SPRING PRECIPITATION AND FLUCTUATIONS IN ATTWATER'S PRAIRIE-CHICKEN NUMBERS: HYPOTHESES REVISITED

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Abstract: Two related hypotheses argue that greater than normal precipitation during May alone or spring (Mar–Jun) leads to decreased Attwater's prairie-chicken (*Tympanuchus cupido attwateri*) breeding success, whereas less than normal precipitation during these periods leads to increased breeding success. These hypotheses have been accepted by wildlife managers and, seemingly because of observer expectancy bias, have been used to explain annual variation in Attwater's prairie-chicken numbers. We demonstrate that neither hypothesis is supported by available data. Similarly, alternative hypotheses that May or spring flooding, the date in May when maximum precipitation occurs, or precipitation variability among spring months drives spring breeding numbers also were not supported. We found, however, that breeding success in spring can drive proportional changes in breeding numbers the following spring.

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The Attwater's prairie-chicken was listed as endangered in 1967 by the U.S. Fish and Wildlife Service when approximately 1,070 birds remained (U.S. Fish and Wildl. Serv. 1983). Historically, Attwater's prairie-chicken occupied an estimated 2.4 million ha of coastal prairie from southwestern Louisiana, south, to at least the Nueces River in Texas (Lehmann 1941, 1968; Lehmann and Mauermann 1963). Conversion of coastal prairie to agricultural, commercial, and urban uses is thought to have been the primary cause of the elimination of this species from Louisiana and most of Texas (Lehmann 1941, Cogar et al. 1977, U.S. Fish and Wildl. Serv. 1983). In 1992, only 4 isolated populations of Attwater's prairie-chicken were located in 5 Texas counties with 94% of the birds occurring in 2 of the 4 populations (U.S. Fish and Wildl. Serv. 1993). Because the remaining populations are of relatively small size, an understanding of the mechanisms influencing Attwater's prairie-chicken numbers is urgently needed.

Fluctuations have been observed in Attwater's prairie-chicken populations (Table 1). Similar fluctuations have been documented for other grouse species, and 5 hypotheses have been proposed in explanation (Bergerud 1988). One hypothesis concerns winter cover that may be inadequate to protect fall populations, so the number of grouse above some threshold quantity are vulnerable to predation or will disperse. A second hypothesis concerns the availability of winter food. According to this hypothesis food is variable and in short supply, hence the number of grouse surviving winter is related to the number present in fall and the severity of the winter. According to the third hypothesis, grouse mortality is low when predators are rare, or alternative prey are common. Predators switch to preying upon grouse when alternative prey numbers decline or predator numbers increase, thus increasing winter grouse mortality. A fourth hypothesis is that breeding space is limited, resulting in the death of grouse that cannot successfully compete for space. Finally, breeding success (no. juv/ad in Aug) during spring and summer may drive proportional changes in breeding numbers the following spring regardless of habitat availability, winter severity, density of available alternative prey, or quantity of breeding space (we subsequently refer to this relationship as "Bergerud's breeding success hypothesis"). After reviewing and evaluating each of these hypotheses, Bergerud (1988:656) concluded that breeding success was the dominant demographic variable that altered spring breeding numbers in grouse.

Two widely accepted, yet untested, hypotheses related to precipitation (see above) have been proposed to explain the yearly fluctuations in Attwater's prairie-chicken numbers. We outline the origin of these hypotheses, use available data to test them, suggest and test related alternative hypotheses, and discuss how uncritical

Table 1. Number of Attwater's prairie-chicken in Austin-Colorado, Refugio, and Victoria counties, Texas, 1970–91. In all studies cited, data were collected by counting all displaying males one morning during the peak of the spring breeding season and doubling this number (assuming a 1:1 sex ratio) to yield total population indices.

