Survival and Causes of Mortality for Northern Bobwhites in the Southeastern USA

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Long-term studies are imperative to increase our knowledge of northern bobwhite (Colinus virginianus; hereafter bobwhite) demographics. During 1992-2005, we determined survival and cause-specific mortality of bobwhites on 10 study areas in southern Georgia and eastern Alabama, USA. We radio-tagged 7,105 bobwhites and determined 49 annual (Oct-Sep) and 110 seasonal survival estimates to examine spatial and temporal variation in survival. Annual survival for all sites and years combined averaged 0.196 (SE = 0.011) and ranged from 0.08 to 0.40. Over-winter (Oct - Mar) seasonal survival estimates (n = 51) averaged 0.541 (SE = 0.019) and ranged between 0.25 and 0.82, while breeding season (Apr-Sep) survival estimates (n = 59) averaged 0.352 (SE = 0.013) and ranged between 0.13 and 0.59. Over-winter mortality (n = 1,473) of known fates was attributed to avian predation (0.572 ± 0.040), mammal predation (0.265 ± 0.044), harvest (0.156 ± 0.028), snake predation (0.001 ± 0.002) and other (0.005 ± 0.002). Breeding season mortality (n = 2138) was attributed to avian predation (0.613 ± 0.026), mammal predation (0.339 ± 0.049), snake predation (0.037 ± 0.006) and other (0.011 ± 0.004). These over-winter survival estimates were higher than previously published estimates for populations on unmanaged lands and/or heavily harvested populations. On managed lands in the Southeast, bobwhite annual survival rates derived from radio-telemetry were reasonable and provided useful information for management and research.


Key words: Colinus virginianus, mortality, northern bobwhite, southeastern USA, survival, telemetry

Introduction

Understanding survival rates and causes of mortality for northern bobwhite (Colinus virginianus) populations is critical for making site specific management decisions as well as for regional recovery efforts. Cox et al. (2004) stated that “the need remains for site-specific, descriptive data on bobwhite survival and mortality because these basic descriptive data are prerequisite for development of sound management strategies.” The need for reliable, long-term demographic information on bobwhites is heightened by their long-term decline throughout most of the Southeast. A number of studies over the years have provided some survival information for bobwhites in the Southeast (Guthery and Lusk 2004); however, the majority of these studies were short in duration and based on small sample sizes (Terhune et al. 2007). In addition, the reliability of these telemetry based survival estimates has recently been called into question (Guthery and Lusk 2004) insinuating that all survival estimates derived with radio-telemetry are biased low. Therefore, it is important to present survival estimates for bobwhite populations in the Southeast from longer term studies derived from those with relatively large sample sizes.

In an effort to produce this much needed long-term data, Auburn University’s School of Forestry and Wildlife Sciences began a long-term investigation of bobwhite population ecology, management,
and hunting on private plantations in South Georgia and Alabama in 1992 commonly known as the Albany Quail Project (AQP). One objective of this long-term radio-telemetry project was to collect reliable data on survival and causes of mortality on properties that were being actively managed for bobwhites. The objectives of this paper are to: (1) present annual and seasonal survival estimates for 10 properties over the first 14 years of the AQP (1992 - 2005); (2) examine the annual variation and long-term means of bobwhite survival both within and among populations; (3) present cause specific mortality estimates for these populations; (4) compare all these estimates to previously published estimates; and (5) determine if our long term survival estimates are biologically reasonable given bobwhite populations on our study areas are stable or increasing.

