Survival of Female Scaled Quail During the Breeding Season at Three Sites in the Chihuahuan Desert

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Scaled quail (\textit{Callipepla squamata}) populations declined markedly across much of their range from 1988-2004, however little research has been conducted to investigate possible causes for the decline. As part of a larger study on scaled quail ecology and management, and in an attempt to determine whether breeding season survival could be implicated in this decline, we monitored survival of radiotagged female scaled quail during the breeding season at sites in Brewster and Pecos counties, Texas, and Sierra County, New Mexico, USA during 1999-2003. Survival rates were calculated using Kaplan Meier analysis for birds living >7 days post capture. Interval survival rates (S) from Mar-Aug ranged from 0.46 to 0.82 for populations in Pecos County, Texas, and from 0.56 to 0.69 in Brewster County, Texas; survival was lower at the New Mexico site (S ranging from 0.22 to 0.48). Predation by mammals was the leading cause of mortality at both Texas study sites, whereas predation by raptors was the primary cause of mortality at the New Mexico site. Several mortalities in Texas were attributed to drowning; 3 in a water trough and 2 others following a flash flood. Survival rates on Texas sites were not affected by moist soil management but were greater than survival on New Mexico sites. Survival on New Mexico sites was greater on areas with access to free-choice quail feeders (S = 0.48) relative to a non-fed site (S = 0.22). Survival rates of scaled quail during the breeding season were higher than those reported for radiotagged northern bobwhite in west Texas at similar latitudes. Survival of female scaled quail during the breeding season does not appear to be a bottleneck to recruitment, at least not on sites where conservative grazing management is practiced.


Key words: \textit{Callipepla squamata}, Chihuahuan Desert, management, New Mexico, predation, radiotelemetry, scaled quail, survival, Texas

Introduction

Abundance of scaled quail (\textit{Callipepla squamata}) declined for undocumented reasons throughout most of their range from 1966-2004 (Schemnitz 1994, Rollins 2000, Sauer et al. 2005) (Figure 1). Predators (Rollins 2000), drought (Wallmo and Uzzell 1958, Saiwana et al. 1998, Pleasant et al. 2006), disease (Rollins 2000), overgrazing (Ligon 1937), changing habitat conditions (Schemnitz 1994, Rollins 2000), or some combination of these factors (Bridges et al. 2001) have been cited as possible mechanisms for declining trends in scaled quail in the Chihuahuan Desert.

Studies of scaled quail have lagged notably behind those of northern bobwhite (\textit{Colinus virginianus}) especially since the advent of radio telemetry (Rollins 2000). Earlier studies by Bent (1932), Wallmo (1956b), Schemnitz (1961), and Campbell et al. (1973) were based on field observations and provided general ecological information about scaled quail, but provided little information on nesting ecology (because of the difficulty of locating nests), movements, or population dynamics (e.g., cause-specific mortality). Recently Pleasant et al.
Survival of Scaled Quail

Figure 1: Scaled quail trends from the Breeding Bird Survey for the Mexican Highlands (Sites 1 and 2 in this study) and Intermountain Grasslands (Site 3), 1968–2005 (Sauer et al. 2005).

(2006) used radiotelemetry to address information voids like nesting ecology and survival. We report survival and cause-specific mortality for 3 populations of radiotagged scaled quail during the breeding season in west Texas and south-central New Mexico. We also report impacts of moist-soil management and supplemental feeding on summer survival of scaled quail.

Study Area

Three study sites were involved: 2 in Texas (Pecos and Brewster counties) and 1 in New Mexico (Sierra County) (Figure 2). Site 1 was the Sherman Hammond Ranch, a 12,000-ha private ranch located about 40 km southwest of Ft. Stockton, Pecos County, Texas. Site 2 was the 18,000-ha Texas Parks and Wildlife Department’s Elephant Mountain Wildlife Management Area located 65 km south of Alpine, Brewster County, Texas. Site 3 was the Armandaris Ranch, a 120,000-ha private ranch located 20 km east of Truth or Consequences, Sierra County, New Mexico. Sites 1 and 2 are located in the Mexican Highlands Bird Conservation Region (BCR) and Site 3 is located in the Intermountain Grasslands BCR.

