AN ABSTRACT OF THE THESIS OF

Darin R. Porter for the Master of Science Degree
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Title: Gut Morphology and Genetic Variation as Predictors of Population Vigor in the Greater Prairie-chicken,

Tympanuchus cupido, in Kansas.

Abstract Approved: [Signature]

Greater prairie-chicken, Tympanuchus cupido, were sampled from populations in the Flint Hills and southeastern Kansas. Populations in the Flint Hills and southeast Kansas were compared for food habits, gut morphology, and genetic constitution. Diet analysis indicated dicotyledonous foliage was consumed in greater volume ($P = 0.04$) in the Flint Hills. Lengths and weights of small intestines and caeca and weights of gizzards were similar between areas ($P > 0.05$). Relationships of gut morphology values and dietary analysis indicate nutritionally adequate food availability. Starch-gel electrophoresis was used to examine genic variation at 22 presumptive loci. Mean levels of heterozygosity ranged from 0.008 to 0.045. Genetic similarity values for the populations indicate clustering by areas, however all populations clustered above 0.98 similarity. F-statistics indicated 95% of the total genic diversity was attributable to differences among individual birds. Based on these analyses, all populations seem to be comparatively similar in vigor with no significant divergence between prairie-chicken from the 2 areas in
Kansas. Therefore, management of the prairie-chicken should not be concerned with the genetic resources, unless population numbers were to decline drastically. Additional dietary and vegetative analysis during other periods of the year might provide useful information.
GUT MORPHOLOGY AND GENETIC VARIATION
AS PREDICTORS OF POPULATION VIGOR IN GREATER
PRAIRIE-CHICKEN, TYMPANUCHUS CUPIDO, IN KANSAS

A Thesis
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by
Darin R. Porter
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Approved by Committee Member

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Approved for Major Department

James I. Wolfe
Approved for Graduate Council
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This thesis is dedicated to my parents, Roy and Donna,
and especially my wife, Joyce, and son, Daniel.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>1</td>
</tr>
<tr>
<td>Materials and Methods</td>
<td>5</td>
</tr>
<tr>
<td>Results</td>
<td>13</td>
</tr>
<tr>
<td>Discussion</td>
<td>25</td>
</tr>
<tr>
<td>Management Implications</td>
<td>31</td>
</tr>
<tr>
<td>Summary</td>
<td>33</td>
</tr>
<tr>
<td>Literature Cited</td>
<td>34</td>
</tr>
</tbody>
</table>
## LIST OF TABLES

<table>
<thead>
<tr>
<th>TABLE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Food contents in the crops of greater prairie-chicken collected in the Flint Hills and southeast Kansas.</td>
<td>16</td>
</tr>
<tr>
<td>2. Mean weights and lengths and standard errors for the digestive structures of greater prairie-chicken collected in the Flint Hills and southeast Kansas.</td>
<td>17</td>
</tr>
<tr>
<td>3. Percentage contribution of each level in the nested analysis, to the total variance for digestive structures weight and length or levels among greater prairie-chicken.</td>
<td>18</td>
</tr>
<tr>
<td>4. Means weights and lengths for digestive structures and F-ratios in greater prairie-chicken in the Flint Hills and southeast Kansas.</td>
<td>19</td>
</tr>
<tr>
<td>5. Allele frequencies of 3 variable loci and heterozygosity by direct count and expected count for populations of greater prairie-chicken collected in the Flint Hills and southeast Kansas.</td>
<td>20</td>
</tr>
<tr>
<td>6. Coefficients of Rogers' (1972) genetic similarity for all populations of greater prairie-chicken examined in the Flint Hills and southeast Kansas.</td>
<td>21</td>
</tr>
</tbody>
</table>
7. F-statistics for each variable locus and the mean across all loci for greater prairie-chicken. ......................... 22
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>FIGURE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Collection sites for populations of greater prairie-chicken <em>Tympanuchus cupido</em> in Kansas</td>
<td>12</td>
</tr>
<tr>
<td>2. Phenogram (UPGMA) based upon Rogers' (1972) genetic similarity values summarizing the genetic relationships among populations of greater prairie-chicken collected in Kansas</td>
<td>23</td>
</tr>
</tbody>
</table>
INTRODUCTION

The evolution and ecology of the prairie ecosystem was strongly influenced by interactions among herbivores, wildfire and the native plants. Changes in any component of this ecosystem can have major effects on the whole ecosystem (Horak, 1985). As prairie grouse evolved within this system, their fate is inextricably tied to the health of the system.