Study Area

These data were collected on 13 separate study sites on 10 large private landholdings in southern Georgia and eastern Alabama (Figure 1) that combined encompass approximately 42,000 ha. All but one of these (site 5) had active and intensive quail management programs in place. Five of these properties (sites 1-5) were contiguous and centered around our headquarters south of Albany, GA in Baker County. Three others (sites 6-8) were scattered around southern GA, and the remaining 2 (9, 10) were in east central Alabama. Following is a brief description of each:

Site 1

The primary study site and headquarters for AQP was a 6,000 ha private plantation in Baker county, GA with a history of quail management dating back to the 1940’s. Typical of the properties in the region, it was characterized by mature old-field pine forests (80%) with a low basal area (3-9 m²/ha) and scattered 1-4 ha fallow fields (20%). Management techniques included maintenance of an open canopy through pine timber thinning and hardwood midstory removal, frequent prescribed burning in the woods, and seasonal disking of fields to stimulate weeds and insects, drum-chopping and mowing, supplemental feeding, and mammalian nest predator control. As a result of this management program, quail abundance estimates in recent years averaged approximately 5 birds/ha. More detailed descriptions of this property can be found in (Yates et al. 1995, Burger et al. 1998, Hughes et al. 2005, Terhune et al. 2006, 2007).

Site 2

The secondary study area for AQP, this 4,400 ha plantation straddles the border of Dougherty and Baker Counties, GA and has a history, management program, and quail abundance estimates very similar to site 1. More detailed descriptions of this property can be found in Simpson (1976), Sisson et al. (2000b,a) and Terhune et al. (2006, 2007).

Site 3

This 4,800 ha plantation in Baker County, GA also has a similar history, management program, and quail abundance estimates as site 1 and 2. This property was divided into 2 study sites (3a, 3b) for a large scale nest predator management experiment in conjunction with United States Department of Agriculture - Wildlife Services, Tall Timbers Research Station, and the University of Georgia. 3a was a 2,000 ha block on the east side of the property and 3b was a 2,000 ha block on the west side. These sites were alternately used as treatment and control sites with data collected and analyzed separately.

Site 4

This 2,800 ha plantation in Dougherty County, GA is within the matrix of plantations south of Albany and also has a history, management program, and bird density very similar to the first 3.

Site 5

This 2,000 ha property was a large private farm with no active quail management program. Located in Baker County, GA this property was dominated by center-pivot irrigated row crop fields (65%) with the remainder a mixture of young planted pines and a large creek swamp. A more detailed description can be found in Hughes et al. (2005) and Terhune et al. (2006).
Site 6
This 3,200 acre property was located in Laurens and Bleckley Counties, GA and was a working row crop farm that was intensively modified to improve it for bobwhite production and hunting. Although in the upper coastal plain, this area was not known for bobwhite abundance therefore it was one of the first in the area to manage specifically for quail. The property was a mixture of agricultural fields, open canopy woodlands, hedgerows, and young planted longleaf. Bobwhite density at the time of the study approached 2 birds/ha. More detailed descriptions of this site can be found in Sisson et al. (2002b) and Terhune et al. (2009).

Site 7
This 1,200 ha property was located in Marion and Schley Counties, GA in the transition area between the Coastal Plain and Piedmont commonly known as the Fall Line. This area was well outside the traditional quail belt in Georgia but was intensively modified by a new owner to create high quality quail habitat. Cover types were a mixture of open canopy woodlands, young planted longleaf, and fallow fields. This was the study site for our wild quail relocation study thereby generating 2 sets of data: 7a) relocated wild birds and 7b) resident wild birds.

Site 8
This 9,200 acre plantation was in southeast Georgia in Screven and Burke County. It has a long history of wild quail management similar to the properties in the Albany area with the main difference being less mature pine woods and more open land, including row crop land, interspersed throughout the quail courses. Bobwhite densities on this property are approximately 2 birds/ha. There were 2 study sites on this property as well. 8a was a mostly open
landscape with a high percentage of the ground under center pivot irrigation while 8b was a more wooded site with no irrigation.

Site 9
This 5,200 acre plantation was located in Russell and Barbour County, Alabama near the town of Hurtsboro. This property was mostly gently rolling pine woodlands interspersed with small fallow fields that made up about 10% of the landscape. History, management, and bird density was very similar to the Albany plantations. The biggest difference was the wet nature and low pH of the soils.