Sites 1 and 2 were used to examine differences in areas with or without moist-soil areas created by water harvesting techniques (i.e., spreader dams). These experiments were conducted in 1999 and 2000 (Site 1) and 2000 and 2001 (Site 2). Site 1 had 3 study populations each separated by >12 km: (1) a “Negative Control”, i.e., an area characterized by the absence of spreader dams; (2) a “Positive Control”, i.e., an area surrounding the ranch headquarters with a 2-ha irrigated lawn (thus providing scaled quail access to green vegetation), and (3) a “Treatment” area characterized by a landscape punctuated with moist-soil sites following rainfall events. Site 2 was similar to Site 1 except no positive control was available and the overall number of moist-soil sites was considerably lower.

Vegetation at Site 1 was dominated by desert scrub and consisted mainly of creosote (Larrea tridentata), tarbush (Flourensia cernua), and honey mesquite (Prosopis glandulosa). Common grasses include tobosa (Pleuraphis belangeri) and bush muhly (Muhlenbergia porteri). The average annual precipitation in Ft. Stockton is 305 mm, with most of it falling between May and October. The average temperature is 8° C during winter and 27° C in the summer.

Major plant communities at Site 2 vary from
Figure 2: Study sites (open circles) relative to range of scaled quail (Sauer et al. 2005) and recent studies on scaled quail in west Texas.

grama (Bouteloua spp.) and tobosa- dominated grasslands to Chihuahuan Desert scrubland. Upland areas contain mesquite and redberry juniper (Juniperus pinchotii). Average annual precipitation at Elephant Mountain WMA from 1986 to 2001 was 363 mm. The driest year during this period was 2001, when only 205 mm of precipitation were recorded. Additional details on Sites 1 and 2 are reported by Buntyn (2004) and Lerich (2002), respectively.

Site 3 was used to evaluate differences in survival between areas with or without year-round supplemental feeding with milo. We monitored scaled quail on 2 areas; a treatment area that featured free-choice quail feeders, and a nonfed control. This experiment was conducted from Oct 2002 -August 2003. The control area was located 7 km north of the fed area, a distance well beyond what scaled quail normally travel, and included feeders that had been active for > 4 years prior to our study. Scaled quail at both sites had access to water via guzzler devices (Rollins et al. 2006). Access to water was not restricted in this study; hence, the presence of guzzlers (i.e., water) was not a treatment variable. Spacing between quail feeders in both the treatment and control areas was approximately 1 feeder per 1.1 km of road. Feeders in the treatment area were constructed of 206-l plastic barrels with 10-12 small (1-cm) holes placed at intervals ranging from 7-25 cm from the bottom of the barrel. These feeders are free choice as milo was available at any time throughout the day and year-round. The 5 feeders in the control were timed feeders, which prior to them being turned off in October 2001 (prior to onset of this study), were on timers set to disburse milo on the ground directly beneath the feeder for 3 seconds at 7 a.m. and 4 p.m. It should be noted that each feeder site (active or not) was a site for trapping, and although feeders were shut off in the control area, approximately a cup of milo remained as bait for each day of trapping. Therefore, a limited amount of milo was available at trap sites in the control area for trapping purposes. Strictly speaking, the control area might be better considered a ‘limited’ feed area and the treatment an ad libitum feed area.
The portion of Site 3 used for this study was a 2,500-ha section near the southern border of the ranch. It was predominantly black grama (B. eriopoda) grassland in good to excellent range condition. Mesquite was the major woody plant and yuccas (Yucca spp.) were primary succulents. Annual precipitation at this site averages 270 mm. The study area was mired in drought for the duration of the study—annual precipitation in 2001 and 2002 was only 53 and 44% of the long-term means, respectively (Western Regional Climate Center 2003). Above normal temperatures prevailed during this time; for example, June 2002 had the highest mean monthly temperature on record.

Methods

Trapping and telemetry

Scaled quail were trapped in funnel traps on each study site during February-April. The study periods were 1999-2000 (Site 1), 2000-2001 (Site 2), and 2002 (Site 3). Female scaled quail were fitted with neckloop telemeters weighing $<7$ g and equipped with mortality sensors. Telemeters from 2 different manufacturers were used; Telemetry Solutions (Concord, CA) was used for Sites 1 and 2, while those manufactured by Wildlife Materials, Inc. (Carbondale, Illinois) were used for Site 3. All quail captured were leg-banded with individually-numbered aluminum bands. Quail were aged and sexed according to methods described by Wallmo (1956a). Trapping and handling methods were approved by the Texas A&M University’s Care of Laboratory Animal Welfare Care and Use Committee.

