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ABSTRACT

Populations of scaled quail (*Callipepla squamata*) and northern bobwhites (*Colinus virginianus*) have declined in North America coincident with global warming. We speculate on a cause-effect relation between global warming and quail declines. Quail are sensitive to operative temperatures >38.7 C, which commonly occur under natural conditions in southern latitudes. Based on empirical results, the laying season for quail may be reduced by as much as 60 days because of high temperatures. We provide mechanistic models that show how reduction in length of the laying season suppresses per-capita annual production. Global warming could be associated with declining quail populations through suppression of reproduction; it also could exacerbate the effects of habitat loss and fragmentation. These possibilities should be explored in field and laboratory research.

INTRODUCTION

Despite controversy over the nature of global warming, the average air temperature on earth has been rising for about 130 years (Gates 1993:2). Increasing temperatures are associated with increases in the quantity of greenhouse gases in the atmosphere (e.g., H_2O, CO_2, CH_4, N_2O, O_3). These gases transmit shortwave radiation (sunlight) but trap longwave radiation, resulting in warming of the atmosphere and cooling of the stratosphere (Schneider 1993).

The warming effect of greenhouse gases is non-controversial. Indeed, life as we know it would not be possible without natural greenhouse warming. However, the rate of addition of greenhouse gases to the atmosphere, due to human activities, and the rate of atmospheric warming, are largely unprecedented in geological history (Schneider 1993).

Populations of scaled quail and northern bobwhites have declined (Brennan 1991, Church et al. 1993) coincident with global warming. Undoubtedly, habitat loss and fragmentation explain declines in some regions. However, in portions of the Southwest, scaled quail populations have dwindled in areas where habitat quantity has apparently been constant. Could there be a cause-effect relationship between global warming and quail declines?

After briefly reviewing the biophysical background, we examine empirical and theoretical effects of higher temperatures on quail. The northern bobwhite serves as our primary model, because the thermal biology of this species is well known. We will demonstrate the importance of heat-driven habitat selection as a process that influences quail abundance and productivity and review the empirical basis for heat effects on reproduction. Finally, we use mechanistic models to explore the process of heat-based suppression of reproduction.

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BIOPHYSICAL BACKGROUND

The physiological goal of warm-blooded animals is maintenance of a stable body temperature. This goal is realized when the following identity holds:

$$\text{rate of heat gain} = \text{rate of heat loss.} \qquad (1)$$

Heat is energy in transit, either moving into or out of an animal's body. Heat always flows from a body of higher temperature to a body of lower temperature, and the rate of heat flow increases in proportion to the difference between the temperatures of 2 bodies. We will use watts (W) to describe rates of heat flow: 1 W = 1 J sec^{-1}, where J = Joule, a measure of energy. In terms of calories, 1 J = 0.2389 cal and 1 cal = 4.186 J. Heat may flow into or out of a quail's body by convection (body-air), conduction (body-solid object), and longwave radiation. Additional sources of heat gain are shortwave radiation (sunlight) and longwave radiation from objects with temperatures higher than that of a quail.

When heat flows into the body, quail may increase the rate of heat loss by evaporation (gular flutter). Under extreme conditions, quail are unable to balance heat loss and gain; the ultimate consequence may be death.

Quail always produce heat by metabolism. The basal metabolic rate for fasting bobwhites in a thermoneutral environment is about 0.95 W (Case and Robel 1974, Curtis 1983, Spiers et al. 1983). In terms of calories, basal metabolism produces about 0.23 cal sec^{-1} (19.6 kcal day^{-1}).

Air temperature provides a poor landmark for determining whether heat potentially flows into a quail's body. A better landmark is operative temperature, T_e, which is a composite of air temperature, wind, and sunlight effects at a fixed orientation of the animal relative to the sun's rays. Operative temperature is similar to the air temperature in a dark room that would be equivalent, in terms of heat flow, to the temperature experienced by an animal standing in sunlight (heat added) with known wind speeds (heat usually subtracted). Operative temperature will be higher than air temperature when an animal is exposed to sunlight and low wind speeds. Operative temperature and air temperature are the same at night with no wind.