Site 10
This 2,620 ha property is contiguous with site 9 and has a similar management program. The land is somewhat different as it is more of a prairie soil with a very diverse groundcover and more of the land is open. There are less fallow fields as well and the bird density here is about 2 birds/ha.

Methods
All sites were part of the on-going work of the Albany Quail Project with research protocols similar among sites. Wild bobwhites were trapped on active study sites twice each year (Mar-Apr and Oct-Nov) during 1992-2005 using standard, baited funnel traps (Stoddard 1931). Each bird was classified by age and sex, weighed, leg banded, radiotagged and released at the capture site. Only birds weighing ≥132g (<5% of body weight) were outfitted with pendant style transmitters (6.0g) equipped with an activity switch (Holohil Systems, Ltd., Ontario, Canada). Trapping, handling, and marking procedures were consistent with the guidelines in the American Ornithologists’ Union Report of Committee on the Use of Wild Birds in Research (American Ornithologists’ Union 1988) and the protocol was approved by the Auburn University Institutional Animal Care and Use Committee, IACUC.

We monitored all birds ≥2 times weekly using the homing method (White and Garrott 1990), and recorded all locations on aerial photographs. Specific causes of predation (raptor, mammal, and snake) were determined when possible by the condition of the transmitter and evidence at the kill site (Dumke and Pils 1973, Curtis et al. 1988). Reporting rates for harvest were virtually 100% because these studies were conducted on private property, hunting and harvest were completely controlled, and records of all harvested birds were put into a large research database (Terhune et al. 2007). When sufficient evidence did not exist to put the cause of mortality into one of these categories, or when evidence existed implicating more than one mortality agent, the cause was recorded as unknown. Any other known sources of mortality (i.e., accidents) were recorded as “other”. Known mortalities therefore were classified as raptor, mammal, snake, harvest, and other.

Seasonal and annual survival estimates were based on a biological year beginning 1 October and ending 30 September. This annual period was divided into 2 seasonal intervals for analysis. The fall-winter interval (1 Oct - 31 Mar, 182 days) began with termination of nesting and formation of coveys. The spring-summer interval (1 Apr - 30 Sep, 183 days) began with covey breakup and initiation of nesting. The Kaplan-Meier staggered entry method was used to produce seasonal and annual survival estimates (Kaplan and Meier 1958, Pollock et al. 1989). An effort was made in every case to insure that birds were randomly sampled across the landscape during trapping and radio-tagging (Pollock et al. 1989, White and Garrott 1990). We used the traditional 7-day conditioning period where birds that died or were censored within 7 days of radio-tagging were excluded from the analysis (Kurzjeski et al. 1987, Pollock et al. 1989). We present causes of mortality by season and site as the probability of loss per known-fate individual (Cox et al. 2004, Terhune et al. 2007). Annual survival estimates were subjected to methods employed by Guthery and Lusk (2004) for determining whether they were reasonable and reliable.

Parts of the data presented here have been published previously. Burger et al. (1998) presented survival and cause specific mortality for one of these sites (site 1) for a 5-year period. They reported...
higher seasonal and annual survival estimates than other previous studies throughout the Southeast. (Sisson et al. 2000a,b) working on another of these sites (site 2) reported higher survival in some seasons for birds receiving supplemental feed, and lower survival for wild birds where a large influx of pen-raised birds occurred. Hughes et al. (2005) compared survival estimates over a 2-year period for 2 of these sites (site 1 and 5) which revealed higher survival on the site being managed for quail than on a farm landscape. Terhune et al. (2007) reported 2 summer survival estimates for site 1 and compared these to wild birds relocated on this site. Together these estimates make up 7 of the 49 (14%) annual estimates presented here and 19 of the 110 (17%) seasonal estimates. They are included here for comparative purposes, to provide a more comprehensive report on survival estimates, and to help derive long term averages for each site. Because our study was observational we focus on means, standard errors, confidence intervals, and graphical interpretation of results to compare among sites and years.

