THE CALLING BEHAVIOR OF

NORTHERN BOBWHITE

MALES

By

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INTRODUCTION

Northern bobwhites (*Colinus virginianus)* are a quail of North and Central America whose primary range in the United States includes the southeastern and midwestern states west to eastern New Mexico, Colorado, and southeastern Wyoming, and north to southeastern South Dakota, southern Wisconsin, and Maine (Johnsgard 1988:61). They are a popular game species that were once abundant, but have experienced long-term population declines over much of their range since 1966, with accelerated losses during the 1980s (Church et al. 1993). One prediction indicated possible extinction of this species by the year 2005 (Brennan 1991).

Considering this negative population trend, it is necessary to carefully monitor northern bobwhite populations (hereafter bobwhites). For accurate monitoring, it is essential to reevaluate and make improvements to monitoring techniques. For this research, I studied the calling behavior of bobwhite males to make improvements in and recommendations for deriving indices using spring and summer call-counts of males. Improving the call-count technique is desirable because of the ease and practicality of conducting aural counts compared to more labor-intensive and expensive methods of population monitoring, such as mark-recapture or kill methods in conjunction with the Lincoln Index and direct visual counts.

Spring and summer call-counts for male bobwhites have been used by scientists and land managers to monitor and study population trends (Kabat and Thompson 1963, Snyder 1984, Stauffer 1993), and as a sampling method to test hypotheses (Baxter and Wolf 1972, Edwards 1972, Brady et al. 1993). Typically, call-counts are conducted on designated county-road routes at locations 0.8-1.6 km apart. Counts begin at or near sunrise and continue for 1-2 hours. At each count location, observers listen and record the number of males making the "bobwhite" call for 2-3 minutes (Bennitt 1951, Kabat and Thompson 1963, Snyder 1984). This protocol is similar to that used in the North American Breeding Bird Survey (Bystrak 1981).

I studied the daily and seasonal phenology of the calling behavior of wild populations during the breeding season, and assessed the effects of weather (temperature, wind speed, humidity, and light intensity) on this behavior. The relationships examined by this procedure are like those examined by Elder (1956) and Robel et al. (1969). Once the effects of time and weather on the calling behavior were determined, meaningful suggestions for designing better call-counts could be made.

In addition to the effects of time and weather, the number of males heard has been found to increase when a recording of a female call is used as an elicitation during counts (Coody 1991). In this study, I tested Coody's hypothesis that call-playbacks increase the number of males heard to determine the usefulness of incorporating this technique into call-count design.

LITERATURE REVIEW

General Ecology and Behavior

Optimum bobwhite habitat can be described as heterogeneous: a mosaic of native grasslands, pastures, cropland and other vegetated yet open areas interspersed regularly with patches of trees or shrubs (Brady et al. 1993). Within this habitat across their range, bobwhites find a variety of foods depending on availability and time of year.

During winter in the southeastern U.S., for example, the diet may include woody plant seeds such as acorns (*Quercus* spp.), pine (*Pinus* spp.), various legumes (e.g., *Lespedeza* spp.), sedge (e.g., *Scleria* spp.), grass seeds, and other herbaceous plant seeds. In the summer, greater quantities of invertebrates, green plant leaves, and fleshy fruits are taken in addition to seeds and nuts (Reid and Goodrum 1979).

Besides providing bobwhites with a variety of foods, a patchy environment gives quail access to woody cover for thermal protection (Johnson and Guthery 1988), predator refugia, roosting, and snow-free foraging areas in the northern parts of its range (Johnsgard 1988:62). When sufficient amounts of suitable habitat exist, food is not known to be limiting for these quail (Guthery 1997). However, snow and ice storms may make food resources unavailable to the birds (Errington 1945). Stoddard (1931:20-21) found that 74% of 602 nests monitored were within about 16 m of some sort of clearing, further emphasizing the importance of a patchy landscape.

From late summer and early fall to late spring, bobwhites form and live in coveys of 10-15 birds (Johnsgard 1988:62). These coveys are of mixed ages and sexes with variable degrees of relatedness (Stoddard 1931:180, Agee 1957). Bobwhites reach varied densities across their range: from ≥ 2.5 - ≤ 17.3 birds/ha (Leopold 1933:52) to 0.4-0.6 birds/ha (Leif and Smith 1993). It was once widely accepted that bobwhites were a relatively sedentary species, making only seasonal, short-distance movements to exploit different food resources in the fall and after covey break-up in the spring. Stoddard (1931:175-176) found that the majority of birds in a band-recapture study conducted in Georgia and Florida were recaptured within 0.8 km of the capture site;

the furthest roving individual was recovered 11.3 km from the original trap-site. However, Duck (1943) determined from leg-band returns that quail in northwestern Oklahoma moved on average 15.7 km in the fall, and 1 individual moved 41.9 km. A recent telemetry study, also in western Oklahoma, revealed individuals moving ≤ 59.6 km in the fall and 25.8 km in the spring (DeMaso et al. 1997), although movements of 16.1-24.2 km and 6.4-8.1 km, respectively, were more common.

Breeding season begins in spring and can continue through early fall. DeMaso et al. (1997) reported seeing chicks with adults as early as 17 April and as late as 1 November in western Oklahoma. More commonly, initiation of egg-laying begins in late April and ceases by early September (Klimstra and Roseberry 1975). Some of the pair formations likely occur while birds are still in coveys during spring, and males become more intolerant of each other at this time (Stoddard 1931:15). Pairs may spend 2-4 weeks together before the first egg is laid (Stoddard 1931:19). A behavior known as "tidbitting" seems to function in female attraction and pair-bond maintenance. A male firsts attracts a female with this behavior by pecking at, without eating, an insect or other food item while giving an associated call, and the behavior continues periodically while pairs are together (Stokes 1967). This behavior was noted to occur within coveys and by parents with broods to alert others of a food source, but it took on sexual display characteristics during the breeding season. During a state of strong sexual motivation, a male would arch his back, ruffle his feathers, fan his tail and stand high on his feet while tidbitting; females, and occasionally other males, were attracted (Stokes 1967).

Twelve to 16 eggs are laid, approximately 1 per day (Johnsgard 1988:64), in a nest completed in about a week (Rosene 1969:58) built by both sexes (Klimstra and Roseberry 1975). Incubation averages 23 days (Johnsgard 1988:64) and can be initiated by either sex. Once a bird has initiated incubation, this individual continues to incubate until hatching, without trading this duty with its mate. Males incubate 20-34% of all nests (Stoddard 1931:30, Curtis et al. 1993, Suchy and Munkel 1993, Burger et al. 1995, DeMaso et al. 1997). Traditionally, it had been thought that bobwhites mate monogamously, and generally raise only 1 brood. Recent studies indicate that bobwhites have a variable, ambisexual, polygamous mating system (Curtis et al. 1993, Burger et al. 1995), and raise multiple broods (Curtis et al. 1993, Suchy and Munkel 1993, Burger et al. 1995, DeMaso 1997). A female may raise a brood for 3-4 weeks and then abandon or leave it under the care of a male while she lays a new clutch (Curtis et al. 1993). Unmated males readily adopt abandoned chicks when they encounter them (Stoddard 1931:65-66, Curtis et al. 1993). The chicks fledge at about 2 weeks of age (Johnsgard 1988:64).

Bobwhite Calling Behavior

Stokes (1967) documented the social and mating behaviors and the complex vocabulary of pen-reared bobwhites. The calls that can be heard easily by a human listener and are of particular interest for this study are the "bobwhite" call of the male, and the assembly call of both sexes (also known as the separation or scatter call).

The assembly call, with 3 forms phonetically described as "hoy-poo", "hoy", and "koi-lee", is used year-round by males and females in several situations (Stokes 1967, Korchenderfer 1971). The "koi-lee" call is given at dawn and dusk, ostensibly to notify other coveys of location and to serve as a spacing mechanism. It is also used by a female separated from her mate or by an unmated female, uttered in rapid succession 5-10 times. Similarly, the "hoy" or "hoy-poo" call functions to unite separated pairs and covey members and is heard when new birds are encountered. The "koi-lee" form is considered the loudest form, followed by "hoy-poo" and "hoy" (Stokes 1967, Korchenderfer 1971). The assembly call develops from the high-pitched "peep" calls of the chicks (Kochenderfer 1971). Low-frequency sounds travel farther than high-frequency sounds, and the relatively high frequency of alarm calls given by young birds, coupled with the lack of intensity differences in these calls, make localization of the source difficult (Marler 1955). In bobwhite chicks, the call undergoes frequency modulation and reduction, thus enhancing localization over longer distances at the time the birds fledge (Baker and Bailey 1986*b*). This call is unique for individuals (Bailey 1978) and inheritance is largely responsible for its distinguishing characteristics (Baker and Bailey 1986*c*). Young birds recognize the assembly call of covey mates (Baker and Bailey 1986*a*), and there is evidence that the phenotypic variations of this call, as a result of inheritance, produce covey dialects over a region (Goldstein 1974, Bailey and Baker 1982). Stokes (1967) observed that, during the breeding season, females recognize the separation calls of their mates and will only respond to their calls.

