

JUVENILE LESSER PRAIRIE-CHICKEN GROWTH AND DEVELOPMENT IN SOUTHEASTERN NEW MEXICO

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ABSTRACT.—We examined growth rates and physical development of four body characteristics (mass, wing chord, bill length, and head width) of Lesser Prairie-chickens (*Tympanuchus pallidicinctus*) 3 to 111 days post-hatch in southeastern New Mexico. Growth rates, inflection points, and selected growth curves (logistic and Gompertz) associated with body mass and wing chord were similar between Lesser Prairie-chickens in New Mexico and Kansas. The asymptotic body mass (713 ± 7 g) was less for female and male yearling Lesser Prairie-chickens in New Mexico than for either yearling females or males in Kansas (male: 789 ± 4 , female: 719 ± 6). Juvenile Lesser Prairie-chickens in New Mexico achieved 90% of their asymptotic body mass 7 days faster than Lesser Prairie-chickens in Kansas. Received 18 October 2005. Accepted 9 October 2006.

Most populations of prairie grouse in North America have declined alarmingly (Silvy and Hagen 2004). In particular, the population size of Lesser Prairie-chickens (*Tympanuchus pallidicinctus*) has decreased by an estimated 97% since the 1800s; there has also been a 92% reduction in the species' historic range and a 78% reduction in occupied range since 1963 (Crawford 1980, Taylor and Guthery 1980). The status of the Lesser Prairie-chicken as "warranted but precluded" for listing as threatened or endangered under the Endangered Species Act (U.S. Department of Interior 2004) warrants a clear concern over this species, and as habitat becomes more fragmented it will be necessary to consider the importance of discrete populations.

Basic natural history data have become increasingly more important for formulating prairie grouse conservation plans. Natural history data provide a baseline for detecting demographic changes due to nutrition, genetics, climate, or other extrinsic factors. Until re-

cently, basic natural history data for Lesser Prairie-chickens, such as growth and development of juveniles were not available. Natal growth rates of Lesser Prairie-chickens have been described in Kansas at the northeastern extent of the species' distribution (Pitman et al. 2005). Thus, growth rates from the disconnected population in New Mexico may provide insight to developmental variability across the range of the Lesser Prairie-chicken. Growth and development data are essential for captive breeding efforts, evaluating development of birds considered for reintroductions, describing adaptive strategies for survival, and monitoring any changes in a population as a result of being genetically isolated.

Our objectives were to: (1) provide growth estimates at approximately equal time intervals for body mass, bill length, wing chord, and head width for juvenile Lesser Prairie-chickens in southeastern New Mexico; (2) describe growth rates of body mass and wing chord from hatch to the first breeding season; and (3) compare growth rates of Lesser Prairie-chickens between New Mexico and Kansas populations to answer questions regarding morphometric change through isolation that may only be detectable in growth analysis.

METHODS

Study Area and Chick Capturing.—Our study was conducted on 24,484 ha of relatively intact sand shinnery oak (*Quercus havardii*) habitat in southern Roosevelt County, New Mexico ($33^{\circ} 40' N$, $103^{\circ} 06' W$) during summers in 2002 and 2003. The area was used primarily for grazing and 86% of the land was

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privately owned. Public land included 3,296 ha of prairie-chicken management areas owned by the New Mexico Game Commission. Sand shinnery oak plant communities dominated the region (Peterson and Boyd 1998). The climate was semi-arid continental with an average frost-free growing period of 200 days extending from mid-April to late October (Wright 2003).

We captured 3- to 5-day-old chicks 1.5 hrs after sunrise by locating and flushing radio-marked females. Chicks were captured by hand and two randomly selected chicks from each brood were marked with radio transmitters (Holohil Systems, Carp, ON, Canada; 0.75 g, 30-day battery life; Larson et al. 2001). If any of the radio-tagged chicks were lost (i.e., predated, transmitter failure or both), an additional chick within a brood was captured and radio-marked. We measured body mass of all captured chicks to 0.5 g using a Pesola spring scale. Calipers were used to measure bill length and head width, and a wing chord ruler was used to measure wing chords to the nearest millimeter. Bill length was measured from the edge of the cere to the tip of the bill, and head width was measured directly behind the eyes (Baldwin et al. 1931). Unflattened wing chord was measured from the distal end of the carpal joint to the tip of the longest primary (Pyle 1997).