Results

From 1992-2005 we monitored 7,105 radio-tagged bobwhites that survived the 7 day censor period. The years of study, number of radio-tagged individuals, and the number of seasonal and annual survival estimates generated for each site is presented in Table 1. Continual radio-telemetry monitoring yielded 49 separate annual (Oct - Sep) survival estimates. Annual survival for all sites and years combined averaged 0.196 (SE = 0.011; range: 0.08-0.40). We observed annual survival rates sufficient to maintain stable populations (defined as production [juveniles/adult] required to stabilize the population ≤7) for 38 of these 49 (78%) individually derived annual survival estimates (Figure 2). Average long-term annual survival by site ranged from

### Table 1: Years of study, sample size, and number of annual and seasonal survival estimates for radio-tagged northern bobwhite on 13 study sites of the Albany Quail Project in Georgia and Alabama 1992-2005.

<table>
<thead>
<tr>
<th>Site</th>
<th>Years of Study</th>
<th>n</th>
<th>Annual</th>
<th>Fall - Spring</th>
<th>Spring - Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1992-2005</td>
<td>2383</td>
<td>13</td>
<td>13</td>
<td>14</td>
</tr>
<tr>
<td>2</td>
<td>1993-2005</td>
<td>1596</td>
<td>10</td>
<td>11</td>
<td>11</td>
</tr>
<tr>
<td>3a</td>
<td>1999-2005</td>
<td>671</td>
<td>6</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>3b</td>
<td>2000-2005</td>
<td>562</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>4</td>
<td>2000</td>
<td>50</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>5</td>
<td>1998-2000</td>
<td>154</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>6</td>
<td>1999-2002</td>
<td>507</td>
<td>3</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>7a</td>
<td>2003-2004</td>
<td>120</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>7b</td>
<td>2003-2004</td>
<td>120</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>8a</td>
<td>2003-2005</td>
<td>219</td>
<td>2</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>8b</td>
<td>2003-2005</td>
<td>200</td>
<td>2</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>9</td>
<td>2002-2005</td>
<td>269</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>10</td>
<td>2002-2005</td>
<td>254</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>TOTAL</td>
<td>1992-2005</td>
<td>7105</td>
<td>49</td>
<td>51</td>
<td>59</td>
</tr>
</tbody>
</table>
Figure 2: Annual estimates (Kaplan-Meier) of survival for northern bobwhites on 10 study sites of the Albany Quail Project in Georgia and Alabama 1992-2005. The darkened point represents the mean of the annual estimates for each site. The horizontal line represents annual survival of 0.125 below which necessitates a stabilizing age ratio ≥7 for population stability.

0.11 (SE = 0.028) to 0.272 (SE = 0.031; Table 2) with a mean (n = 10) of 0.192 (SE = 0.017). Eight of these 10 (80%) were deemed sufficient to maintain stable populations (Figure 2). Over-winter seasonal survival estimates (n = 51) averaged 0.541 (SE = 0.019; Table 2) and ranged from 0.25 - 0.82 (Figure 3); while breeding season survival estimates (n = 59) averaged 0.352 (SE = 0.013; Table 2) and ranged from 0.13-0.59 (Figure 4).

The cause of mortality was determined from 3,580 known fate individuals and was unknown for an additional 801. Over-winter seasonal mortality (n = 1,473) was attributed to avian predation (0.572 ± 0.040), mammal predation (0.265 ± 0.044), harvest (0.156 ± 0.028) snake predation (0.001 ± 0.004) and other (0.005 ± 0.002; Table 3). Breeding season mortality (n = 2,138) was ascribed to avian predation (0.613 ± 0.026), mammal predation (0.339 ± 0.049), snake predation (0.037 ± 0.006), and other (0.011 ± 0.004; Table 3).