Antiphonal calling or duetting occurs primarily when a mated pair calls back and forth rapidly, and has been reported for bobwhites (Stokes and Williams 1968). This behavior is noted mostly in tropical bird species (Morton 1996:258), including some quail (Stokes and Williams 1968, Johnsgard 1988:34-38). Antiphonal calling in bobwhites occurs via both males and females using the separation call; males may also use the "bobwhite" call (Stokes and Williams 1968). This behavior may have several functions such as spacing of males, formation of pairs, and reuniting of separated pairs (Stokes and Williams 1968).

Stoddard (1931:97-101) and Stokes (1967) described the "bobwhite" call as being strictly a sexual solicitation call used during the breeding season by males, although Stokes (1967) reported that one female in his captive flock gave the "bobwhite" call when separated from her mate. Stoddard trapped the few consistently calling males in an area using a hen as bait. He then noted the lack of "bobwhite" calls afterward, despite an abundance of nests in the area, and concluded that unmated males make the "bobwhite" call most frequently. Stokes also reported the cessation of male "bobwhite" whistles after birds had paired. However, some researchers believe that mated males may give this call regularly at certain points during the breeding season, or at least occasionally when separated from their mate for extended periods such as during incubation (Kabat and Thompson 1963, Ellis et al. 1972). Stokes observed the latter reaction when he removed the female of a pair from the male for several hours. Similarly, Stoddard (1931:100) was alerted to dead females within his captive pairs by the whistling of the mate. Korchenderfer (1971) concluded that the "bobwhite" call is related to and probably derives from the juvenile separation call. It was first given by birds at 15 weeks and coincided with sexual maturity in her study of captive birds. Females in this study began laying eggs at 16 weeks of age (Korchenderfer 1971).

However, a separate study of captive birds found that the average age for first egg-laying was 223.7 days, or about 7-7.5 months (Kulenkamp and Coleman 1968).

A south Texas study indicated that perches from which male bobwhites whistle contain consistent habitat characteristics (Johnson et al. 1990). These include brush canopy coverage within 30 m of about 20%, visual screening 12-20 dm aboveground at 20-40%, perch heights of 1.5-2.5 m, and overhead cover in 79% of cases observed.

Another call made by bobwhites during the breeding season is the caterwaul. It is defined as a strongly antagonistic call uttered by males and less commonly females, elicited at close range by the sight and sound of other bobwhites (Stokes 1967). Stokes believed that of all calls, the caterwaul most closely functioned as a territorial song, because it was used to repel rival males from a female (and vice versa) or when a strange bird was introduced to a previously established group. Stokes concluded the "bobwhite" call was not a spacing mechanism, and therefore not a true territorial song, because males would whistle in close proximity to one another without any apparent antagonism, unless a female was introduced. However, Rosene (1969: 60-63) reported that males were seen at least 15.2 m apart while giving the "bobwhite" call in natural situations, and believed it was a spacing mechanism for the somewhat territorial species.

Sound Production and Perception

Sound is described as mechanical waves, which can travel through a gas, liquid, or solid (Halliday and Resnick 1988:418). Sound waves have 3 general characteristics with which I will be concerned. These characteristics are frequency (the number of oscillations or cycles per unit of time), wavelength (the distance between crests or depressions in the wave), and intensity (the average rate per unit area at which energy is transmitted by the wave), expressed in watts per meter squared (W/m^2) (Halliday and Resnick 1988:423). For convenience, intensity is often converted to decibels (dB) by this equation:

$$dB = (10dB) \log I/I_0 .$$

The symbol I_0 equals 10^{-12} W/m^2, the lower limit of human hearing. Attenuation refers to the decrease in intensity with distance. This equation also can be manipulated to determine intensity (I) if decibels are known. Sound wave energy, or power at a point source (P), is expressed in watts and can be determined if intensity (I) and distance in meters from the source is known:

$$P = I\,(4\pi r^2)$$

The surface area of a sphere ($4\pi r^2$) is used because sound waves are usually described as being emitted uniformly in all directions from a source. When power is known, the maximum distance at which a sound can be heard is:

$$r = \sqrt{P/4\pi I_0}$$

However, this equation describes the maximum distance over which a sound can be heard with attenuation only being caused by spherical spreading. In real situations, physical features and atmospheric conditions surrounding a sound source (e.g., trees and relative humidity), and the frequency of the broadcast sound contribute to additional attenuation. Generally, sounds travel faster in warm, humid air than cool, dry air. High-frequency sounds have shorter wavelengths, and are more easily scattered and absorbed by their surroundings than low-frequency sounds (Catchpole 1995:72-77).

The assembly call in bobwhites ranges between 0.6 and 1.8 kHz (Bailey 1978), and the chick's lost call falls between 3.0 and 3.5 kHz (Barton et al. 1984). This corresponds well with the frequencies to which bobwhites are most sensitive (Barton et al. 1984). The auditory threshold curves (sensitivity to a range of frequencies) of some birds, including bobwhites, are similar to humans (Schwartzkopff 1955, 1968:41-44). However, Schwartzkopff (1968:42) suggested that birds possess a much more finely tuned sense of temporal resolution, allowing them to detect changes in frequency at speeds too fast for human perception.

Call-Counts as Indices and the Playback Technique

An index, unlike a census or population estimate, compares relative abundance between areas or within 1 area over time (Bolen and Robinson 1995:60). An index is a number assumed to be linearly correlated with population size or density. Call-counts as population indices have been used extensively as the most feasible way to monitor avian populations (Link and Sauer 1998). They also have been used in studies of bobwhites (Kabat and Thompson 1963, Bennitt 1951, Rosene 1957, Robel et al. 1969, Ellis et al. 1972, Curtis et al. 1989). The reported validity of this technique as an index varies among researchers and seems complicated by several factors. Two of these factors are observer hearing ability (Link and Sauer 1998) and observer ability to distinguish among individuals or individual units (Ellis et al. 1972, DeMaso et al. 1992). Other factors include the effects of environmental and temporal variables (i.e., daily and seasonal phenology) on the calling rate, on the number of birds calling, and on the detection ability of the observer (Robel et al. 1969, Elder 1956, DeMaso et al. 1992). A final factor is the soundness of assumptions inherent in creating an index (Norton et al. 1961, DeMaso et al. 1992). In other words, when developing an index, certain assumptions are always made regarding the relationship between the independent variable measured and the dependent variable predicted, and therefore, an index is only valid if those assumptions are true.

An observer's hearing ability places an obvious bias on a call-count; it is directly proportional to the radius of audibility and thus the area sampled. Bias is introduced in a count by the experience and skill of a listener (Link and Sauer 1998). Weather conditions and habitat characteristics (Catchpole 1995:72-77) also affect the radius of audibility. For example, Robel et al. (1969) found that wind speed was inversely proportional to the number of bobwhite whistles heard, at least partly, they induced, because the radius of audibility was reduced as wind speeds increased. Wind can increase the radius of audibility in the direction the wind is blowing, by increasing the velocity of sound wave (Wiley and Richards 1982:157), and by bending sound waves down towards the ground (White 1975:63-64). However, wind usually acts as turbulence because of inconsistent speed, or due to contact with irregular surfaces, and thus causes sound waves to scatter (Wiley and Richards 1982:140-141). Also, wind speeds that differ with distance from the ground, producing a layered effect, can create various patterns of inaudible and audible zones at ground level (White: 1975:66).

Other weather variables may affect the number of birds calling and the frequency of calls. Elder (1956) found a significant negative correlation between temperature and the number of bobwhites heard. Robel et al. (1969) found a negative correlation between the number of calls and temperature after the seasonal calling peak and a negative correlation between the number of calls heard and humidity before and after the seasonal peak. Bennitt (1951) found no correlation between cloudiness or humidity and the bobwhite call index, but did find a negative correlation between temperature and the number of birds heard.