Year	Austin-Colorado	Refugio	Victoria	Source
1970	470	310	112	Jurries 1977
1971	710	440	234	Jurries 1977
1972	530	166	166	Jurries 1977
1973	474	192	224	Jurries 1977
1974	442	356	242	Jurries 1977
1975	998	336	342	Jurries 1977
1976	822	530	218	Jurries 1977
1977	364	550	110	Jurries 1977
1978				No survey completed
1979	514	742	126	U.S. Fish and Wildl. Serv., unpubl. data
1980	512	726	64	U.S. Fish and Wildl. Serv. 1983
1981	418	658	64	U.S. Fish and Wildl. Serv. 1983
1982	526	438	64	U.S. Fish and Wildl. Serv. 1983
1983	612	646	112	U.S. Fish and Wildl. Serv. 1993
1984	416	838	116	U.S. Fish and Wildl. Serv., unpubl. data
1985	360	810	94	U.S. Fish and Wildl. Serv. 1993
1986	344	340	48	U.S. Fish and Wildl. Serv., unpubl. data
1987	392	582	54	U.S. Fish and Wildl. Serv. 1993
1988	268	562	34	U.S. Fish and Wildl. Serv., unpubl. data
1989	136	246	20	U.S. Fish and Wildl. Serv. 1993
1990	126	292	10	U.S. Fish and Wildl. Serv., unpubl. data
1991	126	310	8	U.S. Fish and Wildl. Serv. 1993

acceptance of such hypotheses can impede conservation efforts.

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ORIGIN OF HYPOTHESES

Oscillations in Attwater's prairie-chicken numbers have been attributed to the quantity of spring precipitation (Lehmann 1941, Jurries 1979, U.S. Fish and Wildl. Serv. 1983). This relationship was first articulated by Waddell (Lehmann 1941:32), who observed the Austin-Colorado-Wharton County, Texas, prairie-chicken population (1925–37). He categorized the number of young reared annually as good, fair, or poor according to the number of birds observed on frequent trips through their range, seen by other reliable observers, bagged by hunters, and counted on spring booming grounds (Lehmann 1941:32). No definition of what constituted a good, fair, or poor number of young was given. Waddell concluded that prairie-chicken production was (1) good in spring months when precipitation was below average, (2) fair to good when precipitation was average or only slightly above average, and (3) poor, very few young being reared, when the nesting season was abnormally wet (we subsequently refer to this relationship as "Waddell's spring precipitation hypothesis") (Lehmann 1941:32). No quantifiable definitions of Waddell's precipitation categories (e.g., abnormally wet) were given, so the hypothesis cannot be tested without making assumptions about his categories.

Lehmann (1941:32–33) used 1 prenesting survey (1937), 2 summer surveys (1936, 1937), and spring (Mar–Jun) precipitation data from the National Weather Bureau Station at Columbus, Texas (1925–37), to examine Waddell's hypothesis. He concluded that only May precipitation was a satisfactory index of breeding season productivity for Attwater's prairie-chicken (no statistical evaluation was attempted). Lehmann (1941:33–34) provided 3 reasons as background for his hypothesis: (1) hens whose nests were destroyed by flooding in March and April could usually renest, while hens whose nests were destroyed in May seldom renested; (2) chicks hatching in April do not have a serviceable covering of feathers—hence are more vulnerable to wet and cold; and (3) most chicks hatch in May, hence May flooding could potentially destroy a larger proportion of annual production than could flooding during other spring months. He did not give quantifiable definitions for descriptors (e.g., usually, seldom, most).

Although Lehmann (1941:34) noted that environmental conditions were not identical throughout the coastal prairie, he maintained that they were similar enough that one could assume that May rainfall was key to prairie-chicken reproduction throughout coastal Texas. From this assumption, Lehmann (1941:24–25) proposed 4 categories of prairie-chicken reproductive success that could be predicted by total May precipitation (we subsequently term this "Lehmann's May precipitation hypothesis"): good, May precipitation ≥3.8 cm less than normal; fair, May precipitation <3.8 cm less than, yet <5.1 cm greater than, normal; poor, May precipitation ≥5.1 cm greater than, yet less than twice, normal; bad, May precipitation at least twice normal. Lehmann (1941:33) used May precipitation and departures from normal (the Natl. Oceanic and Atmos. Adm. defines normal precipitation as mean precipitation for the 30-year period preceding the current decade) recorded at the U.S. Weather Bureau Station at Columbus, Texas (1925–37).