Monitoring

Radiotagged birds were tracked via homing 2-3 times per week using 3-element Yagi antennas with portable receivers. Radiotagged quail were monitored $<3$ times a week from time of capture (mid-February-March) until time of death, or censoring from the study, through the breeding season (i.e., August) during each year. At the onset of incubation, quail were monitored daily, while attempting to not disturb the nesting hen. All mortality signals were investigated upon detection and cause of death was determined using criteria described by Carter et al. (2002). Cause-specific mortality was reported as avian, mammalian, snake, exposure, or unknown.

Data analyses

Interval survival was calculated using Kaplan and Meier (1958) analysis for birds living $>7$ days post-capture. Staggered entries of individual quail were analyzed as described in Pollock et al. (1989). Individuals lost to emigration or radio failure, were censored (Pollock et al. 1989). A log-rank Chi-square test was used to evaluate differences in survival between treatments (or years) at a particular site. Assumptions included: (a) censorship of individuals was random and survival times were independent for all radiotagged birds; (b) survival of quail was not affected by capturing, handling, or radiotagging; (c) survival times were independent; (d) radiotagging did not influence future survival; (e) censoring mechanisms were random; and (f) newly radiotagged quail had the same survival function as previously radiotagged quail (Pollock et al. 1989).

Results

Site 1 - Pecos County, Texas

We trapped a total of 269 birds in 1999 and 228 birds in 2000. The 1999 sample consisted of 154 females (57%) and 115 males (43%); most (72%; $n = 193$) were adults. Of these, 120 females (75% adults) were radiotagged (40 per study site). The 2000 sample included 136 females (59%); 42 (11%) were adults and 186 (89%) were subadults. A total of 90 females were radiotagged (30 per study area). The population trapped in 2000 was consistently younger across all study areas, with adults comprising only 16% of the sample across study areas.

Survival across all sites was similar between years (Figure 3) and across treatments in 1999 (Table 1). In 2000, survival in the Positive Control ($S = 0.47 \pm 0.38$) was lower than that in either the Treatment ($S = 0.81 \pm 0.02$) or Negative Control areas ($S = 0.82 \pm 0.03$) ($\chi^2 = 14.3, v = 1, P < 0.005$).

A total of 20 mortalities were observed in 1999...
Figure 3: Survival of female scaled quail during spring and summer at 3 sites in the Chihuahuan Desert, 1999–2002.

(Figure 4); most \((n = 14)\) were attributed to mammalian predators while raptors accounted for 4 kills. The remaining 2 mortalities were caused by exposure (flooding). Predation by mammals was also the leading agent of mortality in 2000, accounting for 18 of 23 mortalities; raptors accounted for 4 kills and 1 bird was killed by a western diamondback rattlesnake \((Crotalus atrox)\). Predation was similar between years and among sites with the exception of the Positive Control in 2000, where 6 mortalities were attributed to free-ranging cats. All 6 mortalities were recorded within 500 m of the ranch headquarters and their telemeters were retrieved from areas frequented by cats. We estimated the free-ranging cat population to consist of 5 individuals in 1999 and 13 individuals in 2000.

The 2 mortalities related to exposure in 1999 were observed following a flash flooding event from a heavy rain that occurred on 17 June 1999 about 6 km up the watershed. Rainfall totaling 15 cm fell during a short period causing a sheet of water to blanket the Positive Control site. The following day, 2 mortalities were recorded—we attributed both to the flash flood event. Each bird’s carcass was located under a layer of silt \((>10 \text{ cm})\). Each of the hens involved had a brood of chicks \((<10 \text{ days of age})\) at the time.
Survival of Scaled Quail

Table 1: Breeding season (March–August) estimates of survival for radio-tagged female scaled quail at various sites in the Chihuahuan Desert, 1999–2002, including estimates from other recent studies.