The greater prairie-chicken (Tympanuchus cupido) was probably the most common of all prairie grouse in Kansas (Christisen 1969, Horak 1985). Their distribution and abundance appears to be affected by grassland composition, as they are positively associated with native, warm-season plants and inversely associated with exotic, cool season plants (Christisen 1969, Christisen and Krohn 1980); possibly from the standpoint of nutrition (Kirkpatrick 1980). Since settlement of the state, the conversion in land-use from grassland to cropland has influenced prairie-chicken habitat (Baker 1953) and thus prairie-chicken populations. Populations of greater prairie-chicken initially increased, but later decreased as land was converted from prairie to cropland (Aldrich 1963). Because of ranching and little rowcrop farming in the Flint Hills of Kansas, large tracts of grassland are found. The Flint Hills of east-central Kansas (Fig. 1) now contain the largest populations in Kansas, with smaller populations to the east and west (Horak 1985). Habitat suitable for
prairie-chicken is discontinuous to the east and west of the Flint Hills and is considered marginal habitat relative to that found in the Flint Hills.

Physiological condition affects survival and reproductive success (Breitenbach et al. 1963, Barrett and Bailey 1972). By affecting the physiological condition of birds, food quality and quantity can be an important factor in determining population size. Birds consuming low quality, fibrous foods, such as foliage, had longer guts and caeca than those consuming high quality foods such as seeds and fruits (Leopold 1953, Moss 1972). This presumably is because coarser, indigestible foods demand greater rates of intake and digestive abilities. More fibrous foods also require increased maceration by the gizzard and thus the gizzard is comparatively heavier (Miller 1975). By examining gut morphology of the greater prairie-chicken, the quality of the diet of birds found in each area can be indirectly compared for a specific time period. Any difference in food quality and consequently gut morphology may be useful in assessing the quality of habitat between optimal and marginal habitat.

A second part of this study is to examine genetic variability in populations of prairie-chicken to assess effects due to possible inbreeding due to small population size. The genetic resources of a species exists at two fundamental levels, genetic differences between individuals
within a local population and genetic differences among populations.

Isolation by distance (Wright 1943) plays a major role in promoting genetic divergence between populations and can ultimately lead to extinction as well as speciation among related populations. Genetic analyses of numerous species document the lack of continuous gene flow among populations separated by short geographic as well as longer distances (Selander 1970, Manlove et al. 1976, Ryman et al. 1980, Chesser et al. 1982a, 1982b). Stochastic events or differential selection pressures may cause heterogeneity (Smith et al. 1983, King et al. 1985, Brown 1986). Without genetic diversity, a population runs the risk of becoming inbred.

Inbreeding results in a decrease in vigor, viability, and fecundity and an increase in the number of abnormalities in offspring that result from breeding between close relatives in a normally outcrossing species (Chambers 1983). The loss of genetic variability in a population decreases the populations potential adaptability. Without the exchange of reproductively successful individuals among populations, these small populations continue to become inbred and genetic drift leads to changes in allele frequencies from generation to generation. Male prairie-chicken tend strongly to return each spring to the lek on which they had previously established themselves
(Hammerstrom and Hammerstrom 1973). Hens also return to the same leks, although not as persistently as the males (Hammerstrom and Hammerstrom 1973). It is possible that local extinction could occur over small areas because of the reduced genetic variability caused by population division, and because of the lack of genetic resources to adapt to new environmental conditions. Fragmentation of habitat or the presence of different habitat types, usually as a result of human activities, may reduce gene flow between adjacent populations. Since man-made changes in environmental conditions are seldom gradual over time, populations that are able to respond adaptively should be populations that are (1) genetically flexible, (2) have high genetic variability pre-existing in the population, or (3) have large population sizes. By assessing the genetic variation of greater prairie-chicken within and among large populations in the Flint Hills and smaller populations in southeastern Kansas, the extent of genetic differentiation can be determined.
METHODS AND MATERIALS

Male prairie-chicken were collected by shooting in Lyon County, 4 - 11 May 1989; and in Lyon, Chase, Butler and Greenwood counties Kansas, 29 March - 7 May 1990 (Flint Hills region). Prairie-chicken were collected from Labette, Linn, and Bourbon counties, 13 April - 2 May 1990 and from Allen County 12 - 15 May 1989 (southeast region).