Because Lehmann (1941) completed only one survey during the breeding season, and Waddell's impressions of prairie-chicken reproduction were not quantified, Lehmann had insufficient data to test either precipitation hypothesis and he attempted no such tests. However, use of these intuitively appealing hypotheses (Jurries 1979:21, Lawrence 1982:87–88, U.S. Fish and Wildl. Serv. 1983:9) has tended to transmute them into what appear to be empirical rules without the benefit of scientific evaluation (Romesburg 1981), and this rule has been used to explain changes in Attwater's prairie-chicken breeding numbers (Horkel 1979, Lawrence 1982, Lawrence and Silvy 1987).

We test Waddell's spring and Lehmann's May precipitation hypotheses using total spring (Mar–Jun) and May precipitation, respectively. Because precipitation categories other than total spring or May precipitation could explain the same general ideas proposed by Waddell and Lehmann, we tested 4 alternative hypotheses:

H_1: Flooding in May leads to a proportional decrease in Attwater's prairie-chicken breeding numbers the following spring.

H_2: The date in May when the maximum amount of precipitation falls, and the related quantity of precipitation, controls proportional change in breeding numbers the following spring.

H_3: Flooding in spring (Mar–Jun) leads to a proportional decrease in breeding numbers the following spring.

H_4: Precipitation variability among spring (Mar–Jun) months controls the proportional change in breeding numbers the following spring.

Finally, because Waddell's spring and Lehmann's May precipitation hypotheses explain altered breeding success, we test the appropriateness of Bergerud's more inclusive breeding success hypothesis for explaining fluctuations of spring numbers.

Our treatment of hypotheses explaining fluctuations of spring breeding numbers among years is not exhaustive. We do not imply that additional hypotheses relating precipitation variables and proportional changes in breeding numbers could not be formulated or that hypotheses independent of precipitation, including some of those reviewed by Bergerud (1988), might not be applicable to Attwater's prairie-chicken populations.

STUDY AREA AND METHODS

We used Attwater's prairie-chicken populations occurring in Austin-Colorado, Refugio, and Victoria counties, Texas (Table 1). These populations were selected because they were isolated from one another, included the 2 largest remaining populations, encompassed the population from which Waddell's spring and Lehmann's May precipitation hypotheses were derived (Austin-Colorado), and were surveyed either by the same biologist each year or by replacement biologists trained by the initial investigator. We obtained precipitation data from Columbus (28°43′N, 96°32′W), Refugio (28°24′N, 97°17′W), and Victoria (28°51′N, 96°55′W), Texas, weather stations for March–June 1969–91 (Natl. Oceanic and Atmos. Adm.). Each station was within, or adjacent to, these prairie-chicken ranges. As did Lehmann (1941:33), we used the National Oceanic and Atmospheric Administration's definition of normal May precipitation for each weather station (mean May precipitation, 1951–80). We used population data collected by Texas Parks and Wildlife Department and U.S. Fish and Wildlife Service employees, 1970–91 (Table 1). We conducted statistical analyses at the $P < 0.05$ level of significance unless otherwise stated.

If Waddell's spring precipitation hypothesis is supported by the data then spring (Mar–Jun) precipitation should be negatively correlated with the proportional change in prairie-chicken breeding numbers in spring (calculated as $(\hat{N}_2 - \hat{N}_1)/\hat{N}_1$; where $\hat{N}_1$ and $\hat{N}_2$ are the numbers of prairie-chickens derived from the spring survey in year 1 and year 2, respectively). This hypothesis was tested for the 3 populations using linear regression (the Pearson's correlation coefficient associated with the linear regression model was used for these and subsequent linear regression models). No data transformations were necessary for these or subsequent linear regression models because residuals were randomly distributed.

If Lehmann's May precipitation hypothesis explaining annual fluctuations of breeding numbers is supported by the data then 2 criteria must be met. There must be a difference in the proportional change in Attwater's prairie-chicken numbers from the spring survey in which the precipitation data were collected and that of the subsequent spring among Lehmann's (1941:34–35) 4 precipitation categories. Secondly, if such a difference exists, then the direction of change in numbers should agree with Lehmann's ordinal precipitation categories.

To test Lehmann's May precipitation hypothesis, we constructed a contingency table using Lehmann's (1941:34–35) precipitation categories as rows, the Austin-Colorado, Refugio, and Victoria counties Attwater's prairie-chicken populations as columns, and the proportional change in prairie chicken numbers as the dependent variable. We evaluated the hypothesis, using a Kruskal-Wallis test.