Besides excess sound wave attenuation, habitat may affect the number of calls heard in other ways. In a study comparing roadside (visual) quail surveys and male whistle-counts for suitability in predicting fall harvest, roadside surveys were determined to be better predictors (Schwartz 1974). It was speculated that this result was found in part because the whistle-count route was located in prime quail habitat, while ring-necked pheasant (*Phasianus colchicus*)-survey routes were used for the roadside quail surveys (i.e., poor or marginal habitat for bobwhites). Thus, it was thought that roadside routes more clearly showed population fluctuations compared to prime quail habitat, which always had relatively higher densities of bobwhites. Higher population densities may have a negative effect on call-count accuracy (Ellis et al. 1972, Snyder 1984). These researchers believed that determining the exact number of whistling males became difficult when >7 were calling; this number is quite speculative though, because they did not know the number of males within the radius of audibility.

Temporal variables, both daily and seasonal, seem responsible for the greatest changes in the number of bobwhite whistles heard, but the nature of these changes is not entirely clear. Elder (1956) and Robel et al. (1969) reported a general pattern of peaks in whistling activity within the hour after sunrise, although there were exceptions in both studies. Elder found that the second hour after sunrise often contained maximum peaks in whistling activity. In 1 year of a 3-year study, Robel et al. (1969) reported a bimodal calling rate pattern, with a peak at sunrise and a peak 1 hour after sunrise, and fewer calls overall. They determined that these observations were caused by cloudier (i.e., cooler) and windier weather during that year; they found no correlation between light intensities and quail whistling activity. The other 2 years of the study by Robel et al. (1969) showed peaks in the calling rate only at or near sunrise. Three studies (Rosene 1957, Speake and Haugen 1960, Robel et al. 1969) found strong correspondence between nesting activity (mid-June to mid-July) and peak whistling activity, with peaks in whistling occurring at approximately the same time as peaks in nesting activity, but declining sharply after hatching peaks.

Norton et al. (1961) analyzed data collected in Illinois and reanalyzed data collected by Bennitt (1951), Reeves (1954), and Rosene (1957). The results of Norton et al.'s (1961) analysis contradicted the earlier researchers' findings, in that the whistling-male count was not found to be a reliable predictor of autumn covey populations within the same areas in different years. Norton et al. (1961) recommended that these counts only be used to predict relative abundance of autumn populations over similar areas not sampled within the same year, unless regular trends were recognized. In other words, the call-index used for the first year could not be used the second year in the same area. DeMaso et al. (1992), in research comparing covey density with the number of covey calls heard, found only a weak correlation between covey calls and absolute density, most likely because assumptions used in developing the index did not hold. These assumptions were that individual quail call at the same intensity, the proportion of coveys calling is the same over space and time, and observers can accurately identify individual coveys (DeMaso et al. 1992:99).

Evidence suggests that reproductive status of males may affect calling rate (Stoddard 1931:97-101, Stokes 1967). There remains some debate as to whether unmated male bobwhites call (Rosene 1957 1969:75, Ellis et al. 1972). It has been shown for the mourning dove (*Zenaida macroura*) that reproductive status affects calling behavior. In this species, paired males called less often than unpaired males (Staicer et al. 1996:431). Additionally, Guyomarc'h and Guyomarc'h (1998) discovered that the sexual call in European quail (*Coturnix coturnix*) varies in inter-syllable duration, coincident with reproductive condition and age, and thus provides a mechanism for conveying this information to conspecifics.

The playback recording technique has been used to elicit calling of certain bird species that may be difficult to detect in the field (Marion et al. 1981). Bobwhites have been shown to respond by calling to a recording of the assembly or separation call (Bailey 1978), especially sexually motivated males (Stokes 1967, Coody 1991). Coody (1991) found the use of a recording of the assembly call during call counts (i.e., the call-playback technique) increased the number of males heard.

STUDY AREA

Call-count locations were selected on the Oklahoma State University Cross Timbers Experimental Range, and on nearby county roads adjacent to private lands. The Cross Timbers Experimental Range and nearby county roads are 21-24 km west of Stillwater and south of Lake Carl Blackwell in Payne County, Oklahoma. All study sites were in an ecological region known as the Cross Timbers that occupies a band 10-180 km wide south from the southern edge of the bluestem (*Andropogon* sp.) prairie of Kansas, across Oklahoma to the Trinity River in north Texas (Sims 1988:273). The Cross Timbers is characterized by rolling hills of post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*), creating a woodland interspersed with native tallgrasses in undisturbed areas (Sims 1988:273). Some of the grass species listed by Sims (1988: 273) are little bluestem (*Schizachyrium scoparium*), hairy grama (*Bouteloua hirsuta*), yellow Indian grass (*Sorghastrum nutans*), big bluestem (*Andropogon gerardii*), and sideoats grama (*B. curtipendula*) (nomenclature following Scott and Wasser 1980). This vegetation was historically maintained with fire, and eastern redcedar (*Juniperus virginianus*) has become common with recent fire suppression. Other shrubs and trees include smooth sumac (*Rhus glabra*), dogwood (*Cornus* sp.), and elm (*Ulmus* sp.) (Lochmiller and Engle 1991). Soil associations and orders of the study area are Stephenville-Darnelle-Niotaze Alfisols and Inceptisols, Renfrow-Kirkland-Grainola-Bethany Mollisols and Alfisols, (Carter and Gregory 1996).

The climate in the Cross Timbers in northern Oklahoma is classified as moist and subhumid (Oklahoma Water Resources Board 1972). Temperatures range from a mean daily minimum of –5.0°C in January to a mean daily maximum of 35.0°C in July and August. Average precipitation is about 69.9 cm per year with 31.8 cm of snowfall. January is typically the driest month and May the wettest (Oklahoma Water Resources Board 1972).

METHODS

Daily Phenology, Seasonal Phenology, and the Effects of Weather

Five points were selected for conducting call-counts. Each point had an implied 400-m radius because this is a generally accepted radius of audibility (Stoddard 1931:102, Coody 1991). The points were placed so that different proportions of the surrounding area were covered by one of 2 kinds of cover, one assumed to be used and preferred by quail and one that was not or was less so. For example, a point could contain 50% tall grass and brush and 50% plowed field; or it mightcontain75% tall grass and brush and 25% plowed field might. The purpose for this design was to account for and distribute the effects of preferred vs. less-preferred habitat on the call-counts. Cover within the 400-m radius area was determined by ground observations and by examining aerial photographs. Cover was classified as usable and preferred by bobwhites if it consisted of grasslands with brush or resprouting hardwoods and junipers, and a few large trees; less-usable space was covered with open grassland lacking shrubs or resprouting trees, or closed canopy forest. The entire 50.3-ha areas, including the center points, are referred to as sites throughout the text.

Site 1 was covered by 50% closed canopy oak forest (less usable), and 50% brushy grassland with scattered oaks and cedars (more usable). Approximately 75% of site 2 was covered by brushy grassland with oaks and cedars (more usable), 12.5% by open grassland (less usable), and 12.5% by closed canopy oak forest (less usable). Site 3 had a dense north-to-south band of cedars and other trees (less usable) that covered about 5% of the area and divided the remaining area in half. The western half was covered by brushy grassland with a heavy sumac (*Rhus* sp.) component (more usable), and the eastern half was covered by open grassland with a few isolated, large trees (less usable). I judged sites 4 and 5 to be covered entirely with relatively usable space (brushy grassland with small clumps of oaks and cedars). Sites 2 and 3 were partially burned during a controlled burn between January and April 1999.

I collected data from mid-May to mid-August 1998 and 1999. A count for each point began 45 minutes before sunrise and continued for 4 hours and 15 minutes thereafter. The number of calling males and the number of full "bobwhite" calls made by each male were tallied in 5-minute intervals, and the location of each male when first heard was marked on a spot map (Guthery 1986:139) to help prevent double-counting. Weather variables were recorded every hour beginning at the start of the daily call-count period and concluding at the end of the last hour. Counts took place under all weather conditions except continuous rain, because an objective was to determine the influence of weather variables on the call-count index. Each site was sampled 12 times per year, approximately once per week.

Weather data included temperature (°C), relative humidity (%), wind speed (m/sec), light intensity in lumens/m^2 (lux), and proportion of cloud cover. Equipment used for taking weather data and keeping time included a Thermo-Hygro humidity and temperature pen, a Turbo Meter electronic wind speed indicator by Davis Instruments, and a digital light meter and stop watch by Extech Instruments. Temperature measurements were made in the shade. I estimated cloud cover by holding my arm out at a 45° angle from the perpendicular and pointing my index finger. I then rotated 18° 20 times to complete a full circle, and counted each instance my finger appeared to cover clouds (cumulous only), resulting in a measure of proportional cloud cover. For example, if my finger appeared to cover clouds in 5 of the 20 rotations, the proportion of cloud cover was recorded as 0.25. This method of quantifying cloud cover was designed to eliminate some of the variability and bias likely in subjective estimates. However, some bias in estimating proportion of cloud cover by this method still remained (e.g., high, thin clouds; clouds on the eastern horizon), and was partly accounted for by light intensity measurements. Light intensity was measured by facing north and holding the meter horizontal to the ground and out of shade.

