INVERTEBRATE CONSUMPTION BY BREEDING NORTHERN BOBWHITES AND ITS RELATION TO PRODUCTION

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ABSTRACT—The cause of variability in quail recruitment in semiarid environments is unclear but variability is associated with precipitation. We hypothesized that variation in the protein and energy nutrition of hens, resulting from variation in the biomass of invertebrates in diets, causes variation in the proportion of reproductively active females in the population. We tested predictions of the hypothesis that: 1) reproducing female northern bobwhite (*Colinus virginianus*) will consume greater biomass of invertebrates than males and nonlaying females, and 2) the proportion of laying females is related to standing invertebrate biomass. Data were collected from 2 sites in the Gulf Coast Prairies (1992–1993) and 2 sites in the Rio Grande Plains (1993) of Texas. Diets of laying females had 3 to 12.5 times more invertebrates than diets of males and 2.3 to 4.0 times more invertebrates than diets of nonlaying females. Although the mean dry mass (kg/ha) of invertebrates was 2.0 to 5.5 times higher in the Gulf Coast Prairies than in the Rio Grande Plains, the percentage of females laying (60 to 73%) was similar between region-years. Other hypotheses regarding reproductive failure of female quail should be investigated.

RESUMEN—La causa de la variabilidad en el reclutamiento de las codornices en ambientes semiáridos sigue siendo indeterminada, pero la variabilidad se asocia con la precipitación. Propusimos que la variación en la proteína y la energía nutritiva de las gallinas, que resulta de la variación en la biomasa de invertebrados en sus dietas, causa la variación en la proporción de hembras reproductivamente activas en la población. Probamos las predicciones de la hipótesis de que: 1) la codorniz colín de Virginia hembra (*Colinus virginianus*) activa reproductivamente consumirá más biomasa de invertebrados que los machos y las hembras que no son reproductivas, y 2) la proporción de hembras reproductivamente activas se relaciona con la cantidad existente de biomasa invertebrada. Se colectarón datos en 2 sitios en las praderas de la Costa del Golfo (1992–1993) y en 2 sitios en las llanuras del río Grande (1993) de Texas. Las dietas de gallinas reproductivamente activas tuvieron de 3 a 12.5 veces más invertebrados que las de los machos y 2.3 a 4.0 veces más invertebrados comparadas con las de las hembras no reproductivamente activas. Aunque el promedio de la masa seca (kg/ha) de invertebrados fue de 2.0 a 5.5 veces más alto en las praderas de la Costa del Golfo que en las llanuras del río Grande, el porcentaje de hembras que pusieron huevos (60–73%) fue similar entre las regiones-años. Otras hipótesis con respecto al fracaso reproductivo de codornices hembras deben ser investigadas.

Annual recruitment of fauna in arid and semiarid environments fluctuates with precipitation (Serventy, 1971). Variability in production is especially evident in gallinaceous birds: Gambel's quail (*Callipepla gambelii*; Swank and Gallizioli, 1954; Gullion, 1960; Hungerford, 1964), California quail (*C. californica*; Francis, 1970; Leopold et al., 1976), scaled quail (*C. squamata*; Campbell et al., 1973), and northern bobwhites (*Colinus virginianus*; Jackson, 1962; Kiel, 1976) exhibited fluctuations associated with patterns and amounts of precipitation.

Food resources, which are often linked to precipitation during the breeding season, might affect recruitment in northern bobwhites. Previous research on dietary factors associated with reproductive variation has focused on levels of vitamin A (Hungerford, 1964; Francis, 1970), phytoestrogens (a reproduction suppressor; Leopold, 1977:129–132; Cain et al., 1987), phosphorus (Cain et al., 1982), and water (Koerth and Guthery, 1991; Guthery and Koerth, 1992; Giuliano et al., 1995). Each factor has been discounted as a sole causative agent inducing variation in quail production. Nevertheless, Case (1972) reported that the energy requirements of laying bobwhite females nearly doubled in comparison with nonlaying females held at the same temperature, and Giuliano et al. (1996) reiterated the importance of protein and energy on the reproductive condition of bobwhites in controlled experiments.

