Am. Midl. Nat. 153:389–395

Survival and Growth of Northern Bobwhite Chicks in Western Oklahoma

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ABSTRACT.—Knowledge of chick ecology is essential for understanding and managing populations of northern bobwhites (*Colinus virginianus*). We report on chick survival and growth in western Oklahoma during 1997–2002. We used Cox proportional hazard models to estimate chick survival rate. Covariates included mass at time of capture, Julian day of capture and year. Chick mass was the only significant covariate in the model. Survival depended on time since capture because survival increased with chick mass, which concomitantly increased with time since hatch. Because of the dependence of survival on chick mass, we modeled chick growth as a function of age using a logistic model ($r^2 = 0.98$). Growth-rate was highest at day 35 post-hatch, which was around the mean capture-to-death survival time for chicks (30.0 ± 4.4 d SE). Our results suggest that the 30–35-d period post-hatching is a critical period in chicks' lives.

INTRODUCTION

The number of bobwhites in the autumn population is the sum of the number of adults and juveniles surviving through the breeding season. To date, adult survival has received the most research attention, and the survival rate of chicks is among the least investigated aspects of bobwhite ecology (Roseberry and Klimstra, 1984; Guthery, 2002). Knowledge of the demography of bobwhite chicks during the first few weeks of life is essential for understanding fluctuations in autumn populations.

For short-lived species such as the bobwhite, population growth rate is most sensitive to changes in fecundity (Lebreton and Clobert, 1991) and, in as much as it is related to fecundity, recruitment. For bobwhites, 66% of the variation in recruitment was explained by the number of chicks hatched per hen (fecundity) (Klimstra and Roseberry, 1975). Increasing juvenile mortality by 45% (from 15 to 60% mortality) had a 2.5× greater impact on recruitment than a 60% increase (from 20 to 80% mortality) in adult mortality (Roseberry, 1974). Roseberry and Klimstra (1984) suggested that, because of this relationship between fecundity and recruitment, juvenile survival might play a secondary role in determining autumn population size. However, the effect of juvenile survival on recruitment and autumn population size is still considerable; Roseberry (1974) reported that fecundity and juvenile survival were equally important to recruitment.

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Further, such information will provide wildlife managers with a better understanding of the ecology of the bobwhite. Our objectives were to model chick survival rates as a function of mass at capture, Julian day of capture and year. We used radiotelemetry to track individually marked chicks during 1997–2002. This allowed us to follow survival of chicks past the brood-rearing stage. We modeled survival using a Cox proportional hazards model. Given our best survival model, we then modeled the growth rate of bobwhite chicks as a function of time since hatch to better understand the relationship between mass and survival rate through time. We also derived an estimator of hatch-to-November survival of chicks that was independent of telemetry data; this was done to check telemetry-based survival estimates, which are usually biased low for bobwhites (Guthery and Lusk, 2004).

METHODS

Study area.—This study was part of a long-term (1991–2002) research program conducted on the Packsaddle Wildlife Management Area in southern Ellis County, 40 km north of Cheyenne, Oklahoma. The Packsaddle encompassed 6475 ha of mixed-grass prairie. DeMaso *et al.* (1997; and references therein) provided a detailed description of the Packsaddle.

Capture and telemetry.—This study was initiated in 1997 as an extension of the work done by DeMaso *et al.* (1997). However, rather than estimate chick survival by following radiomarked adults, we monitored radiomarked chicks continuously during 1997–2002 until death, disappearance or entrance into the adult population. Nests, found by following radiomarked adults, were monitored to determine hatch date, and chicks were caught 1–5 d after hatching. This was done by first triangulating the radiomarked adult's position at night around the suspected hatch date. After being located, the adult and brood were trapped by placing a 121-liter canister over them. The canister had a 30-cm diameter hole cut into the bottom that was covered with mesh netting with a slit in it to allow access to the chicks. Each chick was weighed to the nearest 2 g using a 200-g finger scale and marked with patagial bands (National Band and Tag Co., Newport, Kentucky, USA). Age was recorded as days from hatch. Chicks were recaptured at 12–23 d post-hatch by homing in on the radioed adult and using a 124.5 cm diameter net attached to a 3 m pole. Recaptured chicks were reweighed, and some were radiomarked with a 30–35-d transmitter (0.7–0.9 g, American Wildlife Enterprises, Monticello, Florida, USA; 1.2 g, Holohil Systems, Inc., Carp, Ontario, Canada) if the transmitter was $<5\%$ of the chick mass. Most transmitters were necklace-style transmitters, but 2–3 chicks received backpack-style transmitters during the first year of the study. In some cases, multiple recaptured individuals from the same brood were radiomarked without noting that they were in the same brood. Therefore, fates of some individuals (*i.e.,* those from the same brood) were not independent, but such non-independence should only bias estimates of variability in survival rate (Pollock *et al.*, 1989). After radiomarking, chicks were released and were relocated ≥ 5 d/wk, including the day immediately after tagging.