Call-playback Response

A route with 10 400-m-radius points was selected on county roads for testing male response to call-playbacks. Each point was placed ≥1.6 km from the next to prevent overlap of birds heard. The route was selected so points would have approximately equivalent amounts of usable habitat. A recording of a female making the assembly call (recorded by Don Scott, Lake Charles, Louisiana) was used for the call-playback on 5 randomly selected points. On the days that the route was tested for male response to the taped call, I used a version of the protocol developed by Coody (1991). For the 5 call-playback points, the number of calls and males heard were counted for 3 minutes prior to using the call-playback, then counted for 1.5 minutes after the recording had been broadcast at high volume (90 dB) in the cardinal directions. This 1.5-minute post-playback session was repeated for a total of 6 minutes of counting time at each point. Birds and calls heard were marked on a spot-map (Guthery 1986:139). The 5 remaining points were treated as controls with no call-playback used, recording the number of calls and males heard in 1 3-minute and 2 1.5-minute sessions, for a total of 6 minutes of counting time at each point. The route was started at a different point each time it was sampled (starting point chosen randomly) to control for the effects of time of day on the counts. The 10-point route was sampled 12 times; every point was used as the starting point at least once. Counts were not conducted in the rain. I made these counts from mid-May to mid-August 1998 and 1999.

Statistical Analyses

Data were analyzed using Prostat (Polysoftware International, Salt Lake City, Utah, USA) and Systat version 8 (SPSS Inc., Chicago, Illinois, USA). Significance for all tests was set at $P \leq 0.05$.

Daily Phenology. –To analyze daily trends in the number of males heard, the number of males for each 5-minute time interval was ranked (Kendall and Ord 1990:24) within day and site separately for each year. Ranking standardized the number of males heard among sites, because there were different densities of bobwhites on different sites by design. The mean rank for each time interval was then calculated. It was not necessary to test for the presence of a daily trend, because the existence of a trend was confirmed by earlier studies (Elder 1957, Robel et al. 1969). Rather, an analysis was performed to determine the nature of the daily trend on my study sites.

A 3-point moving average of the mean ranks and the standard deviations of mean ranks were created to reveal approximate trend lines. The 3-point moving averages were plotted against daily time class (i.e. 5-minute interval) to determine times for maximum number of calling males and least variation in number of calling males. A third 3-point moving average was created from the ratios (means/standard deviations), and was plotted against time class for an index of precision. This measurement combined the 3-point moving averages for maximum number of calling males and least variation in 1 value, and thus when plotted against time, indicated the best times to sample on the basis of precision. By identifying the peaks in the 3-point moving averages for maximum number of calling males by site, I identified time classes when ≥70, ≥80, and ≥90% of the maximum occurred. For example, if the peak in maximum number of calling males for a site was found to be 40, 40(0.9) was calculated. The time classes occurring before and after the time class containing 40, whose maximum number of calling males were $\geq 40(0.9) = 36$, identified the start and stop times for hearing 90% of the maximum on an average daily basis.

Call-playback Response. – Differences between call-playback call-counts and control call-counts were tested using analyses of covariance (ANCOVA)(Systat, SPSS Inc. Chicago, Illinois, USA). The number of males heard during the second 3-minute listening period for each point was used as a response variable, and the number of males heard during the first 3 minutes for each point was used as a covariate in 1 test. A second analysis of covariance used the number of calls heard during the second 3-minute listening period as a response variable and the number of calls heard during the first 3 minutes as a covariate. This test was conducted to remove some of the bias possible in identifying individual males (Ellis et al. 1972, Snyder 1984). A third analysis of covariance, using the number of males heard during the first 3 minutes as a covariate and the number of males heard during the second 3 minutes as a response variable, was performed on a truncated data set. This data set consisted of the 3 points per day sampled closest to 45-55 minutes past sunrise; the time frame determined from other analyses to have the greatest number of calling males with the least amount of variation. A test for parallelism was performed prior to conducting ANCOVAs. Testing for parallelism is important because it determines if the independent variable (in this case the number of males or calls heard during the first 3-minutes) has the same magnitude of effect on the treatment and control groups. Therefore, if the slopes of the treatment and control groups are different, then no meaningful comparisons of the dependent variable means for the 2 groups can be made (Sokal and Rohlf 1995:513).

Artificial Neural Network Modeling. – Seasonal trends and the effects of weather on the number of calling males were examined using an artificial neural network (ANN) model. These models were originally designed to simulate the functions of neurons (Hagan et al. 1996:8), and have been used for research in physics, chemistry, medicine, molecular biology, and ecology (Lek and Guegan 1999). Artificial neural networks work by predicting a dependent variable from multiple independent variables for data it is naïve to. For further information on ANNs, refer to Hagen et al. (1996) and Smith (1996).

Neural modeling was conducted with Neural Connection (SPSS Inc., Chicago, Illinois, USA) software. Model architecture included 7 input nodes, 4 hidden nodes, and 1 output node. The input nodes (independent variables) were Julian day, hour (1, 2, 3, 4, 5), temperature (°C), relative humidity (%), wind speed (m/sec), proportion of cloud cover, and light intensity (lux). Mean hourly values (start and end) were used for the weather variable inputs, because weather data were collected hourly. The standard normal deviate of the mean number of males heard calling during 5-minute intervals in 1-hour periods was the output node (dependent variable), and was specific for site and year. The standard normal deviate for a site and year was calculated as follows: (1) the mean number of males heard calling for each hour was calculated based on 12 5-min intervals/hour and 12 days/site/year, (2) the mean and standard deviation for all hours on a site within a year was calculated based on 12 sampling days/site/year × 5 hours/sampling day ($n = 60$), and (3) the standard normal deviate for any hour within a site and year was calculated as (hourly mean – grand mean) / SD. Calculation of the standard normal deviate permitted pooling of data among the 5 sites within a year, resulting in a sample size of 300/year. Models for each year were trained using a randomly drawn data set comprising 80% of the total yearly data; validation was conducted on the remaining 20%.

The effects of each variable in the input layer on the standard normal deviate of hourly means of calling males were analyzed by holding all other inputs at their 2-year means and modeling the variable of interest. Two-year means were set at 178 for Julian day, 25 °C for temperature, 72% for relative humidity, 1.2 m/sec for wind speed, 36,500 lux for light intensity, and 0.25 for proportional cloud cover. The relative sensitivity of the standard normal deviate to an input node was indexed by calculating the range of response (maximum – minimum) predicted within a reasonable range of values for the input variable.

RESULTS

Daily Phenology

The average maximum across 5 sites in the 3-point moving average for ranked mean number of calling males was calculated to occur during time class 95 (45 minutes past official sunrise) in 1998 and time class 100 (50 minutes past official sunrise) in 1999 (Figs.1, 2; Table 1). The average maximum in the ratio of means/standard deviations was calculated to occur during time class 105 (55 minutes past official sunrise) in 1998 and time class 100 (50 minutes past official sunrise) in 1999. The ratio values used to calculate the average maximum were roughly coincident with times for peak calling males. Thus, the time of peak calling coincided roughly with the time that maximum precision in the call index could be obtained. However, this coincidence was subject to considerable variation (Figs. 1, 2).

Weather and Seasonal Effects

Neural models explained 55% and 41% of the variation in the training data for 1998 and 1999, respectively; they explained 64% and 24% of the variation in the validation data in 1998 and 1999, respectively (Fig. 3). Thus, the neural models found

Fig.1. Daily phenology of calling intensity (top), variability in calling intensity (center), and precision in calling intensity (bottom) for northern bobwhites in central Oklahoma, 1998. The points represent statistics for ranks of the number of calling males within 60 5-min intervals/day as calculated over 12 sampling days/site. The lines are 3-point moving averages of the statistics.