<table>
<thead>
<tr>
<th>Site</th>
<th>Years</th>
<th>N</th>
<th>S</th>
<th>SE</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Irion Co., Texas</td>
<td>1994</td>
<td>17</td>
<td>0.7</td>
<td>Not reported</td>
<td>Rollins 2000</td>
</tr>
<tr>
<td>Bailey Co., Texas</td>
<td>1999</td>
<td>66</td>
<td>0.38</td>
<td>Not reported</td>
<td>Pleasant et al. 2006</td>
</tr>
<tr>
<td>Bailey Co., Texas</td>
<td>2000</td>
<td>72</td>
<td>0.30-0.43</td>
<td>Not reported</td>
<td>Pleasant et al. 2006</td>
</tr>
<tr>
<td>Pecos Co., Texas</td>
<td>1999</td>
<td>120</td>
<td>0.8</td>
<td>0.03</td>
<td>This study</td>
</tr>
<tr>
<td>Pecos Co., Texas</td>
<td>2000</td>
<td>90</td>
<td>0.71</td>
<td>0.08</td>
<td>This study</td>
</tr>
<tr>
<td>Brewster Co., Texas</td>
<td>2000</td>
<td>62</td>
<td>0.63</td>
<td>0.05</td>
<td>This study</td>
</tr>
<tr>
<td>Brewster Co., Texas</td>
<td>2001</td>
<td>46</td>
<td>0.67</td>
<td>0.04</td>
<td>This study</td>
</tr>
<tr>
<td>Sierra Co., New Mexico, fed</td>
<td>2002</td>
<td>132</td>
<td>0.48</td>
<td>0.08</td>
<td>This study</td>
</tr>
<tr>
<td>Sierra Co., New Mexico, not fed</td>
<td>2002</td>
<td>77</td>
<td>0.22</td>
<td>0.08</td>
<td>This study</td>
</tr>
</tbody>
</table>

Site 2 - Brewster County, Texas

We radiotagged a total of 72 birds in 2000 (70 females, 2 males) and 46 birds (25 females, 21 males) in 2001. Seasonal survival was similar between years and between sites in both 2000 ($S = 0.69 \pm 0.09$ and $0.56 \pm 0.10$) and 2001 ($S = 0.67 \pm 0.10$ for both sites) (Figure 3). Cause-specific mortality for 2000 was attributed to mammalian predators ($n = 7$ kills), unknown predators ($n = 6$ kills), raptors ($n = 2$ kills), and drowning ($n = 3$ deaths) (Figure 4).

Site 3 - Sierra County, New Mexico

We trapped a total 532 scaled quail; the sex ratio of birds trapped in 2002 was 1.04:1 females:males (271 females and 261 males). The age ratio of this sample was 2.86:1 subadults:adults (i.e., 74% subadults). A total of 209 hens were radiotagged: 132 (46 adults, 86 subadults) in the treatment area and 77 (20 adults, 57 subadults) in the control area. Survival on site 3 was lower than on sites 1 and 2 but was higher in the fed area ($S = 0.48 \pm 0.08$) than the area not fed ($S = 0.22 \pm 0.08$; $\chi^2 = 4.57, 1 v = 1, P = 0.03$) (Figure 3). The 2 populations survived similarly until late-April when hens in the control portion of the ranch began suffering greater mortality.

A total of 88 mortalities of radiotagged quail were observed; 34% ($n = 30$ kills) were attributed to mammals, 53% ($n = 47$ kills) to raptors, and 7% ($n = 6$ kills) were characterized as unknown (Figure 4). Five mortalities (6%) were attributed to handling, i.e., where the telemeters were initially fitted too tightly. Cause-specific mortality was similar between fed and non-fed sites. Aside from a kit fox ($Vulpes macrotis$) that killed 3 juvenile cocks in a trap, we did not observe any mortalities at or immediately adjacent to quail feeders.

We experienced chronic problems with battery failure in the telemeters used (both brands) at Sites 2 (Telemetry Solutions) and Site 3 (Wildlife Materials, Inc). The batteries seldom, if ever, lasted as long as described by the manufacturer (270 days). Typically, collars lasted <120 days making it difficult to obtain long-term data series for specific females.

Discussion

Data from these telemetry studies suggest survival rates of female scaled quail during spring and summer were quite high, especially at the 2 sites in Texas. Rollins (2000) documented survival of a small sample ($n = 17$) of scaled quail at 0.70 from January-August in Irion County, Texas, in 1995 (about 225 km east of Site 1). Pleasant et al. (2006) reported survival of female scaled quail in Bailey County, Texas (about 200 km north of Site 1) during the same time period of our study (1999-2000) ranging from 0.30-0.43.