Southeast Kansas collection sites were a mixture of cool season and warm-season grasses, with large amounts of agricultural ground. Prairie-chicken populations tended to be found in the larger tracts of native grass in Bourbon and Linn counties, while in Labette County, prairie-chicken habitat was primarily cool season grass pasture and agricultural fields with limited native grass pastures nearby. Two of 3 leks were located in agricultural fields in Labette County. Conservation Reserve Program (CRP) acres enrolled in warm-season grasses were being utilized by prairie-chickens in Linn and Labette counties. Allen County prairie-chickens were located in an area of limited native warm-season vegetation with large amounts of agricultural fields.

In the Flint Hills region, Chase and Lyon counties were typical native grass range with limited interspersed agricultural ground. The Lyon County collection site (Fig. 1) is not located within the Flint Hills region (Self 1978), but is comparable in habitat. The area in Butler and
Greenwood counties was primarily native range. Cool season grass was limited in the Flint Hills region.

A maximum of 4 male prairie-chicken was collected from each of 3 locations (leks) less than 8 km to one another in 7 separate areas (3 in Flint Hills and 4 in southeast). Each group of leks was assumed to represent different breeding populations.

Upon collection fresh body weight was recorded when possible and the birds were labeled and frozen for laboratory analysis. In the laboratory, heart and liver tissue were removed and frozen for genetic analysis and stored in an ultracold freezer at -60 C.

DIET--Crops were emptied and contents weighed to the nearest 0.01 g. Crop contents were identified as to the type of food present, primarily to determine the amount of foliage and seeds in the diet, though specific plant and animal identification was made when possible. Seven categories of food were designated: (1) animal matter, (2) agricultural seeds, (3) dicotyledonous foliage, (4) flowers, (5) legumes, and (6) monocotyledonous foliage and (7) seeds. Food items were counted and volumes were measured by volumetric displacement in a graduated cylinder (Swanson and Bartonek 1970) with volumes recorded to the nearest 0.01 ml. Food items were dried for >48 hours at 50 C and weighed to the nearest 0.001 g. Aggregate percent weight and volume were totaled for category percentages.
Student t-tests was used to compare mean percent volume and mean percent weight of food items between the 2 areas. To ensure normality, the values were arcsine transformed before analysis.

GUT MORPHOLOGY--The digestive tract and gizzard were removed and separated. The gizzard was emptied of food contents and reweighed. The caeca and small intestines were measured to the nearest 0.01 cm and then rinsed of all contents, blotted and weighed. Care was taken to ensure that the structures were straightened but not stretched (Moss 1983). Both caeca were measured separately and were added together to obtain a combined total length. A model I nested analysis of variance was used to 1) test if the mean lengths and weights of gut structures were equal between the Flint Hills and southeastern Kansas and 2) examine the percent contribution of populations, leks, and individuals to the total variance. The BIOSTAT I statistical package was used for the computation (Pimentel and Smith 1986).

GENETICS--The electrophoretic techniques, buffers and stains follow those of Selander et al. (1971) or Harris and Hopkinson (1976). All gels were prepared using hydrolyzed potato starch (Sigma Chemical Co., St. Louis, MO). In multiple locus systems, the isozyme migrating most anodally was designated as "1". Peptidase loci were designated for their substrate specificity. Alleles were scored by designating the most anodally migrating allele as "A". All
other alleles at a locus were assigned alphabetic
designations in order of decreasing anodal mobility.

Genetic variation at 22 loci was determined using the
following systems. Esterase-1, -2 (EST-1, -2; 3.1.1.1),
general protein (GP), superoxidase dismutase-1,-2 (SOD-1,
SOD-2; 1.15.1.1), xanthine dehydrogenase (XDH; 1.2.3.2),
alcohol dehydrogenase (ADH; 1.1.1.1), sorbitol dehydrogenase
(SDH; 1.1.1.14), aspartate-amino transferase (AAT; 2.6.1.1),
peptidase glycyl-leucine (P-GL; 3.4.11), peptidase leucyl-
glycyl-glycine (P-LGG; 3.4.11), and peptidase leucyl-leucyl-
leucine (P-LLL; 3.4.11) were scored on lithium hydroxide gel
buffer (pH 8.2). Isocitrate dehydrogenase (IDH; 1.1.1.42),
and malate dehydrogenase-1, -2 (MDH-1, MDH-2; 1.1.1.37) were
scored on tris-citrate gel buffer (pH 6.7).
Phosphoglucomutase (PGM; 2.7.5.1), purine nucleoside
phosphorylase (NP; 2.4.2.1), glucose phosphate isomerase
(GPI; 5.3.1.9), glycerol-3-phosphate dehydrogenase (GPD;
1.1.1.8), creatine kinase-1, -2 (CK-1, -2; 2.7.3.2), and
hexokinase (HK; 2.7.2.2) were scored on tris-citrate gel
buffer (pH 8.0).