We used long-handled nets to recapture radio-marked chicks at both 30 and 90 days post-hatch. We attempted recaptures at night at 30 and 90 days post-hatch by locating radio-marked birds and individual chicks with spotlights. Morphometrics were recorded from recaptured birds and transmitters were replaced with models that had longer life-expectancies (Holohil Systems, Carp, ON, Canada; 2.0 g, 90-day battery life [30 days post-hatch]; Telemetry Solutions, Concord, CA, USA; 15 g, 20-month battery life [90 days post-hatch]).

Statistical Analysis.—We compiled a table of age-specific means and standard errors to report growth estimates for body mass, bill length, wing chord, and head width measurements at 5- or 6-day intervals. We fitted growth curves to describe and compare growth rates to prairie-chicken body mass and wing chord measurements. We used the two

most commonly applied growth equations for birds (Ricklefs 1973):

$$(1) \text{ Gompertz: } W = A \exp[-e^{-K(t-I)}] \quad \text{and}$$

$$(2) \text{ logistic: } W = \frac{A}{1 + e^{-K(t-I)}},$$

where W represents size (g or mm) at time t (days), A is the final size or asymptote, I is the inflection point at which 37% (Gompertz) or 50% (logistic) of asymptotic size is achieved, and K is a constant proportional to the overall growth rate (Ricklefs 1968, Zach and Mayoh 1982). We also report the time required to grow from 10 to 90% of the asymptotic body mass because K is not comparable directly between the Gompertz and logistic models (Ricklefs 1967). Wing chord at hatching is greater than 10% of the asymptote and we report the time required to grow from 50 to 90% (t_{50-90} ; Pitman et al. 2005) of the asymptote for that morphometric. All modeling procedures were completed using SAS, Version 9.1 (SAS Institute, Inc. 2003). Growth data for bill length and head width are lacking in the literature and we report only means and standard errors, and not growth rates for these two morphometrics.

Measurements from known-age birds (of unknown gender) were used to fit logistic and Gompertz equations to observed body mass and wing chord length data. We pooled data across both years because of small sample sizes. Parameters (K and I) were estimated by least squares using the Marquardt algorithm. We fixed A for both morphometrics using mean values of an equal number (males: $n = 16$, females: $n = 16$) of randomly selected spring-caught yearling male and female Lesser Prairie-chickens from another ongoing study at the same site (Sutton Avian Research Center, unpubl. data). Model fit was closely examined for birds <50 days post-hatching because these models were developed primarily to describe the early growth of juvenile Lesser Prairie-chickens. Model fit often was poor for this portion of the curve (measured from residual plots) due to heterogeneous variance between birds of different ages (morphometrics were more variable for older birds). Therefore, we placed greater weight on observations from younger birds during the modeling process (Draper and Smith 1981)

forcing the model to describe this portion of the curve more accurately. The model (and weighting if necessary) combination that provided the best fit (measured from residual plots and least sums of squares error) for birds <50 days post-hatching was selected as the final model.

Our models were created with non-independent observations (i.e., multiple measurements from broods and individual birds) and we used a bootstrap-resampling procedure (Manly 1998) to obtain 95% confidence intervals for each estimated parameter. We conducted 5,000 iterations where broods were resampled with replacement to match the total number of broods in the original data set. The selected model was refit to the resampled data set and all parameters re-estimated. Sampling distributions were developed for each estimated parameter and 95% bootstrap bias-corrected and accelerated (BCA) confidence intervals were taken from the resulting distributions (Pitman et al. 2005).

RESULTS

We measured body mass of 46 chicks in 15 broods, bill length of 43 chicks in 15 broods, wing chord of 43 chicks in 15 broods, and head width of 11 chicks in 4 broods. We recorded measurements from birds ranging from 3 to 111 days post-hatch. Means (± SE) were calculated at 5- or 6-day intervals (depending on sample size) for 11 growth periods prior to 111 days post-hatch (Table 1). Data were not collected at 16–24, 46–60, 66–100, and 106–110 days post-hatch.

The logistic equation best described gains in Lesser Prairie-chicken mass (Fig. 1A), whereas change in wing chord was best described with the Gompertz equation (Fig. 1B). Wing chord achieved 90% of asymptotic size 13.5 days faster than body mass using the inverse Gompertz and logistic growth equations, respectively.