Laboratory experiments indicate that at an operative temperature between 35 and 40 C, the maximum possible rate of heat dissipation falls below the rate of heat gain; as a result, body temperature increases. At 35 C bobwhites may use gular fluttering to increase heat loss via evaporation (Spiers et al. 1983). Bobwhites exposed to 40 C for >24 hours may die from hyperthermia (Case and Robel 1974). We estimate from models that the minimum operative temperature that leads to hyperthermia is about 38.7 C for bobwhites. This temperature is below mean body temperature of about 41.5 C (Spiers et al. 1983, White 1995). An operative temperature below body temperature may lead to hyperthermia because of heat produced by metabolism (see earlier).

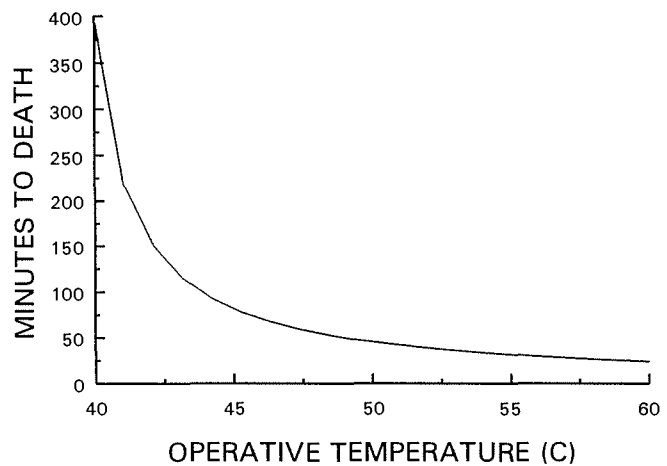Quail are said to have low thermal inertia, because

Fig. 1. Approximate time to death from hyperthermia (core body temperature = 46.5 C) as a function of operative temperature for northern bobwhites. The function is based on a 180-g bobwhite.

a small quantity of heat gain produces a marked response in body temperature. The specific heat of quail tissue is estimated to be 3.43 J g^{-1} C^{-1} (Goldstein 1984). This number means that a net gain of 3.43 J of energy will raise the temperature of 1 g of tissue by 1 C. Heat capacity is the product of body mass times specific heat. For a Texas bobwhite (*C. v. texanus*), the heat capacity is about 160 g times 3.43 J g^{-1} C^{-1} = 549 J C^{-1}. This latter number implies that if a Texas bobwhite's body gains 549 J of energy, its body temperature will rise by 1 C. The heat capacity of bobwhites in northern climes is around 686 J C^{-1} based on a 200-g body mass.

The low heat capacity of quail indicates that small quantities of net energy gain may produce severe physiological effects through elevated body temperature. Three outcomes are possible if heat flows into the body. First, the body temperature may rise and stabilize at some nonlethal value above normal body temperature. This will occur if it is possible for the bird to experience net loss of longwave radiation as its body temperature rises above the temperature of surrounding objects. Second, the bird may experience nonlethal hyperthermia and recover as the thermal environment improves, for example, the sun goes down. The third outcome is death from hyperthermia, which probably occurs at a core body temperature of <46.5 C (Goldstein 1984). Time to death varies hyperbolically with operative temperature (Figure 1).