By categorizing May precipitation (a continuous variable), Lehmann could have obscured a relationship between May precipitation and the proportional change in spring breeding numbers. Therefore, using linear regression we tested the hypothesis that May rainfall was negatively correlated with proportional changes in prairie-chicken numbers among years for the 3 populations.

For the first alternative hypothesis (H_1) we calculated the maximum amount of precipitation measured during any 48-hour period in May as an index of potential flooding (max. 48-hr precipitation included max. 24-hr precipitation 91% [60/66] of the time). If this hypothesis was supported by the data, then May flooding indicators should be negatively correlated with proportional change in prairie chicken breeding numbers the following spring. Using linear regression, we tested this hypothesis for each of the 3 populations.

We addressed the second alternative hypothesis (H_2) by recording the date when maximum May precipitation was observed and the quantity of precipitation received. We then constructed a multiple regression model that included the May date when maximum precipitation was recorded, the quantity of precipitation received, and an interaction term as independent variables. We pooled data from all 3 populations for analysis. If this hypothesis was supported by the data then the regression model should account for most of the proportional change in Attwater's prairie-chicken spring breeding numbers.

The third hypothesis (H_3) was addressed by calculating indicators of potential flooding consisting of the maximum amount of precipitation measured during any 48-hour period during each spring (Mar–Jun) month. If this hypothesis was supported by the data then the yearly sum of the spring flooding indicators should be negatively correlated with proportional changes in prairie-chicken breeding numbers. Using linear regression, we tested this hypothesis for the 3 populations.

We addressed the fourth hypothesis (H_4) by first calculating the coefficient of variation (CV) (Ott 1988:419) for precipitation among the 4 spring months (Mar–Jun) for each study area by year. If precipitation variability among months was sufficient to account for proportional changes in spring breeding numbers then the precipitation CV should be correlated with the proportional changes in breeding numbers. We used linear regression to test this hypothesis.

Finally, if breeding success drives changes in breeding numbers, regardless of the importance of precipitation-based hypotheses, then the number of juveniles counted per adult in the summer or early fall (Bergerud [1988] used this ratio as a measure of breeding success) should be positively correlated with the proportional change in breeding numbers the following spring. We calculated juvenile-adult ratios from Texas Parks and Wildlife Department helicopter surveys for Austin, Colorado, Galveston, Goliad, Harris, Wharton, and Victoria counties during summers 1972–74 ($n = 11$–133, $\bar{x} = 55.4$