DISCUSSION

The logistic and Gompertz growth equations, respectively, described body mass and wing chord growth patterns for juvenile Lesser Prairie-chickens in Kansas (Pitman et al. 2005) and for our study in New Mexico. Juvenile Lesser Prairie-chickens in New Mexico reached 90% of their asymptotic mass in few-

TABLE 1. Measurements (mean ± SE) of body mass, bill length, head width, and wing chord length for juvenile Lesser Prairie-chickens from hatch to 111 days post-hatch in southeastern New Mexico, 2002–2003. Time intervals of 5 or 6 days were used to summarize the data.

Age (days post-hatch) ^a	n	Mean age	Mass (g)	n	Mean age	Bill length (mm)	n	Mean age	Head width (mm)	n	Mean age	Wing chord (mm)
0–5	27	4.3 ± 0.2	19.4 ± 0.7	23	4.5 ± 0.1	8.7 ± 0.3	6	5 ± 0	15.3 ± 0.2	23	4.5 ± 0.1	40.1 ± 1.6
6–10	11	7.4 ± 0.4	32 ± 1.5	11	7.4 ± 0.4	10.3 ± 0.3	0	— ^b	—	11	7.4 ± 0.4	59.1 ± 1.8
11–15	2	11.5 ± 0.5	44 ± 2	2	11.5 ± 0.5	11.5 ± 0.5	0	—	—	2	11.5 ± 0.5	74.5 ± 2.5
25–30	6	28.2 ± 0.7	151.1 ± 12.1	6	28.2 ± 0.7	15.1 ± 1	3	27.7 ± 1.3	21 ± 1.5	6	28.2 ± 0.7	131.3 ± 5.1
31–35	1	31	177	1	31	16	0	—	—	1	31	140
36–40	2	36.5 ± 0.5	205 ± 41	2	36.5 ± 0.5	18.5 ± 0.5	2	36.5 ± 0.5	21.5 ± 1.5	2	36.5 ± 0.5	153 ± 11
41–45	2	42.5 ± 1.5	243 ± 18	2	42.5 ± 1.5	17.5 ± 0.5	1	41	24	2	42.5 ± 1.5	155.5 ± 3.5
61–65	0	—	—	1	61	20	0	—	—	1	61	196
101–105	2	103.5 ± 0.5	675 ± 25	2	103.5 ± 0.5	21.1 ± 1.1	2	103.5 ± 0.5	26.7 ± 1.9	2	103.5 ± 0.5	210.5 ± 9.5
111–115	1	111	770	1	111	16.9	1	111	26.4	1	111	217

^a No data were collected from chicks between 16–20, 46–60, 66–100, and 106–110 days post-hatching intervals.

^b Dashes indicate null values.

TABLE 2. Parameter estimates and 95% bootstrap bias-corrected accelerated confidence intervals (CI_L, CI_U) for equations describing growth of juvenile Lesser Prairie-chickens in southeast New Mexico, 2002–2003. Growth rate (K) and inflection point (I) were estimated through modeling using the logistic equation for mass and Gompertz equation for wing chord. Time (t) needed to grow from 10 to 90% of the asymptote is presented for mass and 50 to 90% of the asymptote for wing chord.

Morphometric variable	K			I			A^a			t
	Estimate	CI _L	CI _U	Estimate	CI _L	CI _U	Estimate	CI _L	CI _U	
Mass (g)	0.088	0.078	0.096	44	41	48	713	698	727	50
Wing chord (mm)	0.053	0.047	0.059	13	13	14	210	207	213	35
* Male mass (g)	0.078	0.056	0.094	48	52	55	789	—	—	57
* Female mass (g)	0.074	0.058	0.080	51	54	60	719	—	—	61

^a All asymptotes (A) were fixed in our modeling efforts. We estimated asymptotes by arbitrarily selecting a random sample of measurements from 32 juvenile males and females captured on leks the following spring. These values were pooled across genders and years to calculate means, standard errors, and sample sizes for body mass (713 ± 7 g, $n = 32$) and wing chord (210 ± 1 mm, $n = 32$).