Invertebrates, well known for striking annual changes in abundance, are rich sources of metabolizable energy (Robel et al., 1995), protein (Wood et al., 1986), and amino acids (Peoples et al., 1994). We hypothesized that annual variation in the abundance of invertebrates and, hence, possible associated variation in protein and energy nutrition of female bobwhites, might explain some portion of variation in the annual percentage of hens that lays in a breeding season, an important source of variation in annual recruitment of northern bobwhites (Guthery et al., 1988; Guthery and Kuvlesky, 1998).

Evaluation of this macronutrition hypothesis required that we assess the abundance of invertebrates, examine the diet of bobwhites during the laying season, and estimate the percentage of hens laying. Under the hypothesis, we expected to observe greater proportional consumption of invertebrates by laying females than by nonlaying females and males because of greater protein and energy demands of laying females. Herein we examine the research hypothesis and the corollary prediction of differential invertebrate consumption by breeding classes (laying female, nonlaying female, male). We also provide original descriptive data on the diet of breeding classes of bobwhites in southern Texas.

METHODS—We collected data from 2 ecoregions of southern Texas (Gould, 1975) with high contrast in mean annual precipitation: the Gulf Coast Prairies (94 cm) in 1992 and 1993 and the Rio Grande Plains (64 cm) in 1993. We chose 2 study sites/year/region for data collection. The Gulf Coast Prairies study sites were the Welder Wildlife Foundation Refuge in San Patricio County and the Roche-Thompson Ranch in Refugio County. The Rio Grande Plains study sites were on the Chaparral Wildlife Management Area (Texas Parks and Wildlife Department) of Dimmit and La Salle counties. Harveson (1995) provided site descriptions. Annual precipitation for the study sites in the Gulf Coast Prairies was similar for 1992 (122 cm, 130% of annual average) and 1993 (110 cm, 120% of annual average; D. L. Drawe, Welder Wildlife Foundation, unpubl. data), whereas in 1993, the Rio Grande Plains area received 67 cm (104% of annual average; Texas Parks and Wildlife Department, unpubl. data).

Invertebrate biomass and composition were measured concurrently from each study area. Sampling was distributed among 5, 3-week intervals (23 April to 13 May, 14 May to 2 June, 3 June to 22 June, 23 June to 12 July, 13 July to 3 August) within the breeding season (May through July). Invertebrates were collected with a vacuum-suction device (Dietrich, 1961). A random number generator chose x-coordinates and y-coordinates for invertebrate collection points. Four cages 0.5×0.5 m, covered on the sides with 2-mm mesh cloth and a plastic pipe frame, were oriented in a 2×2 grid with 10-m spacing centered on the random point. Cages were set within 3 h of sunrise, and each cage was vacuumed for 2 to 3 min. Invertebrate samples were pooled for each random point (4 cages). Invertebrates were collected from 17 points in each of the 1992 study sites; we increased sampling to 30 points in 1993 to improve precision. Invertebrates were identified to order, dried to constant mass (43°C for $\geq$2 d), and weighed to the nearest 0.0001 g. Total invertebrate biomass was defined as the sum of all invertebrate orders and was pooled by region-year ($n = 3$) to index invertebrate abundance relative to the research hypothesis.

Bobwhites were harvested concurrently from each study site each year during peak breeding season (May through July; Guthery et al., 1988). Bobwhites were located (typically on the ground) within the study sites by driving the extensive road networks at slow speeds. Birds were shot using a small-caliber rifle within 3 h of sunrise or sunset. Specimens were weighed, tagged, stored on ice in the field, and later frozen for storage in the laboratory. Collection took place under scientific permit SPR-0592-525 issued by the Texas Parks and Wildlife Department using protocols approved by the Institutional Animal Care and Use Committee, Texas A&M University-Kingsville.