Statistical analyses.—We used the Cox proportional hazards model in SYSTAT version 10.2 (SYSTAT Software, Inc. Richmond, California, USA) to estimate survival between 1997 and 2001. The Cox proportional hazards model allowed us to incorporate covariates into the models. In addition to a model with no covariates, we also tested models with mass at time of capture, Julian day of capture and mass and Julian day of capture included as covariates. Because we were unable to achieve convergence for models including year as a covariate, we tested for year effects using ANCOVA with year as treatment and mass as covariate.

The Cox proportional hazard model is based on the assumption that covariates are not time-dependent (Lee and Wang, 2003). That is, the effect of the covariate (*e.g.,* mass) on survival is independent of time. Therefore, we tested this assumption by including an interaction term between the covariates and time. If the interaction term is not significant, then the covariate is not time-dependent and the Cox model is appropriate for the data (Lee and Wang, 2003).

We derived the following estimator as an independent check against survival estimated from telemetry data:

$$s_j = \frac{s_a R_f}{R_h},$$

where

s_j = the survival rate of chicks from median date of hatch to 1 November,
s_a = the survival rate of hens from the median date of hatch to 1 November,
R_f = the age ratio (juv/ad hen) on 1 November and
R_h = the age ratio (juv/ad hen) at time of hatch.

Data for estimating s_a and R_f came from Cox *et al.* (2004) and for estimating R_h from unpublished data collected during the Packsaddle study. We estimated s_a from age ratio data rather than from telemetry data because the telemetry estimates were biased low (Cox *et al.*, 2004). Adult survival is related to age ratio by:

$$S_a = 1/(1 + R),$$

where R is the age ratio (Guthery, 2002). The variable R_h was the product (nesting attempts/female) × (average chicks at hatch/attempt) × (probability of nest success).

Because our results (*see* below) indicated that mass, and therefore age, was a significant covariate in the survival model, we modeled growth rate as a function of age to better understand the dynamics involved in this relationship. We used the nonlinear modeling module in SYSTAT version 10.2 to develop the growth model. We used a logistic function,

$$y = \frac{A}{1 + e^{(-K(t-t_i))}},$$

where A = the asymptotic mass, K = the growth-rate constant of the equation, t_i = the inflection point in the growth curve and y = mass of chick at age t (Starck and Ricklefs, 1998). The growth-rate constant is directly related to the rate at which the chick mass approaches the asymptotic mass (Starck and Ricklefs, 1998). The asymptotic mass need not be equal to mean adult mass, but instead is the mass of the bird at the end of the growth curve (Starck, 1993). We used all chicks for which we had mass and age records (n = 136) in order to increase our chances of achieving convergence. We estimated all parameters from the data using the Marquardt technique, as recommended by Starck and Ricklefs (1998). We differentiated the resulting equation with respect to t to obtain the growth rate as a function of age.

RESULTS

Over the study period, 200 bobwhite chicks were radiomarked: 32 (16%) males, 28 (14%) females and 140 (70%) unknown sex. Therefore, we could not conduct sex-specific analyses for survival. Of the 200 chicks in the sample, 32 apparently slipped radio collars, 33 succumbed to presumptive capture-related mortality and 16 had unknown fates, leaving 119 suitable for survival analysis.

There was no year effect (P = 0.312) on survival, despite the significant covariate (mass) in the ANCOVA. The results of the Cox proportional hazards model indicated that mass was the only significant covariate (P = 0.005), and this covariate was independent of time ($P > 0.05$).