OPERATIVE TEMPERATURES IN THE FIELD

On 11 June 1996 we analyzed operative temperatures at 23 points within a brush thicket (350 m^2) on a ranch near Laredo, Webb County, Texas. The brush consisted primarily of regrowth honey mesquite (*Prosopis glandulosa*) ≤3 m tall. Hourly trends in operative temperature near ground level showed considerable variability within and among points (Figure 2).
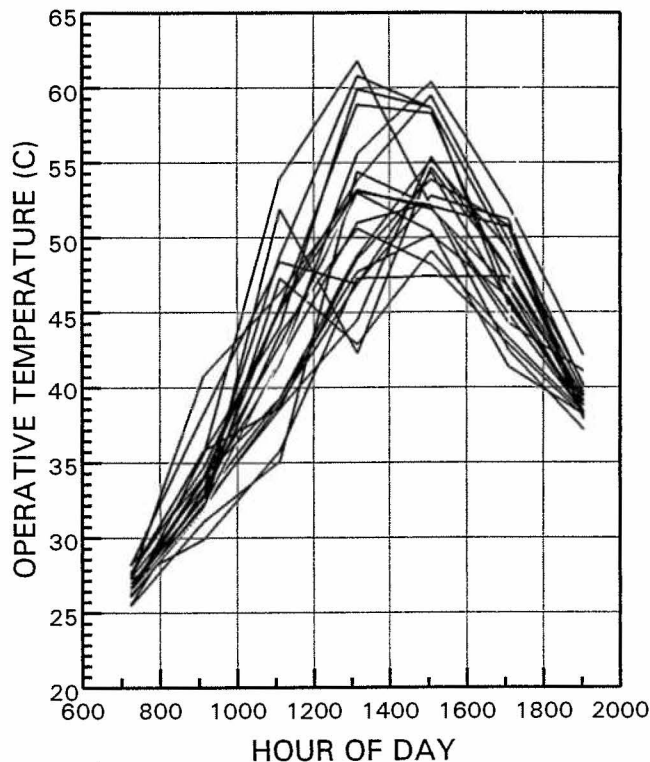
Fig. 2. Hourly trends in operative temperature at ground level at 23 points in a thicket composed of honey mesquite, Webb County, Texas, 11 Jun 1996. Drought conditions prevailed when these data were collected.

This variability arose primarily from variability in shading effects as the sun passed from east to west. All points reached operative temperatures critical to bobwhites (>38.7 C) and probably other quail species. Maximum temperatures observed were potentially lethal to bobwhites in <10 minutes of exposure.

Gambel's quail (*C. gambellii*) in Arizona may die of hyperthermia in <1 minute if they leave shady coverts on hot summer days (Goldstein 1984). This fate accrues because of above-normal beginning body temperature, the added heat load from solar radiation, and increased heat production (metabolism) from activity. Goldstein's (1984) finding shows that in certain environments, heat may be an important factor in quail behavior and habitat selection. In fact, heat avoidance may explain field behavior as well as predator avoidance (Forrester et al. 1998).

EFFECTS OF HEAT ON BEHAVIOR

Habitat Use

Thermal effects on habitat selection, behavior, and productivity of bobwhites have been documented or hypothesized based on field and laboratory research. Bobwhites in the Rio Grande Plains of Texas select loafing coverts with tall, dense canopies during hot days, whereas those selected during cool days have low canopies (Johnson and Guthery 1988). During summer, air temperature at loafing sites (35.7 C) averaged 5.2 C below that at random points. Light in-

tensity was reduced 92.1% at loafing sites in comparison with random points. The intensity of solar radiation decays rapidly as it passes through plant canopies, thereby nullifying a potential source of heat gain.

The calling activity of male masked bobwhites (*C. v. ridwayi*) in Sonora, Mexico, is correlated with relative humidity (W. P. Kuvlesky, Jr., unpublished data); Texas bobwhite males call more frequently after summer showers; they also do this in Florida and elsewhere throughout the southeastern U.S. (L.A. Brennan, personal communication). These observations are consistent with heat-driven behavior, because ambient humidity would be associated with evapotranspiration and evaporation near the ground, both of which dissipate heat. Calling males would have cool thermal refugia to discharge heat and lower body temperature (see Goldstein 1984). Moreover, humidity reduces incident shortwave radiation by absorption.

Kassinis and Guthery (1996) observed shorter flights of bobwhites in summer than in other seasons; this behavior could be associated with body temperature regulation, i.e., longer flights would elevate body temperature more than shorter flights. We have found in southern Texas that bobwhites land at points with cooler temperatures than at take-off points or points in the random environment (N. D. Forrester, unpublished data).