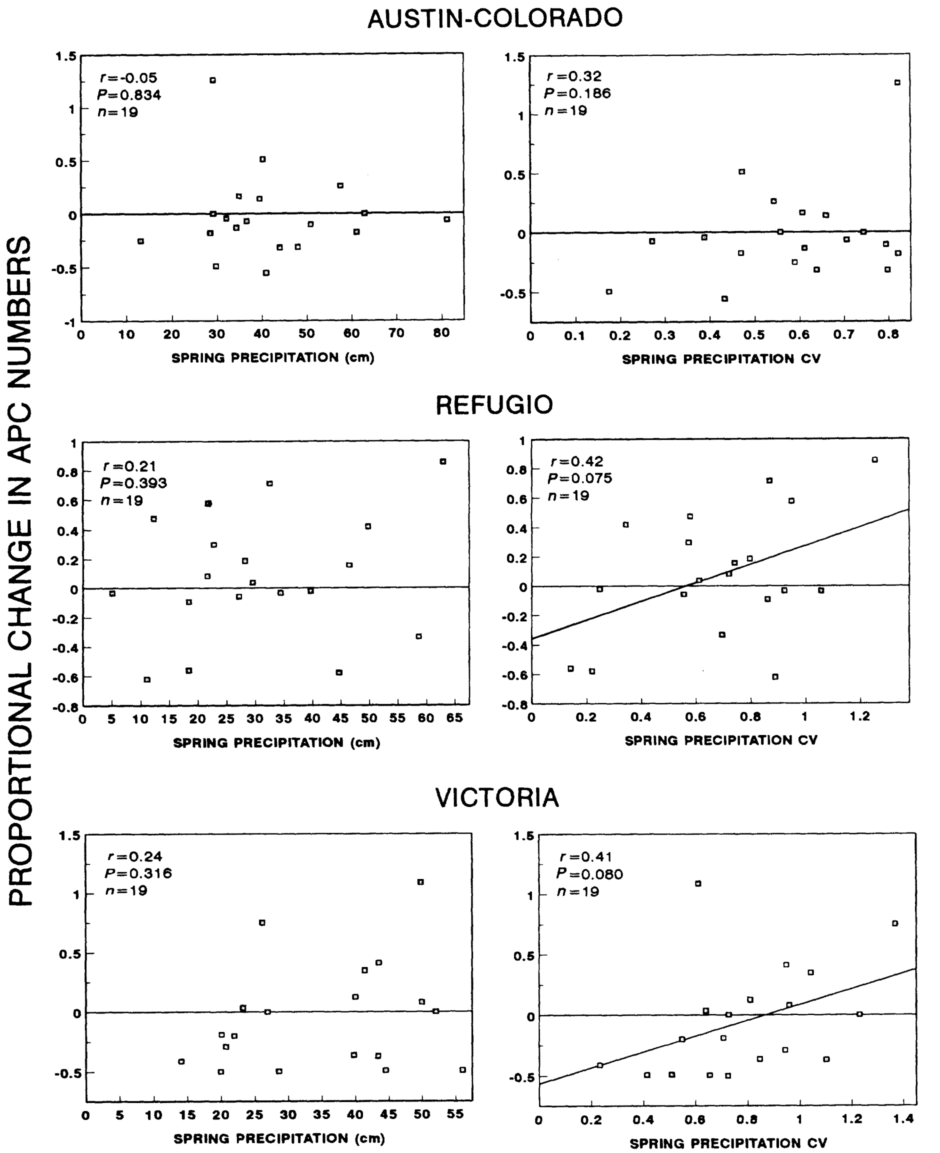

Fig. 1. Proportional change ([$\hat{N}_2 - \hat{N}_1$]/$\hat{N}_1$) in numbers of Attwater's prairie-chicken (APC) on spring breeding grounds, 1970–91, for the Austin-Colorado, Refugio, and Victoria County, Texas, populations as a function of total spring (Mar–Jun) precipitation and the precipitation coefficient of variation (CV) among spring months (Jurries 1977; Natl. Oceanic and Atmos. Adm. records for the Columbus, Refugio, and Victoria, Texas, weather stations; U.S. Fish and Wildl. Serv. 1983, 1993, unpubl. data).

birds observed/survey) (Brownlee 1973*a*,*b*; Jurries 1974). The corresponding proportional changes in Attwater's prairie-chicken breeding numbers were calculated from spring survey data (Jurries 1977). We tested this hypothesis using Spearman's rank correlation.

RESULTS

Waddell's spring precipitation hypothesis was not consistent with the data. Spring precipitation was not correlated with the proportional change in Attwater's prairie-chicken spring breeding numbers for the Austin-Colorado, Refugio, or Victoria County populations (Fig. 1).

There were no differences ($P = 0.060$) in the proportional change of Attwater's prairie-chicken breeding numbers among Lehmann's (1941) May precipitation favorability categories, and the direction of the association did not correspond to Lehmann's ordinal scale (Table 2).

Table 2. Sum of the proportional increases and decreases (calculated as $[\hat{N}_2 - \hat{N}_1]/\hat{N}_1$; where $\hat{N}_1$ and $\hat{N}_2$ are the estimated numbers of prairie-chicken derived from the spring survey in year 1 and year 2, respectively) in Attwater's prairie-chicken numbers for each of Lehmann's (1941:34–45) May precipitation favorability classes for the Austin-Colorado, Refugio, and Victoria County, Texas, populations, 1970–91. The number (n) of spring surveys contributing to the summed proportional change in each category is included.