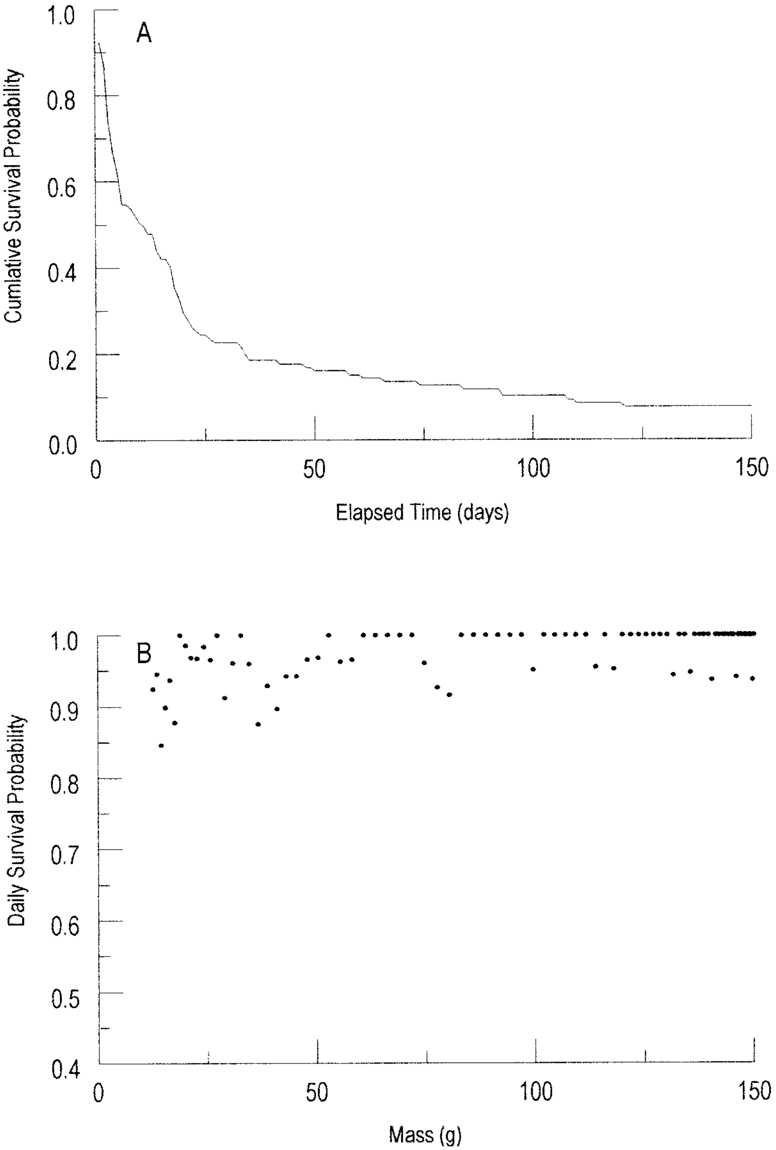

FIG. 1.—(A) Cumulative survival probabilities for bobwhite chicks at the Packsaddle Wildlife Management Area, Cheyenne, Oklahoma, 1997–2002, estimated from the Cox proportional hazard model. (B) Approximate daily survival of bobwhite chicks as a function of mass

Mean survival time from capture to death of chicks in the sample was 30 ± 4.4 SE d (n = 119). The cumulative survival curve indicated that survival leveled out at approximately 30–35 d after capture (Fig. 1A). This means that survival for chicks ≤ 30 days after capture was a function of time since capture. How much of this temporal dependence was due to chicks adjusting to transmitters is unknown.

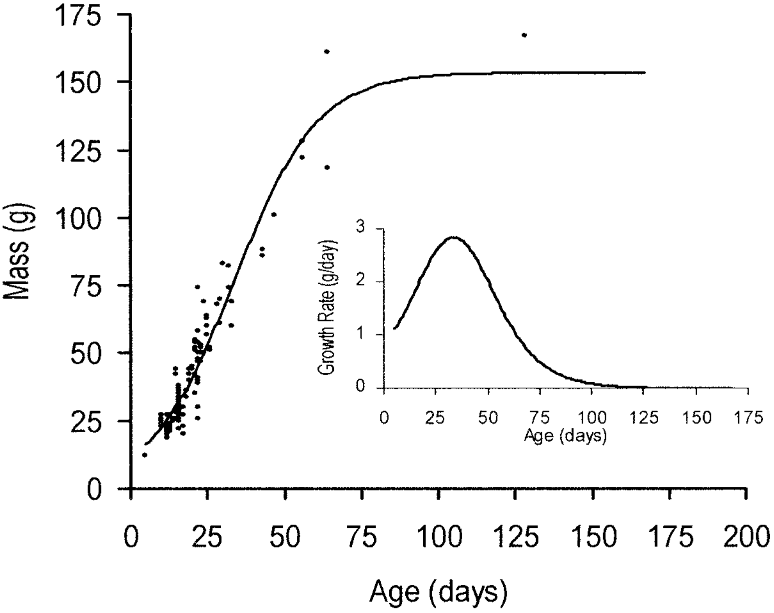

FIG. 2.—Logistic growth model (solid line) fitted to data for bobwhite chicks (filled circles) at the Packsaddle Wildlife Management Area, Cheyenne, Oklahoma, 1997–2002. Inset shows the derivative of the growth model relating growth rate as a function of age