Bobwhites in the western Rio Grande Plains apparently require higher seral stages than those in the eastern Rio Grande Plains of Texas (Spears et al. 1993). This phenomenon is consistent with a thermal response, because higher seral stages in the hotter, drier environments would foster cooler conditions at quail level than lower seral stages. Cooling would occur by the insulating and shading effects of perennial grasses and by evapotranspiration of soil water by deep-rooted perennials. However, it must be noted that alternative hypotheses, e.g., similarity in vegetation structure (Spears et al. 1993), may explain variable seral stage associations of bobwhites in different regions.

Forrester et al. (1998) evaluated operative temperature preferenda of bobwhites in the Rio Grande Plains and Gulf Coast Prairies of southern Texas. During July–September birds exhibited strong selection for operative temperatures within the range 18.8–35.4 C (Figure 3). Forrester et al.'s (1998) results indicate that ≥50% of habitat space-time was thermally stressful (operative temperature ≥39 C). Bobwhites exhibited preferential use in about 28% of available space-time and avoided 72%. In rounded figures, about half of available habitat space-time was thermally stressful (potentially lethal) and about three-fourths was avoided. Management for desirable thermal conditions conceivably could double the habitat space-time available to bobwhites based on these results.

Reproduction

A striking pattern of bobwhite demography in the United States is higher productivity in northern latitudes than in southern latitudes (Figure 4). According-
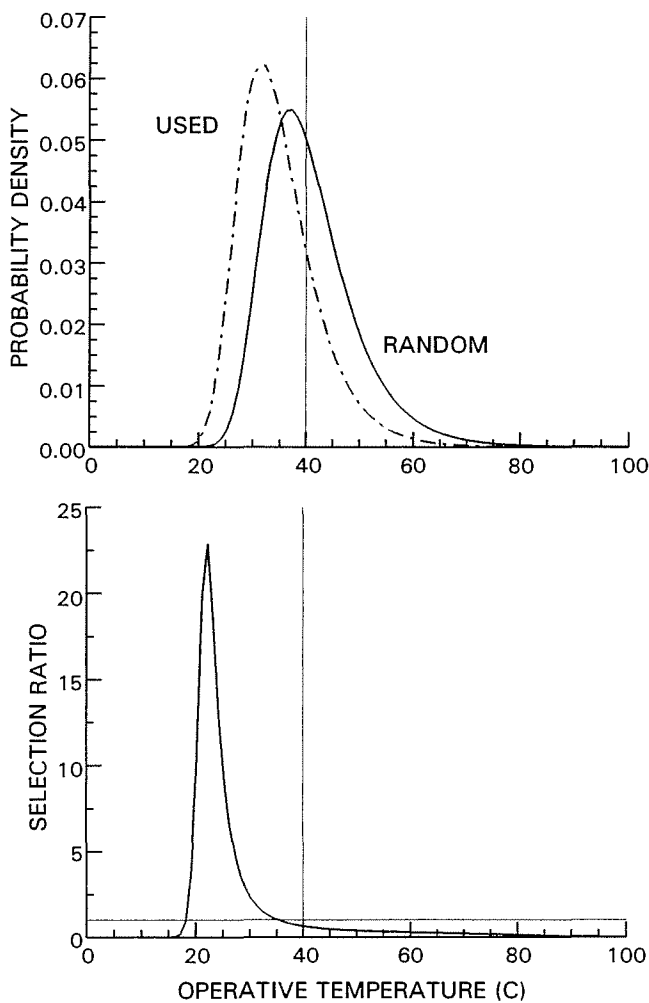
Fig. 3. Probability distributions (top) for operative temperatures at used (flushing and landing, n = 296) and random points (n = 289) for northern bobwhites and the resulting selection ratio function (bottom), Rio Grande Plains and Gulf Prairies of Texas, July–September 1994 and 1995. Values <1 indicate avoidance and values >1 indicate preference for operative temperatures.
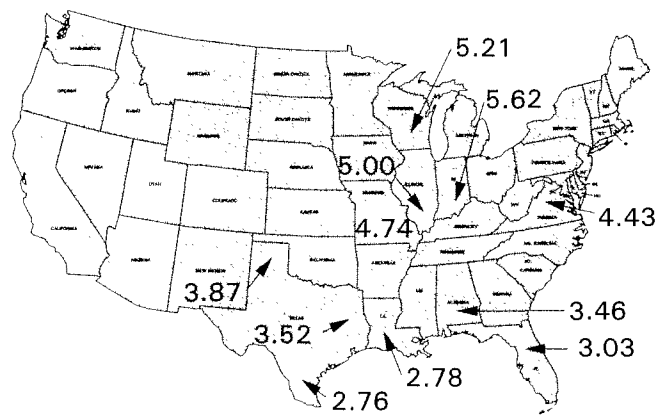