Reproductive status of specimens was determined using several criteria. Females with mature follicles or eggs in the oviduct or having oviduct mass $\geq$3 g were classified as laying females (Kirkpatrick, 1955). Males were considered reproductively active if the

TABLE 1—Mean dry mass (kg/ha) of invertebrate orders collected from invertebrate traps from April through August on study areas in southern Texas, 1992 and 1993.

	Gulf Coast Prairies				Rio Grande Plains	
	1992 (n = 34)		1993 (n = 60)		1993 (n = 60)	
Order	Mean	*SE*	Mean	*SE*	Mean	*SE*
Orthoptera	2.23	0.42	0.64	0.09	0.36	0.08
Hemiptera	0.11	0.03	0.03	0.02	0.04	0.01
Homoptera	0.08	0.02	0.06	0.02	0.00	<0.01
Hymenoptera	0.02	0.01	0.01	0.01	0.04	0.02
Araneae	0.56	0.14	0.22	0.14	0.03	0.02
Coleoptera	0.04	0.01	0.02	0.01	0.08	0.07
Other	0.12	0.04	0.17	0.04	0.03	<0.01
Total	3.16	0.45	1.15	0.18	0.58	0.11

right testis weighed ≥300 mg (Kirkpatrick, 1964). We removed from analysis 2 males that did not meet the gonad-mass criterion.

Crop contents were removed, washed, and separated into seed, foliage, mast, and invertebrate categories. Invertebrates were further separated by order. Crop contents were dried to constant mass (43°C for ≥2 d) and weighed to the nearest 0.0001 g.

Because of recent concern regarding the merit of null hypothesis significance testing in observational studies (Cohen, 1994; Cherry, 1998; Johnson, 1999; Guthery et al., 2001*b*; Burnham and Anderson, 2002), we approached data analysis and interpretation from a descriptive standpoint. We simply report means and standard errors, and judge magnitude of effects (Edwards, 1992) with reference to confidence intervals, estimable probabilities, and established biological processes.

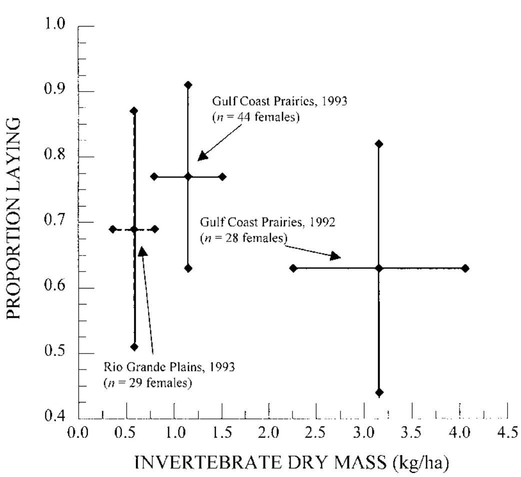

FIG. 1—Proportion of northern bobwhite (*Colinus virginianus*) females that were laying as a function of invertebrate dry mass in southern Texas during breeding seasons of 1992 and 1993. The vertical lines provide 95% confidence intervals for the proportion laying, and the horizontal lines provide 95% confidence intervals for the invertebrate dry mass index.

RESULTS—Total invertebrate biomass was estimated to be 2.0 to 5.5 times greater in the Gulf Coast Prairies than in the Rio Grande Plains. The differences among region-years occurred primarily because of high abundance of orthopterans in the Gulf Coast Prairies in 1992 (Table 1).

The range of invertebrate abundance over which we could assess the macronutrition hypothesis was 2.58 kg dry mass/ha (from 0.58 to 3.16; Table 1). Over this range, we detected no effect of total invertebrate biomass on the proportion of laying females in the sample of females despite strong evidence of differential invertebrate abundance among regions-years (Fig. 1).