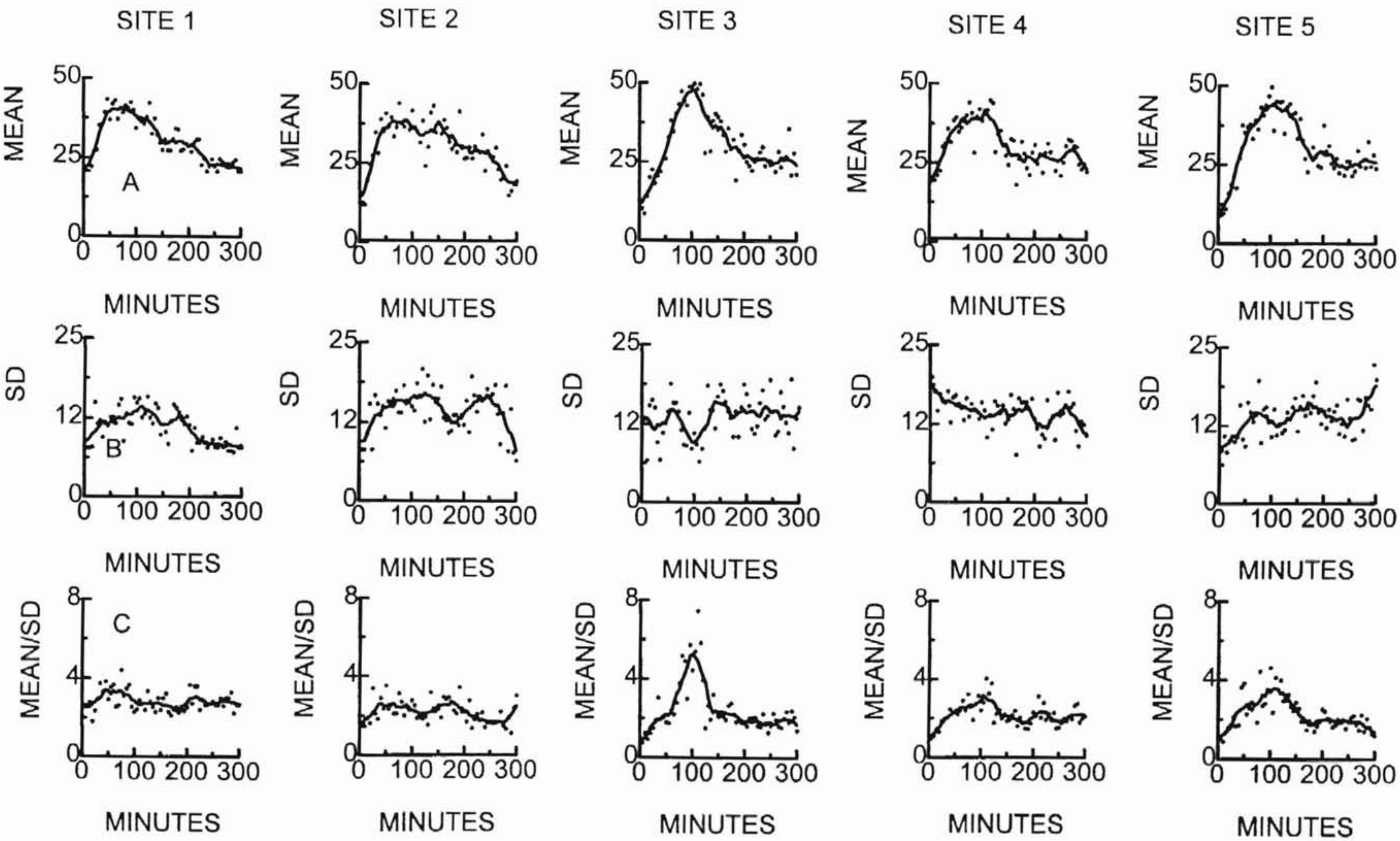
SITE 1
SITE 2
SITE 3
SITE 4
SITE 5
MEAN
SD
MEAN/SD
MINUTES
A
B
C
0
100
200
300
50
25
12
8
4

Fig.2. Daily phenology of calling intensity (top), variability in calling intensity (center), and precision in calling intensity (bottom) for northern bobwhites in central Oklahoma, 1999. The points represent statistics for ranks of the number of calling males within 60 5-min intervals/day as calculated over 12 sampling days/site. The lines are 3-point moving averages of the statistics.

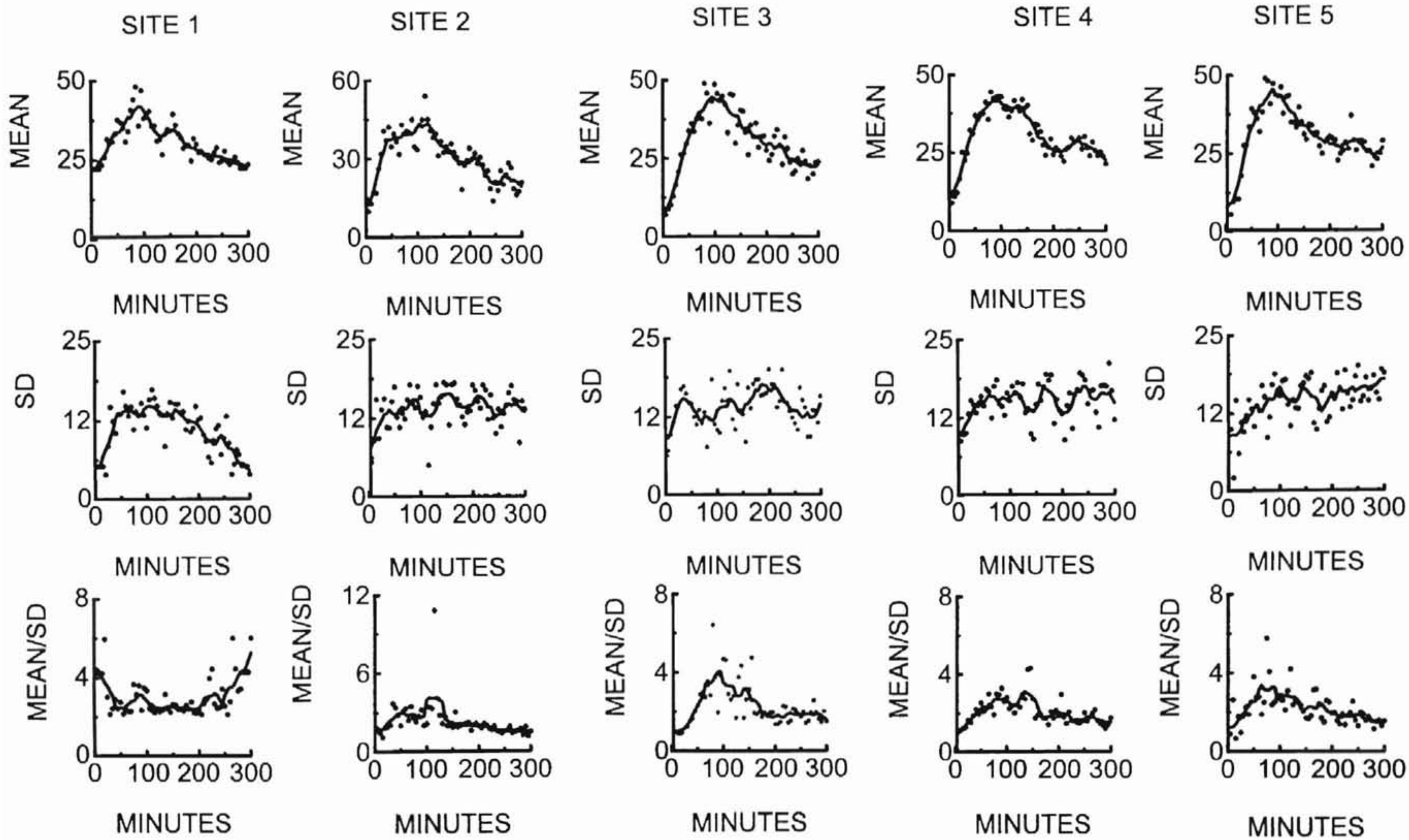
SITE 1
SITE 2
SITE 3
SITE 4
SITE 5
MEAN
SD
MEAN/SD
MINUTES
0
100
200
300
50
25
60
30
12
8
4
6

Table 1. Annual variation in call-count start and stop times relative to sunrise where the 3-point moving average for the mean of ranks of calling bobwhite males within 5-min time classes was ≥70, ≥80, or ≥90% of the maximum 3-point moving average, central Oklahoma, 1998 – 1999.