Fig. 4. Geographic variation in mean age ratios of northern bobwhites. Data are from Jackson (1969:9), Rosene (1969:385–386), Lehmann (1984:133), and Roseberry and Klimstra (1984:218).

ly, annual survival rates must be lower in northern than in southern portions of bobwhite range. One cannot state unequivocally whether survival or productivity lead to the geographic pattern, because these variables are tautologically intertwined. One can hypothesize, however, that lower temperatures in northern latitudes reduce winter survival and foster productivity, whereas these effects reverse in southern latitudes.

High air temperatures have several adverse effects on laying chickens (North 1972). These include decreases in feed intake, egg production, eggshell quality and thickness, and interior egg quality.

Based on direct results and derivations from Case and Robel (1974), high temperatures have similar effects on laying bobwhites. The body mass of laying bobwhites maximizes at about 20.1 C; this temperature provides an estimate of the optimum temperature for laying in the field and is similar to the optimum temperature for domestic poultry (Card and Nesheim 1972). The body mass of female bobwhites declines at 0.174 g C^{-1} for temperatures >20.1 C. The body

mass of males under a 15-hour photoperiod maximizes at 17.4 C and declines at 0.074 g C^{-1} for operative temperatures >17.4 C.

High temperatures suppress the reproduction effort of bobwhites in the wild. Effects in Missouri include earlier completion of hatching and lower autumn age ratios than in normal years (Stanford 1972). Klimstra and Roseberry (1975) showed that each rise of 1 C in the mean maximum daily temperature in July–August reduced the laying season by about 12 days in Illinois. The last clutch was laid in early July during hotter summers (34.5 C for mean daily maximum) compared with early September for cooler summers (30.5 C); i.e., higher temperatures reduced length of the laying season by ≤2 months. In the Rio Grande Plains of Texas, the laying season in a hotter, drier portion of the region (western) was about 2 months shorter than in a cooler, wetter portion (eastern) (Guthery et al. 1988). Based on inferences from Guthery et al. (1988), we estimate the average hen was in laying condition for about 60 days in the hotter environment versus 80 days in the cooler environment.

The effects of a reduction in the number of days in the laying season may be gauged with mechanistic models of production as indexed by an age ratio. The number of nesting attempts per hen (n) is a function of several variables:

$$n = f(m, L, p, D_s, D_f, H)$$

where

m = the elapsed time (days) from start of the laying season to 100% effort (all laying hens laying),
L = the number of days from first to last egg of the season,
p = the probability of success on an attempt,
D_s = the time (days) committed to a successful attempt,
D_f = the time (days) committed to a failed attempt, and
H = the mean number of days in laying condition per hen.

Define $q = 1 - p =$ the probability of nest failure on an attempt.

Let $f(t)$ be a density function that gives the proportion of hens that start laying on day t, $0 \leq t \leq m$. Then the average number of days in laying condition for a hen may be defined as

$$H = \int_0^m [f(t)(L - t)] \, dt. \qquad (2)$$

Equation (2) sums days times probabilities and gives, essentially, a weighted average for hens.