Discussion

We begin by discussing the reliability of our telemetry based survival estimates. The reliability of information collected via radio-telemetry has recently been called into question by Guthery and Lusk (2004) based on their review of the literature and studies in Oklahoma (Cox et al. 2004). This has been countered more recently by researchers in the Southeast however, based on long-term studies and large sample sizes (Terhune et al. 2007, Palmer and Wellendorf 2007). Guthery and Lusk (2004) posited that annual survival estimates from telemetry were biased low because only 10 of 58 (17%) years in the studies they reviewed produced estimates they considered reasonable. The point was reiterated by Cox et al. (2004) where estimates considered reasonable were obtained through telemetry in only 1 of 10 (10%) years for their study in Oklahoma. The benchmark for a reasonable estimate used during these studies was a stabilizing age ratio ≤7, which was considered the upper acceptable limit of production (juvenile/adult) required to stabilize the pop-
Table 2: Over-winter (1 October - 31 March), breeding season (1 April - 30 September), and annual Kaplan-Meier survival estimates on 10 study sites of the Albany Quail Project in Georgia and Alabama 1992-2005.

<table>
<thead>
<tr>
<th>Site</th>
<th>Over-winter</th>
<th>Breeding Season</th>
<th>Annual</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>S  SE (S)</td>
<td>S  SE (S)</td>
<td>S  SE (S)</td>
</tr>
<tr>
<td>1</td>
<td>0.467 0.022</td>
<td>0.411 0.023</td>
<td>0.195 0.017</td>
</tr>
<tr>
<td>2</td>
<td>0.483 0.036</td>
<td>0.324 0.022</td>
<td>0.161 0.022</td>
</tr>
<tr>
<td>3a</td>
<td>0.618 0.051</td>
<td>0.296 0.055</td>
<td>0.207 0.047</td>
</tr>
<tr>
<td>3b</td>
<td>0.686 0.017</td>
<td>0.396 0.059</td>
<td>0.272 0.031</td>
</tr>
<tr>
<td>5</td>
<td>0.305 0.055</td>
<td>0.385 0.055</td>
<td>0.120 0.040</td>
</tr>
<tr>
<td>6</td>
<td>0.570 0.023</td>
<td>0.327 0.033</td>
<td>0.197 0.023</td>
</tr>
<tr>
<td>7a</td>
<td></td>
<td>0.405 0.020</td>
<td></td>
</tr>
<tr>
<td>7b</td>
<td></td>
<td>0.390 0.015</td>
<td></td>
</tr>
<tr>
<td>8a</td>
<td>0.400 0.050</td>
<td>0.303 0.054</td>
<td>0.11  0.028</td>
</tr>
<tr>
<td>8b</td>
<td>0.635 0.015</td>
<td>0.283 0.050</td>
<td>0.19  0.06</td>
</tr>
<tr>
<td>9</td>
<td>0.777 0.034</td>
<td>0.340 0.038</td>
<td>0.267 0.038</td>
</tr>
<tr>
<td>10</td>
<td>0.597 0.078</td>
<td>0.330 0.047</td>
<td>0.203 0.047</td>
</tr>
<tr>
<td>TOTAL</td>
<td>0.541 0.019</td>
<td>0.352 0.013</td>
<td>0.196 0.011</td>
</tr>
</tbody>
</table>

This could have also been interpreted as saying any annual survival estimate generated from telemetry ≤ 0.125 was considered unreasonable for a stable population because it was too low for reproduction to overcome. We use this procedure to critique our estimates.