Specimens with food in their crops included 50 of 60, 73 of 90, and 53 of 60 bobwhites for the Gulf Coast Prairies in 1992 and 1993 and the Rio Grande Plains in 1993, respectively. Diet data were supportive of our corollary prediction (higher invertebrate consumption by laying females; Table 2). Without exception, the raw mean of dry mass invertebrate intake (primarily orthopterans and coleopterans; Harveson, 1995) was higher for laying females than for nonlaying females, but the inferential

TABLE 2—Diet (g dry mass) of northern bobwhites (*Colinus virginianus*) by breeding class from April through August on study areas in southern Texas, 1992 and 1993. Trace (tr) = <0.1 g.

		Females					
		Laying		Nonlaying		Males	
Region, year	Food	Mean	*SE*	Mean	*SE*	Mean	*SE*
Gulf Coast Prairies, 1992[a]	Seed	2.1	0.5	1.8	0.7	1.3	0.3
	Mast	0.2	0.1	tr		0.2	0.2
	Invertebrate	0.5	0.1	0.21	0.1	tr	
	All	2.8	0.6	2.0	0.8	1.3	0.3
Gulf Coast Prairies, 1993[b]	Seed	0.7	0.2	1.3	0.8	0.9	0.2
	Mast	tr		tr		tr	
	Invertebrate	0.4	0.1	0.1	0.1	0.1	0.0
	All	1.1	0.3	1.5	0.8	1.1	0.2
Rio Grande Plains, 1993[c]	Seed	1.1	0.2	0.9	0.8	0.7	0.2
	Mast	0.2	0.0	tr		tr	
	Invertebrate	0.9	0.2	0.4	0.0	0.3	0.0
	All	2.2	0.4	1.4	0.9	1.2	0.3

[a] n = 17, 10, 23, respectively.
[b] n = 30, 9, 34, respectively.
[c] n = 18, 8, 27, respectively.

merit of this occurrence was clouded by overlapping 95% confidence interval coverage. However, if we assume equal intake of invertebrates between laying females and nonlaying females and random sampling, the probability of our results is 0.125, indicating 7:1 odds in favor of greater invertebrate consumption by laying females than by nonlaying females. The intake of invertebrate dry mass by laying females ranged from 3.0 to 12.5 times that of males, with overlapping confidence intervals.

DISCUSSION—Our results did not support the hypothesis that variation in protein and energy nutrition associated with variation in invertebrate abundance explains variation in the percentage of hens laying and, hence, in recruitment for quails in semiarid environments (Fig. 1). However, we had an effective sample size of 3, thus this study is best regarded as first approximation of the relation between invertebrate abundance and laying activity of bobwhites. Nonetheless, within that sample, we had an apparently large range of invertebrate abundance, and the proportion of hens laying seemed independent of invertebrate abundance.

Our findings on the macronutrition hypothesis might hold only within the range of invertebrate dry masses observed (Table 1, Fig. 1). However, the hypothesis might still hold for total invertebrate dry masses below 0.58 kg/ha (the lowest value observed in our study; Table 1), that is, during drier than normal years.

If the macronutrition hypothesis is without merit, then variability in the proportion of hens laying arises from some other source. Possible sources include age composition of the breeding-hen population (e.g., first-year breeders less likely to lay). Francis (1970) found California quail recruitment increased with the percentage of adult females in the population, but he did not specify the mechanism leading to the outcome. Variation in heat loads among breeding seasons (Guthery, 2002) is another possible source of variation in the proportion of hens laying. Higher temperatures are associated with lower production in quails (Heffelfinger et al., 1999; Guthery et al., 2001*a*; Guthery, 2002), and this effect might operate in part by stressing females so that some go out of laying condition and some do not enter it.

Finally, although the percentage of females breeding can be a powerful influence on annual recruitment (Guthery and Kuvlesky, 1998), that percentage is but one of many variables that govern quail production. These variables include probability of nest success, number of nesting attempts, length of the laying season, and chick survival, among others. Our findings in no way reflect on the role of invertebrates in the growth and survival of quail chicks. The findings suggest that invertebrates might not have a major role in the breeding intensity of adult females, given invertebrate abundance higher than the values we reported.

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