The degree of genetic similarity among the 7
populations was analyzed by F-Statistics (Wright 1965, Nei
1977). All F-values were calculated using means and
variances of allele frequencies weighted by sample sizes.
Fst values measure the degree of genetic differentiation
among the populations by comparing expected genotype
proportions from Hardy-Weinberg for the total population. 
F\textsubscript{s} values measure the decrease in heterozygosity due to 
inbreeding within a population. This is the degree of 
genetic differentiation of an individual, from the expected 
Hardy-Weinberg proportions of its subpopulation, and the 
total population.

Coefficients of Rogers' (1972) genetic similarity were 
computed for all possible paired-wise combinations from the 
allele frequency data for each population. A phenogram for 
the 7 populations was obtained from the similarity matrix 
using the unweighted pair group method with arithmetic 
averges option of the BIOSYS-1 package of Swofford and 

Specimens examined.--All specimens were cleaned and 
skeletons were deposited in the Schmidt Museum of Natural 
History. The number in parentheses indicates numbers of 
specimens of greater prairie-chicken collected from each 
locality. Each locality represents a single lek. Kansas: 
Allen Co.; T24S, R19E, NW1/4 SEC. 2 (2), T24S, R20E, NW1/4 
SEC. 7 (2). Bourbon Co.; T26S, R21E, NE1/4 SEC. 24 (2), 
T26S, R21E, SE1/4, SEC. 24 (2), T26S, R21E, SW1/4, SEC. 23 
(2). Butler Co.; T23S, R8E, NE1/4 SEC. 28 (4). Chase Co.; 
T18S, R8E, SE1/4 SEC. 12 (4), T18S, R8E, NE1/4 SEC. 11 (4), 
T18S, R8E, NE1/4, SEC. 24 (4). Greenwood Co.; T23S, R8E, 
SE1/4 SEC. 22 (4), T23S, R8E, SW1/4 SEC. 23 (4). Labette 
Co.; T34S, R19E, SE1/4 Sec. 22 (2), T34S, R19E, NE1/4 SEC.
Fig. 1. Collection sites for populations of greater prairie-chicken Tympanuchus cupido in Kansas. Shaded area indicates the Flint Hills Region in Kansas, according to Self (1978). See the specimens examined for more detailed description of collection sites. 1-Allen Co., 2-Bourbon Co., 3-Chase Co., 4-Butler/Greenwood Co., 5- Labette Co., 6-Linn Co., 7-Lyon Co.
RESULTS

DIET--The composition of the diets of the greater prairie-chicken in the Flint Hills populations and southeast Kansas populations were similar (Table 1.) Plant material made up >98% of the diet with animal matter comprising <2%.

The volume of animal matter consumed was not significantly different \((P = 0.59)\) between the 2 collection areas. Birds in the southeastern region ate Arachnida and Coleoptera whereas birds in the Flint Hills consumed only Lepidoptera.

Agricultural seeds were found in the crops of the prairie-chicken, with sorghum \((\text{Sorghum spp.})\) found only in crops from the Flint Hills, while soybean \((\text{Glycine max})\) seeds were found in birds from both regions. There was no difference \((P = 0.56)\) in the volume of agricultural seeds eaten in both regions.

Foliage of dicotyledonous plants (Table 1) was found in greater percent volume \((P = 0.04)\) and percent weight \((P = 0.03)\) in the Flint Hills than in the southeastern region. Consumption of dicotyledonous flowers by prairie-chicken was found in both areas. No difference in volume \((P = 0.57)\) of flowers consumed existed. Legumes were included in the dicotyledonous percentages and were identified only as trifoliate plants. There was no difference \((P = 0.08)\) in the volume of legumes in the diet. Legumes were not found in the diets of the Flint Hills birds.
Monocotyledonous plant consumption was found in both populations. There was no difference ($P = 0.51$) in volume of foliage or seeds ($P = 0.83$) from monocotyledonous plants in the diets.

GUT MORPHOLOGY--Caeca lengths and weights were 7% and 19% greater in greater prairie-chicken collected from the Flint Hills than those collected from southeast Kansas respectively (Table 2). Small intestine weights in the birds from the Flint Hills were 14% greater while the small intestine lengths averaged 4% less than those from the southeastern region. Gizzard weight was 21% heavier in the Flint Hills (Table 2). The percentage contribution to the total variance was greater at the individual level for the digestive structures (Table 3), however for caeca weight the greatest contribution was at the population level. Variation among leks within populations in general contributed very little to the total variation in digestive structures. There was no significant difference ($P > 0.05$) in the mean for any digestive structure between the birds in southeastern Kansas and the Flint Hills (Table 4).