Survival rates we observed, especially at the
Survival of Scaled Quail

Figure 4: Cause-specific mortality of scaled quail during spring and summer at 3 sites in the Chihuahuan Desert, 1999−2002.

Texas sites, were generally greater than observed for female bobwhites during the breeding season across most of their range. Carter et al. (2002) reported relatively low survival ($S = 0.17$) of 54 radiotagged bobwhites during the breeding season in Irion County, Texas (about 250 km east of Site 1) compared to 0.70 for scaled quail on the same site. Hernandez et al. (2003) reported summer survival rates from 0.17-0.61 in Shackelford County, Texas (about 400 km east of Site 1). Brooks (2005) reported breeding season survival rates of 0.50 for female bobwhites in Fisher County, Texas (about 250 km east of Site 1). Greater survival rates of scaled quail (relative to bobwhites) may be related to less abundant predator populations in more arid environments, or inherent differences between the vulnerability of bobwhite and scaled quail relative to predators (Rollins and Carroll 2001) or hunting (Rollins 2000). Lehmann (1984, :225) considered scaled quail to be more intelligent than bobwhites.

Mammalian predators were the primary cause of mortality for female scaled quail during spring and summer at the 2 sites in Texas, but raptors caused proportionally more mortalities (about twice as many) in New Mexico. Miscellaneous sources of mortality included drowning, rattlesnakes, exposure (hailstorm), and drowning. Hernandez (1999), Carter et al. (2002), and Brooks (2005) reported similar cause-specific mortality sources for female bobwhites during spring and summer in west Texas. Red-tailed (Buteo jamaicensis), and Swainson’s hawks (B. swainsoni) were the 2 most common species of raptors observed at the New Mexico site; neither are regarded as particularly efficient predators of quail. Great horned owls (Bubo virginianus) are common at all sites, and have been
known to prey on scaled quail during the breeding season (Carter et al. 2002). Cooper’s hawks (*Accipiter cooperi*) and northern harriers (*Circus cyaneus*), are present through April in this area, and were likely responsible for most of the raptor-caused mortalities during the spring. Goodwin and Hungerford (1977) indicated that most scaled quail kills in Arizona were made by avian predators including northern harrier, red-tailed hawk, prairie falcon (*Falco mexicanus*), and great-horned owl. Campbell et al. (1973) indicated common scaled quail predators in New Mexico included hawks, owls, coyotes (*Canis latrans*), and snakes.

Scent station indices indicated low diversity and prevalence of mammalian predators at all 3 sites (Lerich 2002, Buntyn 2004, , T. D. Sparks, unpublished data). Low abundance of meso-mammals in this portion of the Chihuahuan desert may have permitted greater survival and hatch rates of scaled quail (Buntyn 2004). The impact of free-ranging cats on scaled quail underscores the potential significance of feral and free-ranging cats on quail.

Rollins and Carroll (2001) discussed impacts predators may have on scaled quail. Sauer et al. (2005) documented a >2.0% increase per year in accipiter abundance over a large area of the U. S. since 1967. Cooper’s hawks, considered to be the most efficient predator of bobwhites, are present throughout the range of scaled quail at least through spring. Northern harriers are common winter residents (through early April) and have been identified as accomplished predators of quail (bobwhite and scaled quail) (Jackson 1947). The only practical approach to minimize raptor losses of scaled quail is to provide adequate loafing and screening cover (Rollins and Carroll 2001). Conservative grazing management was practiced at each of our study sites, which coupled with the presence of suitable screening cover (e.g., catclaw mimosa), likely afforded scaled quail greater survival than which might be expected over much of the Chihuahuan Desert.

The drownings of 2 hens with broods following a flash flood event at Site 1 are intriguing. We speculate the hens’ maternal instincts to brood their young chicks in the presence of rising water precluded their escape. We can offer no other reason why adult birds would succumb to rising flood waters.

Three radiotagged hens drowned in the same water trough at Site 2; 2 in 2000 and 1 in 2001. The trough is <1 m high and approximately 2 m in diameter. Many other bird species used this trough but only scaled quail were found drowned. The water level in the trough was always <3 cm from the rim. It is unclear whether the telemeters had anything to do with their drowning (no other radio-marked quail were found drowned), or if some site (trough) specific factor played a role in the drownings. There are >30 water troughs of the same style spread out on Elephant Mountain WMA and no other quail had ever been found drowned in any of them. These drowning incidents underscore idea by Schemnitz et al. (1998) of making such troughs escapable by quail.