Precipitation favorability class	Austin-Colorado		Refugio		Victoria		Total	
	Increase	Decrease	Increase	Decrease	Increase	Decrease	Increase	Decrease
Good[a]	(0)	1.4 (5)	1.9 (5)	1.8 (4)	0.1 (2)	2.4 (6)	2.0 (7)	5.6 (15)
Fair[b]	1.9 (3)	0.4 (3)	1.8 (3)	0.2 (4)	(0)	0.6 (2)	3.7 (6)	1.2 (9)
Poor[c]	0.4 (2)	0.8 (3)	0.4 (1)	(0)	0.9 (2)	0.9 (2)	1.7 (5)	1.7 (5)
Bad[d]	(0)	0.1 (2)	0.2 (1)	0.3 (1)	1.9 (3)	(0)	2.1 (4)	0.4 (3)
Total	2.3 (5)	2.7 (13)	4.3 (10)	2.3 (9)	2.9 (7)	3.9 (10)	9.5 (22)	8.9 (32)

[a] Total May precipitation ≥3.8 cm less than normal.
[b] Total May precipitation <3.8 cm below, yet <5.1 cm above, normal.
[c] Total May precipitation ≥5.1 cm above, yet less than twice, normal.
[d] Total May precipitation that was greater than twice normal.

There was no difference ($P = 0.283$) in the proportional change in breeding numbers among the 3 populations. When Lehmann's precipitation favorability categories were ignored, the May precipitation hypothesis still was not supported by the data. No correlation was evident between May precipitation and the proportional change in spring breeding numbers for the Austin-Colorado or Refugio populations, but May precipitation was positively correlated with the proportional change in spring breeding numbers for the Victoria population (Fig. 2).

The first alternative hypothesis (H_1) was not consistent with the data. No correlation was seen between the May flooding indicators and the proportional change in Attwater's prairie-chicken breeding numbers for the Austin-Colorado ($r = 0.15$, $P = 0.547$) or Refugio ($r = -0.18$, $P = 0.469$) populations, whereas these variables were positively correlated ($r = 0.61$, $P = 0.006$) for the Victoria County population. Similarly, our second alternative hypothesis (H_2) was not consistent with the data ($r^2 = 0.07$, $P = 0.256$).

Our third alternative hypothesis (H_3) also was not supported. The 4 spring flooding indicators and the proportional change in spring breeding numbers were not correlated for the Austin-Colorado ($r = -0.07$, $P = 0.778$), Refugio ($r = -0.01$, $P = 0.969$), or Victoria ($r = 0.35$, $P = 0.138$) populations. There was no correlation between the CV for precipitation among spring months and the proportional change in Attwater's prairie-chicken numbers (H_4) for the Austin-Colorado, Refugio, or Victoria populations (Fig. 1).

Data were consistent with Bergerud's breeding success hypothesis. Attwater's prairie-chicken breeding success was positively correlated ($r_s = 0.71$, $P < 0.001$, $n = 22$) with the proportional change in breeding numbers the following spring.

DISCUSSION

Although data do not support Waddell's spring, Lehmann's May, or our alternative precipitation hypothesis regarding deleterious effects of precipitation, they are consistent with Bergerud's (1988) more broadly based breeding success hypothesis. Some might consider the correlation between the CV for precipitation among the 4 spring months and the proportional change in Attwater's prairie-chicken spring numbers to be significant for the Refugio and Victoria populations (Fig. 1). In years when high CVs were observed, however, precipitation during 1 of the 4 spring months was typically about twice normal, again demonstrating that increased spring precipitation does not necessarily lead to decreased prairie-chicken numbers.

While our study indicates that precipitation probably does not directly affect annual breeding success by destroying nests (at a time when renesting cannot occur) or killing chicks (e.g., by drowning), as hypothesized by Waddell and Lehmann, it does not follow that spring or May precipitation is unimportant. A bimodal pattern of yearly precipitation is seen in all 3 study areas and most of the former range of the Attwater's prairie-chicken, with a spring precipitation peak in May, much decreased precipitation during the summer, and a fall precipitation peak in September (Carr 1967; also see Natl. Oceanic and Atmos. Adm. data). In addition to hypotheses dealing with the direct effects of too much precipitation, the indirect influences of precipitation should be considered. For example, be-

