, then arguments from a conservation perspective are diminished. However, arguments demonstrating the positive impact of intensive quail management on other species also could be made (Webb and Guthery 1983, Harveson et al. 2000). With more diverse predator and prey communities, we are then required to

Telemetry studies of scaled quail have lagged behind those of bobwhites.

make these decisions in a more complex system (e.g., we are also likely to make mistakes and reduce species that result in no net benefit to quail).

#### Predator control or predation management?

As bobwhite populations continue to decline in the Southeast, there is increasing pressure to implement predator control to increase bobwhite abundance. Some conservation organizations, e.g., Quail Unlimited, are increasingly questioning the "if you build it, they will come" habitat paradigm as the sole means of sustaining bobwhite populations. In calling for broad-spectrum predator control, some in and out of the wildlife profession may be acting prematurely. As Leopold (1953: 60) suggested, "the urge to comprehend must precede the urge to reform." Waterfowl managers have done an admirable job in the quest to understand the ecological implications of predator control and subsequently predation management. Quail managers may be well advised to study such examples. As was suggested by Tapper (1999) and Reynolds and Tapper (1996), we might not even need to see a net reduction in predator numbers to have a positive impact on game bird populations.

As in the northern plains, some predators might adversely impact those predator species that prey heavily upon nesting game birds. For example, coyotes at low densities will displace red foxes, thereby resulting in greater duck nest survival (Sovada et al. 1995). Similar correlations between coyote densities and bobwhites have been reported in Texas (Rollins 1999*a*). Coyotes may suppress smaller, more efficient nest predators (e.g., gray foxes, raccoons), or at least restrict their distribution on the landscape.

### An integrated approach to predation management

We suggest the development of an Integrated Pest Management (IPM) approach for managing predators of quail. The concept of IPM was developed to enhance strategic control of pests in crops (Pedigo 1989) and recognizes that a species of insect may be either a "pest" or "beneficial," depending on the situation involved. Further, IPM introduces the idea of economic thresholds, i.e., the level of pest damage that can be sustained before it becomes economical to provide a corrective treatment. Most IPM strategies include nonlethal (e.g., crop rotations) and lethal (e.g., insecticides) control alternatives. The former is applied as the first line of defense, with the latter being applied in the most "surgical" manner feasible to reduce treatment costs and minimize risks to the environment. Appropriate parallels relative to predator management for quail are numerous.

Messmer et al. (1999) surveyed public opinion in the U.S. about managing predators to enhance avian recruitment. When given specific predator control scenarios, respondents supported control to enhance avian recruitment, except for controlling raptors to protect exotic upland game birds. Their results suggested that public support for predator control is greater when control practices are applied "surgically" rather than applied broadly. Thus, an IPM model for predation management on quail could be supported by the general public.

#### Conclusion

Changes in land management over the last 30 years have resulted in conditions that make it more difficult to maintain high densities of quail (especially bobwhites) over much of their distribution. There is no doubt that land fragmentation will continue and likely accelerate over the next 20 years in bobwhite and scaled quail ranges (e.g., Texas; Wilkins et al. 2000). At the same time, there is evidence that some predators of quail may have benefited from these changes. How these landscape-level changes in land use and predator and prey populations impact the interaction of quail and their predators is unclear at this time. But our challenge as quail managers is apparent: how to maintain (or restore) quail populations in an increasingly fragmented habitat. We suggest that appropriate predation management techniques should be one of the tools considered in such restoration efforts.

Although we have discussed quail population dynamics on a regional scale, the interaction of habitat, predator communities, and quail is likely to be played out on a finer spatial scale. For example, the presence or absence of a hardwood drain in a fire-maintained, longleaf pine (*Pinus palustris*) community might have an enormous influence on the dynamics of a local predator community, regardless of what might be happening on a regional scale. Farther west, the interactions of livestock grazing, drought periodicity, and subsequently nest-site availability may increase the vulnerability of quail to predation.

The potential role of predation as a suppressing agent in quail populations needs additional study. It is crucial to understand how landscape-level changes in land use might change relationships between quail and their predators, as well as change predator and prey communities. What is needed is experimental research to define more clearly the relationships between quail and their predators within the context of current land-use and habitat management. Leopold and Hurst (1994) outlined strategies to study impacts of predators on game bird management. Specifically, the relationships among precipitation, vegetation dynamics (including nest-site availability [i.e., thresholds]), land management (e.g., livestock grazing, brush control), predator searching effectiveness, and consequent nesting success and recruitment need additional investigation (Schemnitz 1994).

An IPM-based approach to predator management for quail needs to be developed. Information is needed to develop economic thresholds and integrated predation management strategies that satisfy biological and political facets of predation management. Recent technology (e.g., radiotelemetry, continuous video surveillance) will continue to expand our knowledge on the relative management importance of various predators. If raptor populations (e.g., accipiters) continue to increase, the efficacy of nonlethal predation management strategies (i.e., habitat management) needs to be quantified. Additional, long-term experimental studies, designed appropriately (Leopold and Hurst 1994), are needed to clarify relationships between quail, their predators, and habitat dynamics. The decline of quail, especially bobwhites, underscores the urgency for such studies.

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Associate editor: Conover