GENETICS--Of the 22 presumptive genetic loci examined, 3 were polymorphic and 19 were monomorphic and fixed for the same allele in all samples (Table 5). Mean levels of heterozygosity ($H$) ranged from 0.008 in Bourbon County to 0.045 in Allen County. Mean heterozygosity in the Flint Hills was 0.029 and 0.023 in the southeast. Mean
heterozygosity across all populations was 0.025. Expected heterozygosity was less than heterozygosity by direct count in Allen County and greater in all other populations indicating some level of inbreeding within populations.

Genetic similarities between pairs of populations ranged from 0.994 to 0.978 (Table 6). The phenetic relationships among populations are summarized in a phenogram (Fig. 2). Populations did not cluster strictly by area, although some grouping does occur between areas, however all populations are genetically very similar and cluster above the 0.98 similarity value.

The mean $F_{st}$ value across all loci was 0.049 (Table 7) for the 7 populations of prairie-chicken. On the average, 5% ($F_{st} = 0.049$) of the total variance in allele frequencies was due to differences among populations. Thus, 95% of the total gene diversity ($1 - F_{st}$) was attributable to differences among individual birds within populations. The mean $F_{is}$ value across all loci was 0.256 for the 7 populations, which again indicates inbreeding within populations.
Table 1. Food contents in the crops of greater prairie-chicken collected from the Flint Hills (F) (n = 18) and southeastern (S) Kansas (n = 21). Food items were grouped into one of 7 categories.

<table>
<thead>
<tr>
<th>Food Category</th>
<th>Number of Food Types</th>
<th>% Volume</th>
<th>% Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>S</td>
<td>F</td>
</tr>
<tr>
<td>ANIMAL MATTER</td>
<td>3</td>
<td>0.29</td>
<td>1.62</td>
</tr>
<tr>
<td>AGRICULTURAL SEEDS</td>
<td>2</td>
<td>41.92</td>
<td>17.02</td>
</tr>
<tr>
<td>DICOTYLEDONOUS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FOLIAGE</td>
<td>13</td>
<td>10.56</td>
<td>50.49</td>
</tr>
<tr>
<td>FLOWER</td>
<td>6</td>
<td>23.60</td>
<td>17.91</td>
</tr>
<tr>
<td>LEGUME</td>
<td>1</td>
<td>19.43</td>
<td>0.00</td>
</tr>
<tr>
<td>MONOCOTYLEDONOUS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FOLIAGE</td>
<td>2</td>
<td>4.11</td>
<td>12.87</td>
</tr>
<tr>
<td>SEED</td>
<td>1</td>
<td>0.07</td>
<td>0.08</td>
</tr>
</tbody>
</table>
Table 2. Mean weights (g) and lengths (cm) and standard errors for the digestive structures of greater prairie-chicken collected in the Flint Hills (F) and southeast (S) Kansas.

<table>
<thead>
<tr>
<th>Area</th>
<th>Caeca  ( n = 62 )</th>
<th>Small Intestine  ( n = 62 )</th>
<th>Gizzard  ( n = 63 )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length ( \bar{X} )</td>
<td>Weight ( \bar{X} )</td>
<td>Length ( \bar{X} )</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>SE</td>
<td>SE</td>
</tr>
<tr>
<td>F</td>
<td>96.28</td>
<td>9.16</td>
<td>116.34</td>
</tr>
<tr>
<td>S</td>
<td>89.97</td>
<td>7.68</td>
<td>121.49</td>
</tr>
</tbody>
</table>
Table 3. Percentage contribution of each level in the nested analysis, variance to the total variance for digestive structures weight (g) and length (cm) or levels among greater prairie-chicken.

<table>
<thead>
<tr>
<th>Level</th>
<th>d.f.</th>
<th>Caeca</th>
<th>Small Intestine</th>
<th>Gizzard</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Length</td>
<td>Weight</td>
<td>Length</td>
<td>Weight</td>
</tr>
<tr>
<td>Individual</td>
<td>43</td>
<td>55.6</td>
<td>31.5</td>
<td>66.6</td>
<td>64.4</td>
</tr>
<tr>
<td>Lek</td>
<td>13</td>
<td>9.6</td>
<td>6.1</td>
<td>33.4</td>
<td>9.2</td>
</tr>
<tr>
<td>Population</td>
<td>5</td>
<td>34.8</td>
<td>62.4</td>
<td>0.0</td>
<td>26.4</td>
</tr>
</tbody>
</table>
Table 4. Mean weights (g) and lengths (cm) for digestive structures and F-ratios in greater prairie-chicken in the Flint Hills (F) and southeast (S) Kansas areas.