The average annual survival we observed (0.192) necessitated production of only 4.2 juveniles per adult, well below the threshold of 7 proposed by Guthery and Lusk (2004) to maintain population stability. In addition, of the 49 annual survival estimates generated during this study, 38 (78%) were above the 0.125 level, and would therefore have been classified as “reasonable” in their analysis (Figure 2). A more sensible approach may have been to look at the long-term average-annual survival by site as opposed to using each year as a separate data point. Even populations considered stable can be expected to fluctuate from year to year (Palmer et al. 2002, Palmer and Wellendorf 2007) along with the survival and reproductive parameters that drive them. Therefore, we believe looking at the average annual survival for a site over time and the subsequent stabilizing age ratio required for that average is more judicious. When examined in this fashion it is revealed that 6 of 10 sites had individual years with annual survival estimates below 0.125, however the average for 8 of 10 of these sites (80%) was above the threshold of what is believed needed to maintain population stability (Table 2 and Figure 2). Incidentally, both of our study sites (site 5, 8a) where the average estimates would be classified as “unreasonable” were from properties with declining populations during the course of a short-term investigation. Site 5 was an unmanaged farm where canopy closure on young pine stands shaded out the ground cover and reduced habitat quality and quail abundance (Hughes et al. 2005, Terhune et al. 2007). This site was typical of the “non plantation” landscape in southwest Georgia and had no harvest pressure.
Over-winter survival on this site was shown to be a function of over-winter survival which in turn was affected by the abundance of native foods (Hughes et al. 2005). Site 8 was a managed property where unusually high avian mortality from Cooper’s Hawks (Accipiter cooperii) during winter caused a population decline as evidenced by our census records (AQP, unpublished data) as well as the plantations hunting records. The other 8 study sites where “reasonable” estimates come from are all from stable or even increasing populations (Burger et al. 1998, Sisson et al. 2002b, a, Terhune et al. 2007). We interpret this disparity in telemetry derived survival estimates as evidence of demographic problems in need of management attention, and not evidence that the estimates are “unreasonable” because they are too low.

Additionally, short-term studies may be conducted during either up or down swings in population trajectory thus giving a false impression of the true long-term demographics. To illustrate, we looked at only the study sites with relatively long term samples (≥5 years) from our data. These 4 sites generated 34 of the 49 (69%) annual survival estimates, including 8 (24%) that are below the 0.125 required to maintain a stable population. Guthery and Lusk (2004) analysis would have classified these 8 as unreasonable and evidence of radio-handicapping. Each of these 4 sites had long-term annual survival well above the threshold (avg. = 0.21, range 0.161-0.272) which leads us to interpret these low estimates as expected fluctuations in population performance. In fact, population abundance estimates have been shown to fluctuate along with these fluctuations in survival (Sisson et al. 2000b, Palmer and Wellendorf 2007).

As a result of this evidence and in combination with the results reported by others (Palmer and Wellendorf 2007, Terhune et al. 2007), we conclude these telemetry based survival estimates are indeed reliable for our study sites. We continue our discussion based on that conclusion.

The survival rates reported herein for these sites are generally higher than many of the previously reported rates for the Southeast, and tend to support and strengthen the arguments of Burger et al. (1998) that these managed populations perform better, demographically, than their counterparts on the typical landscape of the Southeast. The disparity is particularly apparent in over-winter survival when these estimates are compared to the review conducted by
Guthery and Lusk (2004) and the 10-year study on annual survival by Cox et al. (2004). During these studies, low annual survival was generally a function of low over-winter survival from a combination of predation and harvest. On our study sites, harvest was generally low (<10% Burger et al. 1998, Terhune et al. 2007) and the birds resided in a landscape of good habitat where supplemental feed was provided in most cases. Most of the other studies conducted in the Southeast were conducted during a time of population decline (Sauer et al. 2004) caused by diminishing habitat and increasing predator populations (Brennan 1991, Rollins and Carroll 2001). Combine this with the possibility of diminished food resources due to clean farming, less prescribed burning, and increased deer browsing on native food plants (Stokes et al. 1994) it is easy to imagine why many of these other studies reported low over-winter survival. Exceptions to this included Curtis et al. (1988) and Pollock et al. (1989); who both reported over-winter and annual survival estimates similar to ours on managed and un-hunted populations in north Florida. These patterns tend to support the conclusion of Cox et al. (2004) of accumulating evidence that harvest may increase over-winter mortality and decrease breeding populations.