The independent estimate of chick survival from median hatch date to 1 November was based on data pooled over the 1991–2002 study. The median hatch date was 19 June, resulting in an elapsed time of 135 d to 1 November. We observed 1.7 nesting attempts/hen (n = 117 females), 12.3 ± 0.29 chicks/nesting attempt (n = 161) and a probability of nest success of 0.48 ± 0.028 SE (n = 331). Based on age-ratio-derived adult survival, we estimated adult hen survival at 0.51 during 19 June–1 November. The average fall age ratio was about 11 juveniles/adult hen. These data translated to 135-d chick survival estimated at 0.56 (constant daily rate of 0.9957), which was substantially higher than telemetry-derived survival (Fig. 1A). The independent estimate is subject to uncertainty, which could not be estimated because of data pooling.

The logistic growth model ($r^2 = 0.98$, n = 136) was

$$y = \frac{153.5}{1 + e^{(-0.074(t-33.7))}}.$$

The derivative of the model indicated that the maximum growth-rate for chicks on the Packsaddle was 2.83 g/d and was achieved on day 35 post-hatching (Fig. 2). Growth rate became zero at approximately 145 d post hatching. Daily survival was low and variable at masses <50 g; it tended to stabilize near 1.0 for chicks >50 g (Fig. 1B).

DISCUSSION

The survival rate of chicks is generally thought to be lowest during the first 2 (pre-flight) to 4 (pre-thermogenesis) wk of life and to increase subsequently. DeVos and Mueller (1993) reported a daily survival rate of 0.9332 during the first 2 wk of life, which increased during the second 2 wk to 0.9596. DeMaso *et al.* (1997) observed a daily survival rate of 0.9526 during the first 20 d and 0.9983 during days 21–39. Other studies have reported higher survival rates than those reported above. Roseberry and Klimstra (1984) reported typical survival rates of 53–75% for the first 16 wk post-hatching. These rates translate into daily survival rates of 0.993–0.997. Our telemetry-independent estimate of survival over an approximately 19-wk period (56%, daily survival = 0.9957, 61.7% survival for 16 wk) was derived under logic similar to that of Roseberry and Klimstra (1984) and was within the range of their results. Suchy and Munkel (2000) monitored radiotagged chicks aged between 21 and 59 d. They reported a daily survival rate of 0.9943, or 52.7% for 16 wk.

Our survival model indicated that survival rate was an increasing function of mass, which in turn was an increasing function of age (Figs. 1, 2). The assumption that mass was independent of time held for our analysis because chicks of different ages and masses entered the sample continuously throughout the study period, but were given a common starting point (*i.e.*, day 1 after capture). Therefore, for any particular day, the effect of mass on chick survival was independent of time in days because chicks were of varying age.

An interesting point is that growth rate reached its maximum at around day 35 post-hatching (Fig. 2) and that survival became less sensitive to time since capture at around day 30. Since chicks were initially captured between 1 and 5 d after hatching, maximum growth occurred at roughly the same time that survival became independent of time since capture. This relationship was not completely surprising given the relationship between mass and survival. These data suggest that the first 30 d after hatching were the critical period for bobwhite chicks. We elected not to use a conditioning period for the dataset to account for the adjustment period because the adjustment process was insinuated into the development process of the growing chicks and information from the early stages of the bobwhite lifecycle are important to a full understanding of the bobwhite's ecology. However, the reader should note that survival was not independent of time since capture <30 d. It was not clear whether the dependence of survival estimates on time was due exclusively to changes in mass with age or to a prolonged conditioning period, or both.

We add one caveat to the interpretation of our survival analyses. Even after adjusting the survival estimates for the effects of mass, daily survival rates were extremely low (Fig. 1). Given a daily survival rate on day 1 of 0.924 and correcting it for a chick mass of 75 g we obtained an adjusted daily survival rate of 0.984. This translated to 16-wk survival of 0.164. This low survival rate further suggests that there was a prolonged period of stress associated with adjustment to radiotransmitter attachment. Our telemetry-independent estimate of survival supported this conjecture.