		1998			1999		
Percentage of maximum	Site	Start	Stop	Minutes	Start	Stop	Minutes
≥70	1	-25	165	190	-20	135	155
	2	-25	205	230	-20	125	145
	3	10	120	110	0	135	135
	4	-20	95	115	-10	130	140
	5	-5	120	125	-5	120	125
≥80	1	-20	95	115	0	75	75
	2	-20	140	160	-10	100	110
	3	15	85	70	10	105	95
	4	-15	90	105	0	115	115
	5	5	110	105	5	90	85
≥90	1	-10	70	80	15	60	45
	2	-10	65	75	30	85	55
	3	30	75	45	30	80	50
	4	20	80	60	15	100	85
	5	30	90	60	20	70	50

Fig. 3. Comparison of observed and predicted values (artificial neural network) of the calling behavior of northern bobwhite males in central Oklahoma, 1998—1999. The neural models predicted the standard normal deviate of hourly means of calling males as a function of Julian day, hour, temperature (°C), relative humidity (%), wind speed (m / sec), proportion of cloud cover, and light intensity (lux). The validation data show performance of the model on data not used in training the model.

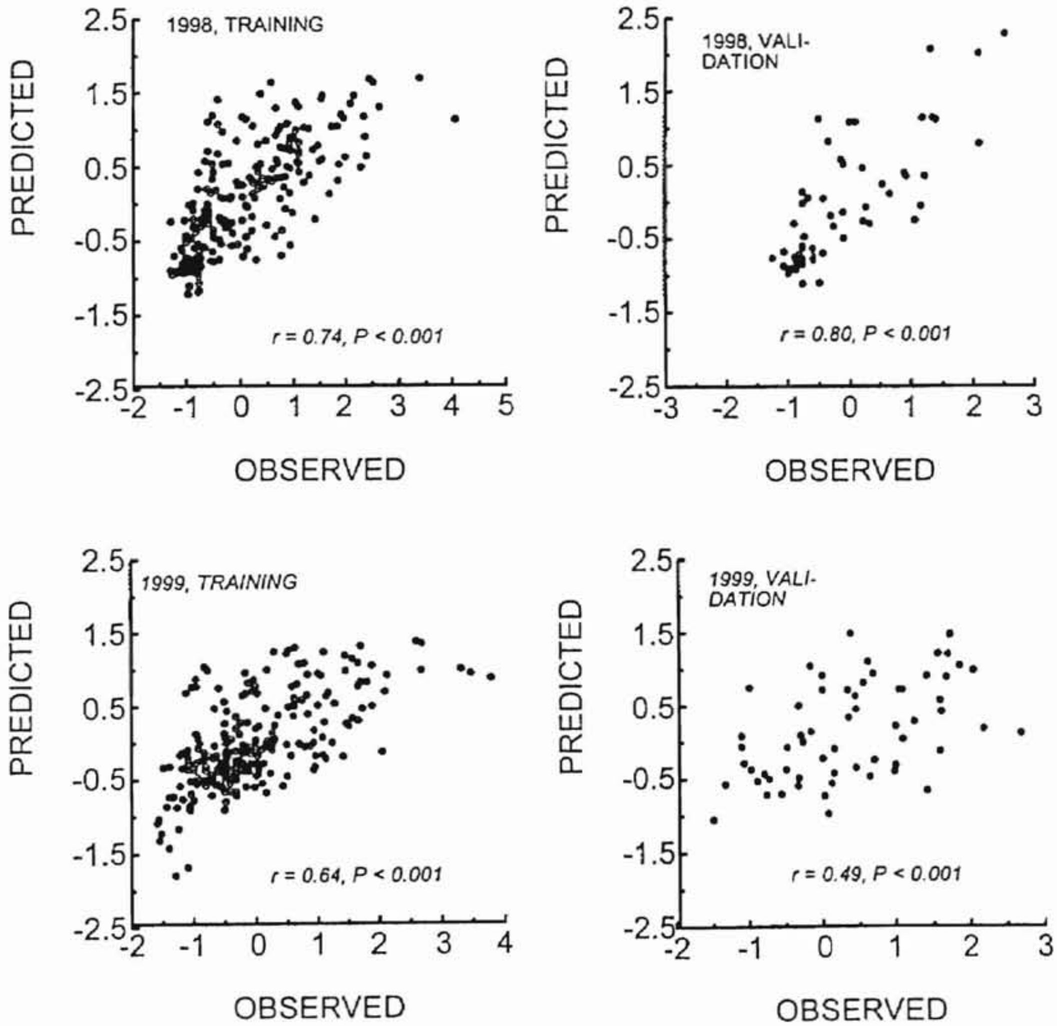
1998, TRAINING
r = 0.74, P < 0.001
1998, VALIDATION
r = 0.80, P < 0.001
1999, TRAINING
r = 0.64, P < 0.001
1999, VALIDATION
r = 0.49, P < 0.001
PREDICTED
OBSERVED

Fig. 4. Artificial neural network predictions of the response of calling by northern bobwhite males to temporal and weather variables, central Oklahoma, 1998—1999. The models predicted the standard normal deviate (deviate) of hourly means of the number of calling males (n = 300/year). The effects of 1 variable were examined by holding other variables constant at their 2-year mean values.

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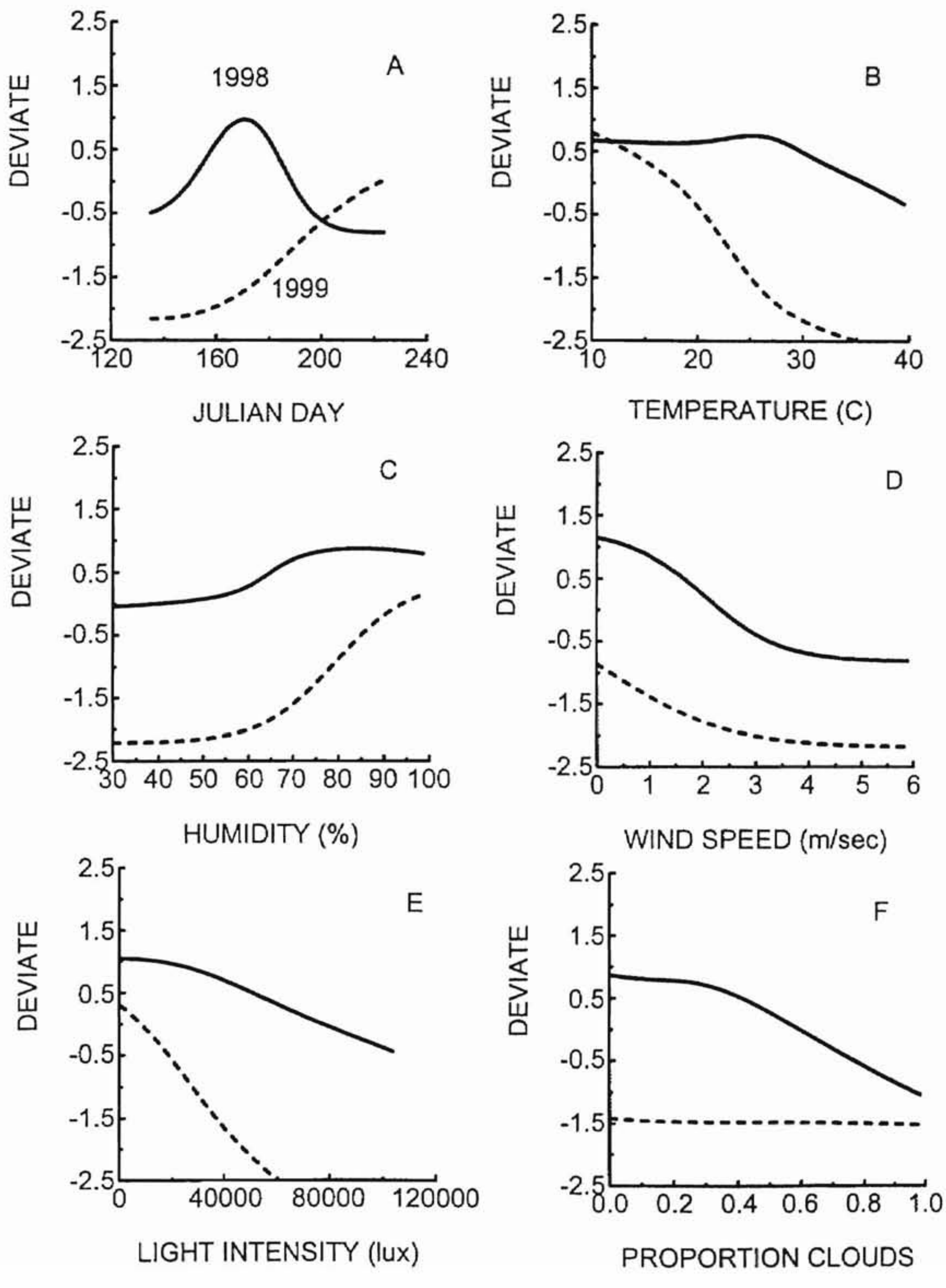
A
1998
1999
DEVIATE
2.5
1.5
0.5
-0.5
-1.5
-2.5
120
160
200
240
JULIAN DAY
B
TEMPERATURE (C)
10
20
30
40
C
HUMIDITY (%)
30 40 50 60 70 80 90 100
D
WIND SPEED (m/sec)
0 1 2 3 4 5 6
E
LIGHT INTENSITY (lux)
0 40000 80000 120000
F
PROPORTION CLOUDS
0.0 0.2 0.4 0.6 0.8 1.0

Table 2. Annual variation in weather variables for 5 sites in central Oklahoma, 1998 – 1999. Each site was sampled 12 times/year and weather data (mean for start and end of 1 hour) were obtained 5 times/site/day, resulting in n = 300/year.