In our study, over-winter survival (0.541) was generally higher than breeding season survival (0.352; Table 2). Breeding season survival as reported herein was similar to many of the previously published studies in the region (Curtis et al. 1988, Puckett et al. 1995, Taylor et al. 2000, Hughes et al. 2005, Terhune et al. 2007) suggesting the major difference in regional demographics was a higher percentage of the population in our study making it to the breeding season. Causes of mortality generally follow the trends observed in previous studies. For all our study sites combined avian predation ac-
Table 3: Over-winter (1 October - 31 March) and breeding season (1 April - 30 September) causes of known mortality for 3,611 radio-tagged northern bobwhite on 10 study sites of the Albany Quail Project in Georgia and Alabama 1992-2005.

<table>
<thead>
<tr>
<th>Causes of Mortality</th>
<th>Season</th>
<th>Avian</th>
<th>Mammal</th>
<th>Harvest</th>
<th>Snake</th>
<th>Other</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Over-winter</td>
<td>Total</td>
<td>843</td>
<td>391</td>
<td>229</td>
<td>2</td>
<td>8</td>
<td>1473</td>
</tr>
<tr>
<td></td>
<td>Percent</td>
<td>57.23</td>
<td>26.54</td>
<td>15.55</td>
<td>0.14</td>
<td>0.54</td>
<td>100</td>
</tr>
<tr>
<td>Breeding</td>
<td>Total</td>
<td>1310</td>
<td>725</td>
<td>0</td>
<td>80</td>
<td>23</td>
<td>2138</td>
</tr>
<tr>
<td></td>
<td>Percent</td>
<td>61.27</td>
<td>33.91</td>
<td>0</td>
<td>3.74</td>
<td>1.08</td>
<td>100</td>
</tr>
</tbody>
</table>

counted for the highest percentage of known mortalities in both winter (0.572) and summer (0.613; Table 3). Mammal predation was the next most important mortality factor and was higher during the spring-summer (0.339) than fall-winter (0.265). The percentage of known mortality attributed to harvest, snakes, and other mortality factors was inconsequential on our study sites compared to these two agents (Table 3). This is in stark contrast to Curtis et al. (1988), Robinette and Doerr (1993) and Cox et al. (2004) who each reported high winter mortality from a combination of avian predation and heavy harvest pressure. Harvest pressure was light (<10%) on all of our study areas and likely helped promote the high over-winter survival estimates.

While our survival estimates were generally higher than most previously reported studies in the Southeast, there was still some variability in both the annual and seasonal estimates (Figure 2 - 4). This was true when compared between sites and between years on the same site. We believe this is partly due to the natural fluctuation of quail populations as discussed previously as well as to site-specific management problems between properties. Several sites with long-term-stable populations have separate years, or series of consecutive years, with low annual survival estimates; while the 2 sites with population problems (5,8a) have consistently low annual survival due to low over-winter survival. These parameters have proven to be a valuable tool for us in developing site-specific management plans as well as in contributing to the knowledge base of quail demographics for the region to aid in species recovery. We further suggest caution when interpreting survival rates of short-term studies as they may provide false impressions of what the population may permit during the long-term.

**Management Implications**

One of our intentions was to dispel the notion that all telemetry based survival information was biased low and therefore unreliable. We disagree that research biologists should be skeptical of information obtained on bobwhite demographics obtained with radio telemetry, but only after the researchers themselves have demonstrated the reliability of the data for their study sites. We caution, however, in drawing too many conclusions from short-term and/or small sample size studies. We have observed that when our estimates are derived over long term and from large samples they are reliable, indicative of what the population is doing, and very helpful...
in making site-specific management recommendations. Perhaps on a regional scale, we should focus more on what previously published low survival estimates are telling us instead of using them as evidence of “radio-handicapping”.

The fact that our survival estimates are higher than the general landscape of the Southeast is no surprise because our study was conducted mostly on properties managed intensively for bobwhite quail with a conservative harvest. However, this inherent management and moderate harvest rate does not preclude the utility of our research from benefiting other sites. Rather, we believe that many lessons can be gleaned from the management programs that yield this high survival (i.e. timber thinning, prescribed burning, hardwood removal, supplemental feeding, and predation management) that may contribute to region-wide species recovery efforts. In short, sound management practices at the landscape-scale level results in improved demographic parameters and population persistence.

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