The telemetry-based survival rates reported herein were relatively low, which probably reflected the combined effects of adjustment to the radio package and changes in survival with increasing mass (*i.e.,* age). Nonetheless, evidence suggested that the first 30–35 d post hatching were critical in chicks' lives. This critical period is considerably longer than the 14 d period—when being relying on flight to escape predators (Stoddard, 1931)—commonly assumed to be most critical for bobwhite chicks. Management to increase survival during this period would enhance recruitment and, therefore, population abundance. Such management might entail cover manipulation that reduces exposure to predation and improves the availability and accessibility of invertebrate foods.

Acknowledgments.—Financial support for this publication was provided by the Federal Aid, Pittman-Robertson Wildlife Restoration Act under project W-149-R of the Oklahoma Department of Wildlife Conservation and Oklahoma State University. Logistical support was provided by the Oklahoma

Cooperative Fish and Wildlife Research Unit (Oklahoma Department of Wildlife Conservation, Oklahoma State University, USGS Biological Resource Division and Wildlife Management Institute cooperating). Additional support was provided by the Department of Forestry, the Department of Zoology, the Oklahoma Agricultural Experiment Station, Game Bird Research Fund and the Bollenbach Endowment. This paper was approved for publication by the Oklahoma Agricultural Experiment Station.

LITERATURE CITED

COX, S. A., A. D. PEOPLES, S. J. DEMASO, J. J. LUSK AND F. S. GUTHERY. 2004. Survival and cause-specific mortality of northern bobwhites in western Oklahoma. *J. Wildl. Manage.,* **68**:663–671.

DEMASO, S. J., A. D. PEOPLES, S. A. COX AND E. S. PARRY. 1997. Survival of northern bobwhite chicks in western Oklahoma. *J. Wildl. Manage.,* **61**:864–853.

DEVOS, T. AND B. S. MUELLER. 1993. Reproductive ecology of northern bobwhite in north Florida. *Proc. Natl. Quail Symp.,* **3**:83–90.

GUTHERY, F. S. 2002. The technology of bobwhite management: the theory behind the practice. Iowa State Press, Ames, Iowa, USA.

——— AND J. J. LUSK. 2004. Radiotelemetry studies: are we radio-handicapping northern bobwhites? *Wildl. Soc. Bull.,* **32**:194–201.

KLIMSTRA, W. D. AND J. L. ROSEBERRY. 1975. Nesting ecology of the bobwhite in southern Illinois. *Wildl. Monogr.,* **41**.

LEE, E. T. AND J. W. WANG. 2003. Statistical methods for survival data analysis, 3rd ed. John Wiley and Sons, Hoboken, New Jersey.

LEBRETON, J. D. AND J. CLOBERT. 1991. Bird population dynamics, management, and conservation: the role of mathematical modelling, p. 105–125. *In:* C. M. Perrins, J. D. Lebreton and G. J. M. Hirons (eds.). Bird population studies: relevance to conservation and management. Oxford University Press, Oxford, UK.

POLLOCK, K. H., C. T. MOORE, W. R. DAVIDSON, F. E. KELLOG, AND G. L. DOSTER. 1989. Survival rates of bobwhite quail based on band recovery analysis. *J. Wildl. Manage.,* **53**:1–6.

ROSEBERRY, J. L. 1974. Relationship between selected population phenomenon and annual bobwhite age ratios. *J. Wildl. Manage.,* **38**:665–663.

——— AND W. D. KLIMSTRA. 1984. Population ecology of the bobwhite. Southern Illinois University Press, Carbondale, Illinois.

STARCK, J. M. 1993. Evolution of avian ontogenies. *Curr, Ornithol.,* **10**:275–366.

——— AND R. E. RICKLEFS. 1998. Avian growth rate data set, p. 381–423. *In* J. M. Starck and R. E. Ricklefs (eds.). Avian growth and development: evolution within the altricial-precocial spectrum. Oxford University Press, Oxford, UK.

SUCHY, W. J. AND R. J. MUNKEL. 2000. Survival rates of northern bobwhite chicks in south-central Iowa. *Proc. Natl. Quail Symp.,* **4**:82–84.

SUBMITTED 13 APRIL 2004 ACCEPTED 15 JUNE 2004