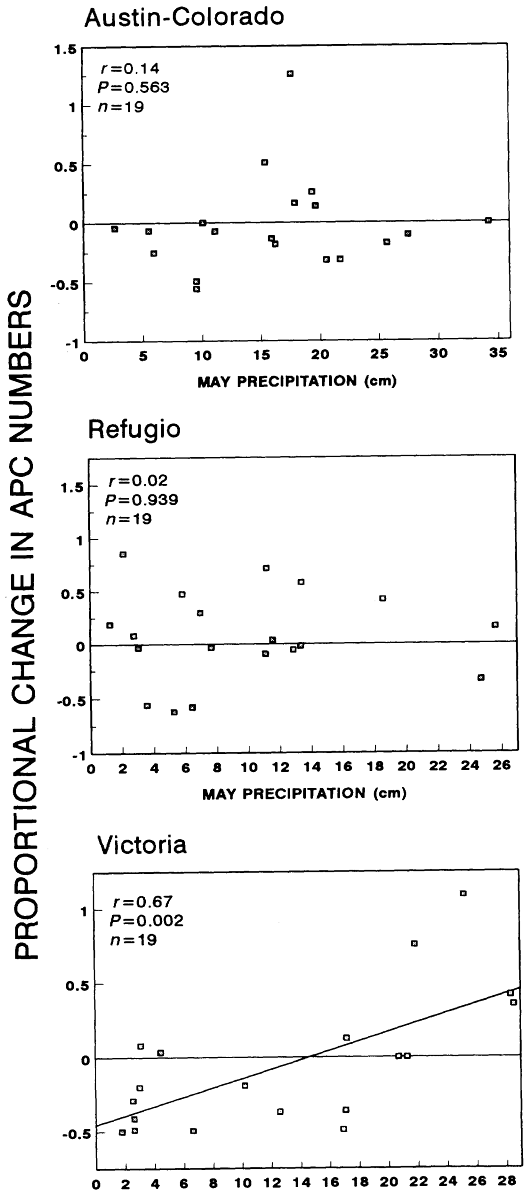

Fig. 2. Proportional change ($[\hat{N}_2 - \hat{N}_1]/\hat{N}_1$) in numbers of Attwater's prairie-chicken (APC) on spring breeding grounds, 1970–91, for Austin-Colorado, Refugio, and Victoria County, Texas, populations as a function of total May precipitation (Jurries 1977; Natl. Oceanic and Atmos. Adm. records for Columbus, Refugio, and Victoria, Texas, weather stations; U.S. Fish and Wildl. Serv. 1983, 1993, unpubl. data).

cause of timing related to prairie-chicken reproduction, spring drought could lead to habitat conditions less conducive to rearing young, such as increased nest and chick predation due to suboptimal nesting and brood-rearing cover and less insect availability due to less plant growth. Some of these conditions have been thought responsible for decreased Attwater's prairie-chicken breeding success (Morrow 1986:78, Silvy and Morrow 1986).

Hypotheses related to precipitation that have been used to explain changes in breeding success of other grouse species could be evaluated for the Attwater's prairie-chicken. For example, Moss (1986) found that the number of capercaillie (*Tetrao urogallus*) chicks in northeastern Scotland was inversely related to the number of days with rain during and shortly after hatching. Bergerud (1988:602–605) established that sharp-tailed grouse (*Tympanuchus phasianellus*) breeding success was positively correlated with a 23-month soil-moisture index in North and South Dakota, but not in Minnesota. He maintained that in the drier Dakotas, a 23-month total was needed to account for both residual and new cover that affected the grouse/predator interaction during nesting and brood rearing. Baines (1991) found that black grouse (*Tetrao tetrix*) females were more likely not to have broods and that less juveniles were reared per hen during cold, wet Junes. Nonprecipitation-related hypotheses also could be developed to account for Attwater's prairie-chicken breeding success.

Although it could be argued that acceptance of the untested spring and May precipitation hypotheses of Waddell and Lehmann was harmless, this process has kept biologists from developing and testing other hypotheses accounting for observed fluctuations in Attwater's prairie-chicken numbers. Because of its endangered status, reliable knowledge concerning processes limiting Attwater's prairie-chicken numbers is needed if we hope to stop this species' decline. An important facet of such knowledge will be the illumination of processes leading to changes in spring breeding numbers—including the mechanisms responsible for the survival of nests and survival and fitness of chicks.

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