<table>
<thead>
<tr>
<th>Digestive Structure</th>
<th>Mean</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>S</td>
<td>d.f.</td>
<td>F-ratio</td>
<td>P</td>
</tr>
<tr>
<td>Caeca Weight</td>
<td>9.16</td>
<td>7.71</td>
<td>1,5</td>
<td>1.04</td>
<td>0.36</td>
</tr>
<tr>
<td>Caeca Length</td>
<td>94.46</td>
<td>90.25</td>
<td>1,5</td>
<td>0.44</td>
<td>0.54</td>
</tr>
<tr>
<td>Sm. Int. Weight</td>
<td>14.49</td>
<td>12.53</td>
<td>1,5</td>
<td>2.66</td>
<td>0.16</td>
</tr>
<tr>
<td>Sm. Int. Length</td>
<td>116.34</td>
<td>121.82</td>
<td>1,5</td>
<td>3.00</td>
<td>0.14</td>
</tr>
<tr>
<td>Gizzard Weight</td>
<td>18.72</td>
<td>15.79</td>
<td>1,5</td>
<td>4.13</td>
<td>0.10</td>
</tr>
</tbody>
</table>
Table 5. Allele frequency at 3 variable loci and heterozygosity by direct count (DC) and expected count (EC) for the populations of greater prairie-chicken in the Flint Hills (F) and southeast Kansas (S). Refer to Fig. 1 for locality designations. Unless otherwise indicated, alleles were present in a population at a frequency of 1.00.

<table>
<thead>
<tr>
<th>Population</th>
<th>n</th>
<th>ES-2</th>
<th>ADH</th>
<th>A-GPD</th>
<th>Heterozygosity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>DC</td>
</tr>
<tr>
<td>1. Allen (S)</td>
<td>4</td>
<td>A/0.38</td>
<td>A</td>
<td>A/0.13</td>
<td>B/0.62</td>
</tr>
<tr>
<td>2. Bourbon (S)</td>
<td>6</td>
<td>A/0.42</td>
<td>A</td>
<td>B</td>
<td>0.008</td>
</tr>
<tr>
<td>3. Chase (F)</td>
<td>12</td>
<td>A/0.25</td>
<td>A</td>
<td>B</td>
<td>0.019</td>
</tr>
<tr>
<td>4. Butler (F)</td>
<td>12</td>
<td>A/0.29</td>
<td>A</td>
<td>B</td>
<td>0.030</td>
</tr>
<tr>
<td>5. Labette (S)</td>
<td>8</td>
<td>A/0.38</td>
<td>A</td>
<td>A/0.06</td>
<td>B/0.94</td>
</tr>
<tr>
<td>6. Linn (S)</td>
<td>9</td>
<td>A/0.33</td>
<td>A</td>
<td>A/0.11</td>
<td>B/0.89</td>
</tr>
<tr>
<td>7. Lyon (F)</td>
<td>18</td>
<td>A/0.25</td>
<td>A/0.89</td>
<td>A/0.03</td>
<td>B/0.11</td>
</tr>
</tbody>
</table>
Table 6. Coefficients of Rogers' (1972) genetic similarity for all populations of greater prairie-chicken examined in the Flint Hills (F) and southeast Kansas (S). For population location, refer to Fig. 1.

<table>
<thead>
<tr>
<th>Population</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Allen (S)</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. Bourbon (S)</td>
<td>0.986</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. Chase (F)</td>
<td>0.984</td>
<td>0.991</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. Butler (F)</td>
<td>0.978</td>
<td>0.989</td>
<td>0.992</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. Labette (S)</td>
<td>0.991</td>
<td>0.994</td>
<td>0.989</td>
<td>0.985</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. Linn (S)</td>
<td>0.990</td>
<td>0.992</td>
<td>0.986</td>
<td>0.985</td>
<td>0.994</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>7. Lyon (F)</td>
<td>0.980</td>
<td>0.987</td>
<td>0.989</td>
<td>0.987</td>
<td>0.986</td>
<td>0.986</td>
<td>-</td>
</tr>
</tbody>
</table>
Fig. 2. Phenogram (UPGMA) based upon Rogers' (1972) genetic similarity values summarizing the genetic relationships among populations of greater prairie-chicken in Kansas.
Table 7. F-statistics for each variable locus and the mean across all loci for greater prairie-chicken.