The mean time (d) committed to a nesting effort may be defined as

$$d = pD_s + qD_f \qquad (3)$$

Equation (3) is a weighted average of days committed to successful and unsuccessful nesting attempts.

The number of attempts per hen is laying days per hen divided by days per attempt, i.e.,

$$n = H/d. \qquad (4)$$

Suppose $f(t)$ may be described as a parabola on [0, m], i.e.,

$$f(t) = at - bt^2.$$

The coefficients a and b are estimated as

$$a = 6/m^2$$

and

$$b = 6/m^3.$$

With these coefficients the area under the curve $f(t)$ from 0 to m will sum to 1.0; i.e., $f(t)$ will be a density function. Then

$$H = \int_0^m [(at - bt^2)(L - t)] \, dt.$$

Solution of this integral and substitution for a and b leads to the simple result,

$$H = L - 0.5m.$$

We may approximate the autumn age ratio ($R =$ juvenile/adult) under single-brooding as (Guthery and Kuvlesky 1998)

$$R = wzc(1 - q^n) = wzc(1 - q^{H/d}) \qquad (5)$$

where

$w =$ the proportion of hens in the adult population,
$z =$ the proportion of hens that lays, and
$c =$ effective clutch size (viable eggs/clutch).

Equation (5) implies production increases asymptotically with the number of nesting attempts, holding the other variables constant.

If we define $L = 150$ days from first to last egg of season, $m = 30$ days for all laying hens to become active, $D_s = 75$ days devoted to a successful nest, $D_f = 40$ days devoted to a failed nest, and $p = 0.3$ for probability of nest success, then under the parabolic model, we obtain

$H = 135$ days hen^{-1},

$d = 50.5$ days attempt^{-1}, and

$n = 2.67$ attempts hen^{-1}.

At $w = 0.45$, $z = 1.0$, and $c = 12$ we obtain an age ratio of

$$R = (0.45)(1.0)(12)(1 - 0.7^{2.67}) = 3.32 \text{ juvenile/adult}$$

Now suppose, hypothetically, the number of days in the laying season declines from 150 to 90 because of a late-summer heat wave. Holding other input variables as specified above, we find the number of days in laying condition for each hen becomes $H = 75$, leading to $n = 1.49$ and $R = 2.23$ juvenile/adult. In this hypothetical example, an empirically reasonable reduction in the laying season of 60 days due to heat (Klimstra and Roseberry 1975, Guthery et al. 1988) reduced per-capita production by 1.09 juvenile/adult.

DISCUSSION

The negative effects of high temperatures on reproduction by gallinaceous birds are well established empirically and theoretically. The effects are based on matters of physics and chemistry, which are not subject to debate at this point in the history of the universe. However, whether global warming could be responsible for declining quail populations remains speculative.

Average temperatures in the atmosphere have increased by about 0.5 C since the current warming trend began (Gates 1993, Schneider 1993). Projections subject to uncertainty indicate mean temperatures may increase by up to 5 C in the next century or so. These increases seem small, but if increases in the average occur primarily because of increases during summer, then a small increase in the average could potentially have strong impact on quail populations.

The global warming trend is consistent with an insidious and widespread decline of quail in warmer climates. If the average length of the laying season in a particular area declines through the years, there might be an early stage where density dependent processes and other adjustment mechanisms result in a stable population. However, with larger reductions in the laying season (1–2 months), adjustments in survival would not be expected to keep pace with reductions in production. This could lead to a slow annual rate of decline. Continued warming might be expected to increase the annual rate of decline in the next century. Under this scenario, global warming would exacerbate the effects of habitat loss and fragmentation in populations subject to global warming effects.

Certain populations may not be susceptible to the negative influence of global warming, if the influence exists. Populations of California quail (*C. californica*), Gambel's quail, and mountain quail (*Oreortyx pictus*) were stable from 1966 to 1991 (Church et al. 1993). The effects of latitude, altitude, and ocean masses could theoretically mitigate global warming effects on these species. This possibility fits Gambel's quail poor-

ly, because they are largely an interior species of low latitudes. Church et al. (1993) reported a decline in Gambel's quail during the decade preceding 1991.