	1998				1999			
Variable	$\bar{x}$	SD	min	max	$\bar{x}$	SD	min	max
Temperature (°C)	26.3	4.9	13.7	36.9	24.0	4.7	10.0	33.9
Humidity (%)	66.5	10.1	32.5	92.5	78.1	9.6	26.0	98.0
Wind (m/sec)	1.2	1.1	0.0	5.8	1.2	1.0	0.0	5.3
Lux (lumens/m^2)[a]	3.7	3.2	0.05	11.0	3.6	3.3	0.04	10.6
Cloud cover (%)	20	32	0	100	30	36	0	100

[a] $\times 10^{-4}$

repeatable patterns in the relationship between calling behavior of bobwhite males and temporal and weather variables.

Neural model predictions for the standard normal deviate of mean number of calling males using Julian day differed between the 2 years (Fig. 4A). A pronounced peak in the mean number of males detected occurred near Julian day 170 in 1998, and a gradual continuous increase in calling activity with increasing Julian day occurred in 1999 (Fig. 4).

The relationships between 4 of the weather variables and number of calling males were similar in 1998 and 1999. Calling activity decreased with increasing temperature, wind speed, and light intensity, and increased with increasing humidity (Fig. 4B, C, D, E). An increase in the proportion of cloud cover resulted in a decrease in the mean number of males in 1998; however, this variable showed no effect in 1999 (Fig. 4F). The sensitivity of the number of males heard to the weather variables were ranked as follows: light intensity > temperature > Julian day > wind speed = humidity > cloud cover. The value for mean number of males detected was more sensitive to increases in temperature in 1999, and more sensitive to cloud cover in 1998; temperatures were higher in 1998, and there was more cloud cover in 1999 (Table 2).

Call-playback Effects

Tests for parallelism revealed parallel lines present between playback points and non-playback points for the number of males heard during the first 3 minutes versus the second 3 minutes in both 1998 ($P = 0.521$) and 1999 ($P = 0.782$) in the full data set. Parallelism was also shown between playback and non-playback points for the number of calls heard in 1999 ($P = 0.585$), but not in 1998 ($P = 0.011$). Parallelism was shown between playback and non-playback points for the number of males heard during the first 3 minutes versus the second in 1998 ($P = 0.664$) and 1999 ($P = 0.965$), in the truncated data set. Analysis of covariance was therefore performed using the number of males heard during the first 3 minutes as a covariate for the full and truncated data sets for 1998 and 1999, and the number of calls heard during the first 3 minutes as a covariate for 1999. Results of the analysis of covariance showed no significant difference in *y*-intercept for the number of males heard between playback and non-playback points in the full data set in 1998 ($P = 0.762$) or 1999 ($P = 0.350$), or for the number of calls heard in 1999 ($P = 0.576$). There was also no significant difference in *y*-intercept for the number of males heard between playback and non-playback points in the truncated data set in 1998 ($P = 0.322$) or 1999 ($P = 0.659$). Thus, there was no apparent benefit in using call-playbacks to index bobwhite abundance.

DISCUSSION

Daily Phenology

Peaks in the maximum number of calling males occurred, on average, within the hour after official sunrise in this study (Table 1). This agrees with the findings of Bennitt (1951) and Elder (1956). The maximum mean number of calls/minutes had an average peak during the first hour after sunrise in the study by Robel et al. (1969). Elder (1956) found that sometimes the second hour after sunrise had the highest number of calling males. I determined that 90% of the maximum could be heard within a time interval extending into the second hour after sunrise (Table 1). Robel et al. (1969) found that the number of calls heard per minute increased rapidly in the minutes before sunrise; Elder (1956) eliminated the 30 minutes before sunrise from analysis of his counts, because of the large amount of variability in calling activity at this time. This study did not find any peaks in the 3-point moving average of maximum calling males before sunrise, although estimated start times of counts to hear 90% of the maximum began before sunrise at some sites in 1998 (Table 1).

The phenomenon of birds singing or calling intensely in the morning is well documented and theories abound as to its possible proximate and ultimate causes (Staicer et al. 1996:426-453). The daily phenology of morning calling has been found to be species-specific and vary between and within season (Berger 1961:170, Shields 1977, Verner and Ritter 1986). It has also been suggested as an important variable to consider in designing aural counts (Hutto et al. 1986). Light intensity appears to be the most important external trigger for the daily initiation of morning calling in birds and is species specific (Armstrong 1963:190-192).

In this study, the daily phenology in number of calling bobwhite males within sites between years was remarkably similar (Figs. 1, 2). Three possible explanations for this result are 1) similar relative population numbers within sites between years, 2) genetic relatedness of site population members, and 3) similar photoperiod and local environmental conditions. The assembly call of bobwhites has unique, genetically transmitted characteristics (Baker and Bailey 1986*b*), and the inheritance of these characteristics can lead to regional dialects (Goldstein 1974, Bailey and Baker 1982). Individual differences have also been found in the male sexual solicitation call of

European quail, Japanese quail (*C. japonica*), and hybrid European × Japanese quail (Collins and Goldsmith 1998). Although it has not yet been demonstrated, it may be possible that bobwhite males in certain areas not only inherit vocal characteristics, but also daily singing patterns. However, perhaps a better expanation for similar daily calling phenology lies in similar relative populations within sites between years. The presence or calling of male birds can stimulate others in the vicinity to call or display; thus the amount of calling may be a function of density (Staicer et al. 1996:434). This effect has been demonstrated or indicated in several gallinaceous birds such as ring-necked pheasants (Gates 1966), European and Japanese quail and their hybrids (Collins and Goldsmith 1998), spruce grouse (*Dendragapus canadensis*) (Keppie 1992), and bobwhites (Rosene 1969: 61). The Cross Timbers study sites appeared to contain similar relative numbers of males in 1998 and 1999, and this may explain the similar daily calling patterns within sites. In addition, because the same sites were sampled in both 1998 and 1999, and site characteristics did not change appreciably between years, photoperiod and other local environmental variables were likely similar within sites, thus affecting resident bobwhites similarly from year to year.

Weather and Seasonal Effects

The peak in the number of males heard calling during the field season occurred at different times in 1998 and 1999. This result seemed to be influenced by the seasonal effects of weather on quail behavior and physiology.

From neural analysis, the seasonal peak in the number of calling males occurred near Julian day 170 (19 June) in 1998 (Fig. 4A). This date agrees with results (number of calls) found by Robel et al. (1969) in their study of quail in Kansas, and with results obtained by Bennitt (1951) in Missouri. These researchers found peaks in mid-June and mid-July. The date of the peak in 1999, as determined by neural modeling, was predicted to occur at the end of the field season, which was consistent with field observations, although smaller peaks also occurred near 19 June. Robel et al. (1969) reported small secondary peaks in late July and early August in 2 of 3 years of their study.

The weather effects I observed were both consistent with earlier studies, and differed from them. The standard normal deviate in number of males heard was determined to be most strongly affected by light, followed by temperature, wind speed and humidity (the effects of which were equal), and cloud cover. Bennitt (1951), Elder (1956), and Robel et al. (1969) all considered temperature to be the most or one of the most influential weather variables of those measured. Robel et al. (1969) were the only researchers to measure light intensity, and it was the least important variable in their multiple regression analysis. They admitted, however, that some of their light measurements might not have accurately represented field conditions. Air temperature is directly related to the amount of incident light, and this, in conjunction with the daily calling phenology of bobwhites, explained the important influence of light in my study. Robel et al. (1969) found wind speeds to be the most important factor affecting the number of calls heard because wind reduced the radius of audibility; in contrast, Bennitt (1951) found little effect due to wind. Elder (1956) did not encounter enough windy days to evaluate its effects fully. Humidity had the most ambiguous relationship to quail calling among studies: Bennitt (1951) and Elder (1956) found no strong effect, Robel et al. (1969) found a negative effect, and I found a positive effect (Fig. 4C). All previous studies of bobwhite calling behavior used linear models, which deal poorly with nonlinear phenomena. Moreover, the effects of temperature, wind speed, and humidity on the propagation of sound are not in question; rather, the magnitude of these effects are of practical interest.