<table>
<thead>
<tr>
<th>Loci</th>
<th>$F_{st}$</th>
<th>$F_{is}$</th>
<th>$F_{it}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>ES-2</td>
<td>0.046</td>
<td>0.221</td>
<td>0.257</td>
</tr>
<tr>
<td>ADH</td>
<td>0.097</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td>A-GPD</td>
<td>0.056</td>
<td>0.267</td>
<td>0.308</td>
</tr>
<tr>
<td>Mean</td>
<td>0.049</td>
<td>0.256</td>
<td>0.292</td>
</tr>
</tbody>
</table>
DISCUSSION

DIET--The spring diet of the prairie-chicken was comprised of both plant and animal matter with less than 2% of the diet composed of animal matter and the remaining composed of plant material. Due to the early collection dates, few insects or spiders would be expected in the diet.

Agricultural seeds included sorghum and soybeans. Sorghum was found only in the diet of Flint Hills birds while soybeans were found in birds from both areas. Consumption of agricultural seeds is restricted by availability. Soybean fields were within 1 km of 2 Lyon County leks and prairie-chickens were observed flying to these fields. Baker (1953) found legumes constituted 20.5% of the diet in prairie-chicken collected in October from Anderson, Woodson and Coffey counties, Kansas.

Monocotyledons or grasses were found in the diets of both populations. Grasses comprised 4.2% and 13% of the diets of populations from the southeast and Flint Hills respectively. Due to the dates of collection of the birds these were thought to be mainly cool season grasses. None of the monocotyledons were identified as wheat although some birds in the southeast were collected on leks that were found on wheat fields.

Plant diversity, excluding woody species, in the 2 areas was site specific and cannot be generalized. Associated with this plant diversity, insect populations may also be expected to be more diversified and in greater
numbers (Jones 1963), thus allowing insects to be expressed in greater numbers in the diets.

Food habits of the greater prairie-chicken by Baker (1953) and Korschgen (1962) showed great variability in the types and amounts of food items eaten during different times of the year. Items such as soybean seeds varied from as great as 33% to a low of 1.2% of the diet. All types of foods were eaten including seeds, foliage, and animal matter. Seasonal variation of diets is dependent upon the availability of specific foods during different times of the year. In addition, certain foods may be scarce during drought years, yet plentiful in moist years as weather patterns change from year to year.

Food consumption analyses by Schwartz (1945) and Yeatter (1943) showed a wide variation in the amount of animal matter in the diet of the prairie-chicken. During the summer months, animal matter comprised nearly 50% of the diet, but was nearly absent the remaining months of the year. The low amount of animal matter consumed by prairie-chicken collected in this study is comparable to their findings, in that many insects and other invertebrates are not easily available for the prairie-chicken during the spring.

Food is not a serious limiting factor to prairie-chicken in Missouri (Korschgen 1962). The diets of the prairie-chicken in the Flint Hills and the southeast show
the same variability and tendencies of multiple food usage as grouse in other regions. Although used, cultivated crops were not the primary food source for the prairie-chicken, thus indicating adequate forage availability.

GUT MORPHOLOGY--Gut weights and lengths and gizzard weights of gallinaceous birds vary with the diet. Birds that eat coarser, more fibrous foods tend to have longer, heavier guts (Leopold 1953, Lewin 1963, Moss 1972, 1974), presumably because coarser foods demand greater intakes and digestive abilities. The variability in the measurements of the guts of birds, indicates differences in the digestibility of different foods eaten by separate populations (Moss 1983). Changes in the weight-length characteristics of the gastrointestinal tracts appear to be mainly the result of changes in the diet (Pendergast and Boag 1973). In those birds whose diet consists of hard material the gizzard is well developed with a powerful muscle and a thick abrasive inner membrane. When the food is soft, the gizzard muscle and lining membrane are thinner and lighter (Akester 1986). Olawsky (1987) found heavier gizzards in lesser prairie-chicken (Tympanuchus pallidicinctus) consuming shinnery oak (Quercus havardii) acorns as opposed to those not consuming the acorns, as the acorns generally require rigorous maceration before reaching a digestible state. Lewin (1963) reported that individuals
within populations exhibit digestive system characteristics that vary seasonally.