* Data from Pitman et al. (2005).

er days (50 days) than gender pooled (54 days) birds in Kansas. However, growth rate estimates K and I were similar (New Mexico: $K = 0.088$, $I = 44$; Kansas: $K = 0.084$, $I = 47$), indicating rates of growth are approximately the same but asymptotic body size was greater in Kansas. In comparison to Kansas, faster growth rate and smaller asymptotic mass in New Mexico are consistent with Ricklefs' (1973) hypothesis about the inverse relationship between asymptotic body size and growth rate. However, our results remain speculative but consistent with the inverse relationship hypothesis because there are no data for the estimated day of inflection. Mean body mass of spring-captured male (789 ± 4 g) and female (719 ± 6 g) Lesser Prairie-chickens in Kansas (Pitman et al. 2005) were greater than our pooled estimate (713 ± 7 g) from New Mexico, suggesting that individuals in northern latitudes achieve greater body mass than those in southern areas. Latitudinal size differences within a species could be attributed to Bergman's Rule (populations in colder climates [higher latitude] have larger bodies than populations in warmer climates [lower latitudes]). However, food availability, genetics, adaptive survival strategies, or climate could contribute to this difference.

Inflection points for wing growth, in addition to differences in asymptotic body mass between the two populations of Lesser Prairie-chickens, approximately corresponded to initial flight capabilities in juvenile Lesser Prairie-chickens as wing chord measurements were 96.5% longer in 0–5 day-old chicks in New Mexico versus Kansas. However, the av-

erage age of birds from which measurements were taken in Kansas was 0.4 days post-hatch compared to 4.5 days post-hatch in New Mexico. Wing growth inflection points from Kansas (Pitman et al. 2005) and our study (12 and 13 days, respectively) were within the range of days when Lesser Prairie-chickens first begin to fly (7–14 days depending on how flight is defined; Ricklefs 1973, Giesen 1998), indicating the rapid period of wing chord growth occurs just prior to when flight capabilities are achieved. Had wing chords been measured identically between our study (not flattened) and Pitman et al. (2005) (flattened), the inflection points for wing chord may have been the same. Other galliform researchers (Milby and Henderson 1937, Lewin 1963) have reported similar flight ages ranging from 7 to 11 days. Our conclusion, that inflection point is indicative of flight capabilities in galliforms, could not be supported as they did not provide growth inflection points.

Our study, the first on growth and development of juvenile Lesser Prairie-chickens in southeastern New Mexico, yielded broadly similar results to that of Pitman et al. (2005). However, there were slight differences as asymptotic body size was greater in Kansas. We cannot identify the source of these differences, which could range from food availability to genetics (either through drift or local adaptation). These differences, however slight, should be monitored and considered if captive breeding programs are established in an effort to repopulate areas where Lesser Prairie-chickens have been extirpated.

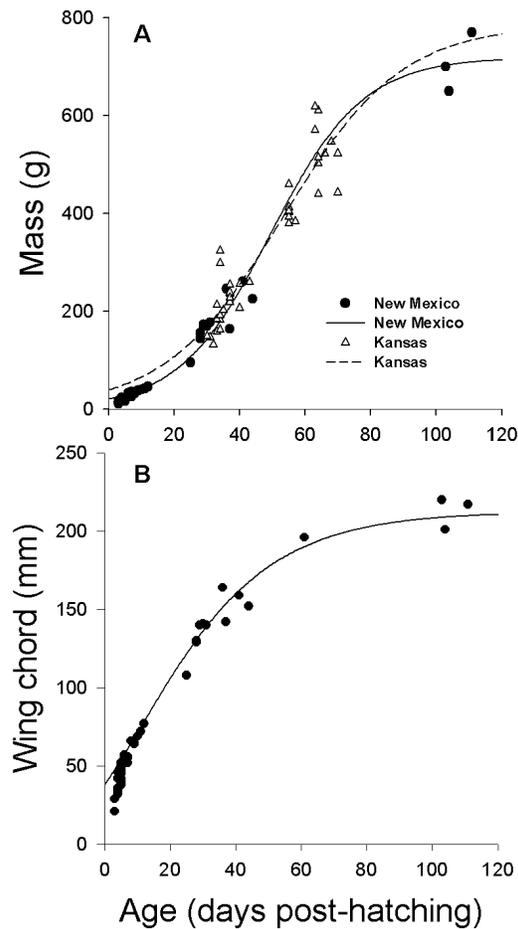


FIG. 1. Changes in Lesser Prairie-chicken body mass (A) (logistic equation, $n = 46$) and wing chord length (B) (Gompertz equation, $n = 43$) from 3 to 111 days post-hatch for birds in southeastern New Mexico, 2002–2003. Body mass of juvenile Lesser Prairie-chickens from southwestern Kansas is included in graph A (Pitman et al. 2005).