**Management impacts on survival**

**Moist-soil management**

We initiated our investigations into breeding season dynamics of female scaled quail in 1999 in an attempt to explain why Site 1 had maintained a viable, hunt-able population during a time period (1990s) when scaled quail abundance had declined markedly across much of their range in Texas (Rollins 2000). During the 1990s the Ranch appeared to have greater quail abundance than those of surrounding ranches. A landscape punctuated by spreader dams was hypothesized to be a major component in the population abundance. The distribution and abundance of spreader dams appeared to offer additional habitat components i.e., cover and possibly additional food resources (arthropods and seeds). Indeed, herbage and arthropod biomass were 25 and 6 times greater, respectively, on moist-soil sites relative to adjacent uplands (Buntyn 2004). However, the presence of spreader dams did not affect scaled quail survival during the breeding season at either Site 1 or 2 in either years when precipitation was above (e.g., 1999) or below normal
Survival of Scaled Quail

(e.g., 2000). During the study period (April-August) spreader dams held water for short periods, yet evaporation eliminated standing water within a couple of days. The availability of free-standing water (i.e., for drinking) has not been shown to increase scaled quail abundance (Wallmo and Uzzell 1958). We recognize that benefits of moist soil management (e.g., increased seed or arthropod production (Buntyn 2004)) may accrue to scaled quail and possibly increase either brood or fall-winter survival, but we did not measure these parameters.

Grazing management

Livestock grazing and its relationship to scaled quail habitat need additional study (Saiwana et al. 1998, Smith et al. 1996, Rollins 2007). Smith (1996) found no scaled quail present on an ungrazed site in the northern Chihuahuan Desert, suggesting that heavy or thick vegetation is not frequented by scaled quail. Scaled quail prefer areas of open ground yet require cover to avoid predation from both mammalian and avian predators. In south Texas, an area of sympatry with bobwhites, scaled quail used areas of sparse vegetation compared to areas of dense herbaceous cover used by northern bobwhites (Wilson and Crawford 1987). Conversely, Rollins (2007) suggested “undergrazing”, i.e., stocking rates perhaps 30-50% below those historically practiced for improving overgrazed habitats for bobwhite and scaled quail in west Texas. Grazing management is especially important during times of drought conditions such as those that characterize the Chihuahuan desert (Campbell-Kissock et al. 1984, Nelson et al. 1997).

Supplemental feeding

We observed greater survival of female scaled quail during one breeding season at a fed site compared to a control site however both sites had survival rates lower than the Texas sites we studied. Providing supplemental feed to quail has typically been dismissed by quail biologists as either ineffective (Guthery 2002, :149), inefficient (Guthery et al. 2004), or too expensive (Campbell 1959). However, some private landowners may have the capital to accommodate supplementation and can control some other factors (e.g., hunting pressure) that cannot be controlled on public land. Rollins (2000) reported frequent visitations of adults and young chicks (<3 weeks old) to feeders in west Texas, and recommended that supplemental feeding be evaluated as a management tool in west Texas. Rollins et al. (2006) recorded scaled quail and their broods using feeders commonly at this study site (19 to 22% of feeder visitations), or about twice as often as bobwhites at 4 sites in west Texas (6 to 10% of feeder visitations; Henson 2006). Feeders are also effective in making quail hunting more predictable and productive (Rollins 2000).

Year-round supplementation with milo, in addition to providing a formulated egg-laying ration, significantly improved survival and reproduction of bobwhites on fed sites in northern Florida (Sisson et al. 2000, Tall Timbers Research Station 2001). Benefits from providing supplemental feed might be more important for scaled quail under weather conditions similar to those we encountered during our study (below normal precipitation and above normal temperatures). Additional research is needed to better elucidate the potential benefits of supplemental feeding for desert quails.

We acknowledge some limitations within our studies. The feeder study on Site 3 was non-replicated, and Sites 1 and 2 were not replications in the strictest sense as no positive control at Site 2 and the number of spreader dams was perhaps 10% of that found on Site 1. The feeder study was conducted during a period of severe drought; whether we would have observed treatment differences in more moderate weather conditions is unknown. Our study sites, especially Sites 1 and 3, were atypical for their respective regions because of their conservative grazing management and subsequent higher seral stages.

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Survival of Scaled Quail


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