Savory and Gentle (1976) concluded that Japanese quail (Coturnix coturnix japonica) on different diets may adjust their guts to the size necessary to maintain a desired rate of digestion. The weights of the gizzards, and lengths and weights of the small intestines and caeca from both areas showed similar values. Although there was a significant difference in the amount of dicotyledonous foliage consumed between the 2 areas, no difference was found in weights or lengths of caeca and small intestine between collection areas indicating similar overall digestibility and nutrition in their diet. The differences in gizzard weights between areas, indicates that the Flint Hills population is consuming food requiring increased maceration, although overall digestibility seems equal. The nested analysis of variance indicates that much of the variance in digestive structures is due to differences among individuals within an area and not due to differences among populations or areas. This indicates that differences in gut morphology are not consistent between regions, but may reflect more individual differences in diet.

GENETICS--Study of geographic variation at allozyme loci in birds has lagged behind that of other vertebrate groups (Zink and Remsen 1986). The mean heterozygosity for prairie-chicken from the Flint Hills and the southeast was
0.025, which is lower than the mean heterozygosity for most birds (0.053) (Barrowclough 1983). Greater prairie-chicken in Kansas have passed through periods when large population numbers were restricted (Bunker 1913). In 1951 and 1952, the only legally hunted populations were in the Flint Hills (Horak, 1985), indicating relatively low numbers of prairie-chicken in other areas of the state. In 1980, the Kansas Fish and Game Commission survey of greater prairie-chicken distribution indicated populations in the Flint Hills were abundant compared to the southeast where greater prairie-chicken were rare to common (Horak 1985). During periods when population numbers in certain areas are decreased or isolated, genetic heterozygosity may decrease, resulting in inbreeding affects due to isolation and the returning of birds to traditional leks used by their ancestors. The phenogram from Rogers' genetic similarity shows 2 slightly distinct groups, the Flint Hills populations and the southeastern populations. The overall similarity value of greater than 0.98 is indicative of no real difference between these 2 groups. The low levels of $F_{st}$ indicate that the populations have not undergone significant differentiation, although high levels of differentiation has been attributed to restricted gene flow in some mammals (Avise et al. 1979). The relatively high $F_{is}$ value indicated some degree of inbreeding within leks, but in association with the low $F_{st}$ value is not likely to be
detrimental to the overall health of the birds within populations. The mean \( F_{Is} \) value across all loci for the 7 populations indicates that there is a deficiency of heterozygous individuals within the populations, which is probably a reflection of the mating system and social structure more than an indication of restricted gene flow due to habitat destruction.
MANAGEMENT IMPLICATIONS

The populations of greater prairie-chicken sampled from the Flint Hills and southeastern Kansas are basically similar in overall diet, gut morphology and genetics. The diets, and digestive tract lengths and weights of the 2 populations are comparable, indicative of generally adequate nutrition. The sampled populations were genetically similar with some inbreeding found within leks, which may be a function of individuals returning to the same ancestral leks each year. The polygynous mating system of the prairie-chicken may also contribute to this inbreeding as a small number of males are responsible for most of the breeding on the leks each year (Hammerstrom and Hammerstrom 1973). Inbreeding within the leks though seems to be of little importance due to overall similarity among all birds.

The vigor of the greater prairie-chicken in the Flint Hills and southeast Kansas is comparatively adequate. The small populations in the southeast are not genetically diverse from those in the Flint Hills. Any translocation of prairie-chicken, such as trap and release, from one area to another would have a neutral affect from a genetic standpoint. Analysis of land use from a dietary point may not provide useful information, due to similar gut morphology, although other factors such as vegetation for nesting and brood cover might indicate differences between areas. Factors other than the genetics and diets of
prairie-chicken seem to be responsible for the their low numbers in southeast Kansas.
SUMMARY

This study reports on the diet, gut morphology and genic analysis for the greater prairie-chicken. Two areas, the Flint Hills and southeast portion of Kansas were sampled representing 7 populations. Diet analysis indicated similar food habits, differing only in greater amounts of dicotyledonous foliage consumed in the Flint Hills. Small intestines and caeca showed no differences in length or weight, or differences in gizzard weight between areas. Horizontal starch-gel electrophoresis was used to examine genic variation at 22 loci. Mean levels of heterozygosity ranged from 0.008 in Bourbon County to 0.045 in Allen County. F-statistics showed 95% of total gene diversity was from differences in individuals with $F_{is}$ values indicating some inbreeding within leks. Genetic similarity showed some clustering by areas, but was thought to be due to the high degree of overall similarity in all individuals.
Literature Cited


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Signature of Author

7 May 1991

Date

Gut Morphology and Genetic Variation as Predictors of Population Vigor in the Greater Prairie-chicken, Tympanuchus cupido, in Kansas

Title of Thesis

Signature of Graduate Office Staff Member

Date Received