ACKNOWLEDGMENTS

We thank P. M. Kizer, W. L. Beggs, J. D. Weaver, and Jim Williamson for property access, and J. A. Sedgwick, C. E. Braun, and three anonymous reviewers for comments that substantially improved the manuscript. L. P. Altman, C. A. Carney, D. M. Davis, C. E. Dixon, J. A. Helm, K. M. Kasik, A. Z. Miller, J. E. Montagna, D. J. Riley, Fumiko Sakoda, C. R. Schermer, J. J. Sinclair, and T. R. Thompson assisted with trapping of prairie-chickens. Financial support was provided by the New Mexico Department of Game and Fish, U.S. Fish and Wildlife Service, National Fish and Wildlife Foundation, University of Oklahoma, Grasslands Charitable Foundation, and ConocoPhillips.

LITERATURE CITED

- BALDWIN, S. P., H. C. OBERHOLSER, AND L. G. WORLEY. 1931. Measurements of birds. Volume 2. Cleveland Museum of Natural History, Cleveland, Ohio, USA.
- CRAWFORD, J. A. 1980. Status, problems, and research needs of the Lesser Prairie-chicken. Pages 1–7 in Proceedings of the First Prairie Grouse Symposium, Stillwater, Oklahoma (P. A. Vohs and F. L. Knopf, Editors). Oklahoma State University Publishing and Printing, Stillwater, USA.
- DRAPER, N. R. AND H. SMITH. 1981. Applied regression analysis. John Wiley and Sons, New York, USA.
- GIESEN, K. M. 1998. Lesser Prairie-chicken (*Tympanuchus pallidicinctus*). The birds of North America. Number 364.
- LARSON, M. A., M. E. CLARK, AND S. R. WINTERSTEIN. 2001. Survival and habitat of Ruffed Grouse nests in northern Michigan. *Wilson Bulletin* 115:140–147.
- LEWIN, V. 1963. Reproduction and development of young in a population of California Quail. *Condor* 65:249–278.
- MANLY, B. F. J. 1998. Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall, London, United Kingdom.
- MILBY, T. T. AND E. W. HENDERSON. 1937. The comparative growth rates of turkeys, ducks, geese and pheasants. *Poultry Science* 16:155–165.
- PETERSON, R. S. AND C. S. BOYD. 1998. Ecology and management of sand shinnery communities: a literature review. General Technical Report RMRS-GTR-16. USDA, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- PITMAN, J. C., C. A. HAGEN, R. J. ROBEL, T. M. LOUGHIN, AND R. D. APPLGATE. 2005. Gender identification and growth of juvenile Lesser Prairie-chickens. *Condor* 107:87–96.
- PYLE, P. 1997. Identification guide to North American birds. Part I. Columbidae to Ploceidae. Braun-Brumfield, Ann Arbor, Michigan, USA.
- RICKLEFS, R. E. 1967. A graphical method of fitting equations to growth curves. *Ecology* 48:978–983.
- RICKLEFS, R. E. 1968. Patterns of growth in birds. *Ibis* 110:419–451.
- RICKLEFS, R. E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115:177–201.
- SAS INSTITUTE, INC. 2003. SAS/STAT software: changes and enhancements. Release 9.1. SAS Institute, Inc., Cary, North Carolina, USA.
- SILVY, N. J. AND C. A. HAGEN. 2004. Introduction: management of imperiled prairie grouse species and their habitat. *Wildlife Society Bulletin* 32: 2–5.
- TAYLOR, M. A. AND F. S. GUTHERY. 1980. Status, ecology, and management of the Lesser Prairie-chicken. General Technical Report RM-77. USDA, For-

- est Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- U.S. DEPARTMENT OF INTERIOR. 2004. Endangered and threatened wildlife and plants: review of species that are candidates or proposed for listing as endangered or threatened. Federal Register 69: 24875–24904.
- WRIGHT, E. 2003. Ecological site description: sandy. Pages 1–15 in USDA, Natural Resources Conservation Service. Site ID: R077XC055NM. <http://esis.sc.egov.usda.gov/>.
- ZACH, R. AND K. R. MAYOH. 1982. Weight and feather growth of nestling Tree Swallows. Canadian Journal of Zoology 60:1080–1090.