The above paragraph demonstrates that any effects of global warming on quail populations will vary with the prevailing climate to which populations are adapted; in other words, the response of quail populations to increased heat loads will vary geographically. Biotic factors including the quantity and quality of thermal refugia will exacerbate variation among populations. This variation will occur despite intrinsic similarity in the bioenergetics (e.g., Guthery 1999) and biophysics of quails.

A question that arises concerning global warming and quail production is whether populations might adapt genetically to higher temperatures. Breeding experiments with domestic poultry indicate little genetic variation with respect to heat tolerance (El-Gendy and Washburn 1995). This finding is perhaps not surprising because heat tolerance has a strong basis in biophysical chemistry. Alteration of laying phenology through natural selection seems feasible; if global warming is affecting quail populations, then selection should favor those individuals that lay earlier in the season when temperatures are cooler. Whether the rate of selection can keep pace with the rate of temperature change remains problematic.

Another potential effect of global warming is a change in the distribution of quails from more southerly (hotter) to more northerly (cooler) latitudes. Biogeographic changes have ample precedent in geologic time (Gates 1993).

Two barriers presently confront a northerly shift in the distribution of wildlife (Gates 1993). First, the vegetation that provides habitat for a species follows climate change at an extremely slow rate relative to the dispersal capabilities of the species. Second, modern fragmented landscapes may prevent distribution shifts for both plants and animals; i.e. modern landscapes contain agricultural and urban areas that represent barriers to dispersal.

We conclude this discussion by observing that there is no single cause of quail declines in the real world, because multiple factors increase mortality and suppress production in declining populations. Selection of any 1 factor from a set of potential factors is arbitrary. The best science can do in a multiple-cause milieu is to estimate the proportional impact of agencies contributing to an effect (Chamberlain 1890). Although global warming could be associated with an accelerated rate of quail decline in some areas, its importance relative to other potential problems remains unknown.

microenvironments may be created by management of herbaceous and woody cover. The more such cover, the better, within the limits of the habitat structure to which quail are behaviorally and morphologically adapted.

The response of individuals and populations to high heat loads is a fertile area for field and laboratory research. Historical data such as breeding bird surveys (Church et al. 1993) or Christmas bird counts (Brennan 1991) might be examined to ascertain population trends in areas more sensitive and less sensitive to global warming. Regions with higher altitudes and latitudes or a marine influence should be less sensitive to global warming than interior regions at low altitudes and latitudes. The global warming hypothesis predicts higher rates of decline in more sensitive than in less sensitive regions.

The research community might want to address the role of heat in variation in quail production. Field data relative to this question are limited and somewhat anecdotal. For example, we have no idea of the dynamics of heat loads in different vegetation types relative to the thermal biology of quails. A critical question is determining whether acute as opposed to chronic heat events suppress production. Suppression could occur by causing hens to quit laying, addling eggs (Leopold 1933:297), or killing chicks (Sumner 1935). Our research group has initiated combined laboratory and field studies to better understand the influence of heat on bobwhite demographics in a subtropical environment.

We suggest that researchers examining the influence of heat loads on quail dynamics pay close attention to the length of the laying season and the proportion of hens that lays in a given season. The proportion that lays has a particularly strong influence on production (Guthery and Kuvlesky 1998). Because the proportion that lays could be misleading, we also recommend analysis of the average number of days in laying condition for hens. This variable can be estimated as the integral of an equation that describes the proportion laying as a function of time (Julian day).

ACKNOWLEDGMENTS

MANAGEMENT IMPLICATIONS

The sensitivity of quail to high temperatures is neither widely recognized nor fully appreciated in applied ecology. If global warming has contributed to the decline of quail populations, then the management response is to reduce temperatures at quail level. Cooler

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