There exists considerable evidence that bobwhite reproduction is affected by weather conditions, specifically the amount of precipitation (Roseberry and Klimstra 1984:118-119), and temperature coupled with precipitation (Robinson and Baker 1955, Speake and Haugen 1960, Guthery et al. 1988). Generally, above-average amounts of precipitation and cool temperatures result in greater production, or a longer potential nesting season. Robinson and Baker (1955) found that either high temperatures coupled with moderate rainfall or moderate temperatures coupled with low rainfall (April-September) resulted in reduced reproductive success, as determined by the ratios of juveniles to adults in the fall harvest. A similar result was found in a study of Gambel's quail (*Callipepla gambelii*); greater reproductive success was associated with years of high rainfall in midwinter, although the effects of low rainfall were mediated by cooler temperatures in this desert species (Heffelfinger et al. 1999). Heffelfinger et al. (1999) also found a stronger calling response was correlated with higher midwinter rainfall. Guthery et al. (1988) studied bobwhite populations in 2 climate types of south Texas, the subtropical steppe and the subtropical subhumid. They found that bobwhites living in the hotter, drier conditions of the subtropical steppe attained reproductive condition earlier in the season, but maintained this condition for a shorter amount of time (3 months) than birds in the subtropical subhumid climate (5 months). In my study, more males and calls were heard for a greater proportion of the season in 1999, and precipitation for May-August in 1999 was twice that measured in 1998 (University of Oklahoma, Oklahoma climatological survey, mesonet data, unpublished data). The 1999 field season was also cooler, cloudier, and more humid than 1998 (Table 2). If the reproductive season was longer in 1999 than 1998, and, if males begin to call "bobwhite" at 15 weeks of age (Korchenderfer 1971), it is possible that the later peak in calling activity observed in 1999 could partly be due to hatch-year males beginning to call.

Quail adjust their behavior during hot seasons to limit exposure to heat; Gambel's quail in California rested quietly in the shade during the hottest times of the day, and spent less time in the sun as days got hotter (Goldstein 1984). Bobwhites in south Texas avoided habitat space-time where operative temperatures were >39°C (Forrester et al. 1998). It is likely that bobwhites in this study also restricted their daily activity, including calling activity, during hotter periods.

Seasonal peaks in calling or the number of calling bobwhite males have been correlated with peaks in hatching (Speake and Haugen 1960, Robel et al. 1969). Initiation of laying generally occurs in late April, but annual termination of nesting appears affected by maximum temperatures in July and August (Klimstra and Roseberry 1975). Hatching dates for 75% of clutches, 17 June – 18 August in a 10-year study in southern Illinois (Klimstra and Roseberry 1975), corresponded well to peaks in calling activity in other studies, and for 1998 in this study. Given that bobwhites are polygamous (Curtis et al. 1993, Burger et al. 1995), and that females incubate 66-80% of all nests (Stoddard 1931:30, Curtis et al. 1993, Suchy and Munkel 1993, Burger et al. 1995, DeMaso et al. 1997), it seems plausible that more males will begin calling and looking for mates as more females begin to incubate. This is the case with the polygamous marsh wren (*Cistothorus palustris*) (Verner 1965); the time spent singing by males (used for mate attraction more than territory defense) increased during the laying and incubation phases of the birds' reproductive cycle.

An interesting characteristic of the neural outputs (Fig. 4) was the annual variation in sensitivity of the standard normal deviate of number of calling males to the weather variables. Possibly, this pattern can be explained by acclimation of the birds to the prevailing weather conditions. Many birds seem to be sensitive to subtle changes in their environment, especially in terms of light and temperature. Armstrong (1963:208) noted that some birds begin singing a few minutes later than usual on cloudy mornings. Similarly, some birds will display courtship behavior during mild spells in the winter, but a sharp change in temperature, rather than the temperature attained, seems most important (Armstrong 1963: 214).

Finally, weather conditions, especially wind, affect the transmission and perception of sounds. The effect of wind is generally to break up and scatter sound waves, as wind is usually a form of turbulence rather than a vector that can increases a sound wave's velocity (Wiley and Richards 1982:140-141, 157). Thus, wind usually attenuates sound. Wind speeds>0 m/sec reduced the number of birds heard in this study (Fig. 4D). The wind's effect on call-counts may also be a behavioral one; some birds decrease or cease singing or calling in winds (Armstrong 1963:210-211). Elder (1956) felt that bobwhites stopped calling during gusty conditions. I, too, noticed that while other birds at similar distances from me as the quail continued calling during windy periods, the bobwhites did not.

Another weather variable measured that can affect the transmission of sound is temperature, specifically temperature gradients and inversions. In cold air, sound travels slower. When air cools as it rises from the ground, horizontally transmitted sound waves within it are refracted upward into zones of lower sound velocity known as a shadow zone (Wiley and Richards 1982:157). Shadow zones are also a product of turbulence. Birds can avoid shadow zones by singing during cooler weather, or in the morning when warmed air is not rising from the ground as rapidly as it does during midday. At night and early in the morning, the air directly above the ground is cooler than the air at higher elevations. The warmer layer of air on top traps the bottom layer, creating a temperature inversion, which refracts sound waves back towards earth (Wiley and Richards 1982:158). The presence of temperature inversions in the morning may partly explain the prevalence of birds singing at this time (Elkins 1983:80).

Call-playback Effects

The call-playback technique had no significant effect on either the number of males or the number of calls heard. In contrast, Coody (1991) found that call-playback significantly increased the number of males and calls detected. Smith (1996:393) defined 4 functionally different responses to playback that vary among species and individuals. First, an individual may remain where it is and reply to the playback with its own song or call, either by calling more rapidly and continuously, or by immediately answering each playback. Second, the bird may approach the recording silently, move away again, and begin to call (a probing approach). Third, a close approach may be made quickly, and the bird then calls, or tries to locate and interact with the source of the sound. Fourth, the bird may approach the recording silently (an investigatory approach). Of these responses, bobwhite males in my study appeared to exhibit the latter two. The playback recording attracted some nearby males: in several instances, males flew in, and landed within a few meters of me; others walked towards the sound on the edge of the road. Some males gave assembly calls in duetting-fashion as they landed or while the recording was still playing; it was not possible to determine if these males had been calling "bobwhite" before, or if other assembly calls heard during the counts were males or females.

Keppie (1992) recommended against using playback for indices of spruce grouse. He contended that using playback requires additional assumptions, namely that birds will respond equally or that differences will occur in predictable proportions.

MANAGEMENT IMPLICATIONS

For call-counts indices to be a reliable measure of population status, they must improve in precision and reliability. The effectiveness of call-counts can be improved by studying calling behavior, and through this study, a better understanding of male bobwhite calling behavior was achieved. It is hoped that this knowledge will allow quail managers to make better decisions about when to conduct summer call-counts, and how to interpret the effects of weather.

To improve precision in the number of males heard, I recommend that managers follow the guidelines presented here: To hear ≥90% of the maximum number of males, counts should begin 10-15 minutes after official sunrise and continue for an hour. Counts conducted between 45 and 55 minutes after sunrise will likely encompass times to hear the greatest number of males with the least variation in number of males. Managers can also consult Table 1 to interpret the results of counts not conducted within the parameters to hear ≥90% of the maximum number of males. The variation in seasonal peak as determined by neural analysis emphasizes the need to replicate counts at individual locations for more reliable measures of abundance.

The neural model results provide bobwhite managers the means to evaluate effects of weather on counts. Of these effects, light intensity had the strongest influence on the number of males heard, followed by temperature, Julian day (time of season), humidity and wind (both affected bobwhites equally), and cloud cover. In general, bobwhite males were heard less during hot, dry weather, and there is strong evidence that the length of the summer calling-season is suppressed by these conditions. Additionally, bobwhites may acclimatize to prevailing weather, and show increased sensitivity to relative changes in it. This means, for example, that after a period of cool, cloudy weather, counts conducted on a relatively warm, sunny day may show a decrease in number of calling males. It is also important for managers to note that the number of calls heard decreased with wind speeds >0 m/s; if time and personnel allow, call counts should not be conducted on days with measurable wind speeds.

Playbacks of female calls did not appear to be an effective technique for eliciting male voice responses; nearby males may approach the source of the calls, but do not increase calling themselves. It is simpler and equally effective to conduct non-playback call-counts.

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