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David L. Otis
Iowa State University

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A Framework for Reproductive Models of Mourning Doves

DAVID L. OTIS

U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Iowa State University, Ames, Iowa 50011

Population models can be used to aid in development and evaluation of harvest management strategies for game species. No current models are available for the Mourning Dove (*Zenaida macroura*), which is considered a migratory game bird in 37 states. A predictive model for annual reproduction is a necessary component of such a model. I used a simple construct based on parameters of the Mourning Dove breeding cycle to develop probability distributions of annual per capita reproduction for each of five geographical regions in the U.S. Confidence intervals for model predictions included average estimates from published studies in all regions except the southeastern U.S. Additional field studies will be required to produce contemporary estimates of model parameters and their spatial and temporal variation. A large-scale survey to estimate age ratios using wings from hunter-harvested doves could be used to evaluate and improve model predictions and structure, but additional research will first be necessary to calibrate harvest age ratios with realized annual productivity. Stochastic computer simulations of population models can be used to evaluate the sensitivity of predicted population trends to individual reproductive parameters.

INDEX DESCRIPTORS: Mourning Dove, *Zenaida macroura*, harvest management, reproduction model.

Informed harvest management of game species is dependent upon population models that can predict annual population numbers or rate of change as a function of demographic parameters of mortality and reproduction (Williams and Johnson 1995). The Mourning Dove is a game bird in 37 states in the contiguous U.S. Annual harvest of this resource exceeds the total harvest of all other migratory game birds combined (Baskett and Sayre 1993). However, no formal population models have been developed to assist in development of long-term harvest management strategies for maximizing harvest while maintaining sustainable population densities. As a first step toward this goal, historical band recovery data have been used to build a set of models that relate annual survival to harvest rates (Otis 2002). The analysis was based upon stratification of the contiguous U.S. into geographical subregions; therefore, survival rate predictions can be made on a regional scale. The objective of this paper is to present an initial model of annual reproduction that can be refined as new data are generated. These regional models can be coupled with survival models to produce a set of population models for use in regional-scale harvest management of Mourning Doves.

Published estimates of various parameters of the breeding cycle of Mourning Doves date back at least 80 years, and several summaries of these results have been compiled (Hanson and Kossack 1963, U.S. Fish and Wildlife Service 1977, Sayre and Silvy 1993). This collection of small scale, relatively short-term studies served to establish bounds on such parameters as length of the nesting season, young fledged per breeding pair, and nest density. However, lack of standardized field sampling methodology and the short study time frames precluded direct use of these data to construct general models of productivity on regional scales. The most comprehensive study of breeding in Mourning Doves was conducted in 1979 and 1980, for the primary purpose of estimating effects of September hunting on nesting success (Geissler et al. 1987). The study involved 106 sites in 27 states and represented the best source of information on nesting chronology and productivity among large-scale geographical units. However, the study was conducted during only two years, and data were pooled over years for analysis and presentation.

Estimates of annual recruitment, in terms of number of juveniles (hatching year; HY) per adult (after hatching year; AHY) in the pre-harvest population, can be derived from age ratios observed in the harvest, corrected for differential harvest vulnerability of age classes (Nichols and Tomlinson 1993). Harvest age ratios are usually derived from collection of wings from surveyed hunters, and long-term surveys are conducted by the U.S. Fish and Wildlife Service for waterfowl species and American Woodcock (*Scolopex minor*). In the case of waterfowl, age ratio data from wing surveys is a key component in development of reproductive models used in the adaptive harvest management program (Johnson et al. 1997). However, no long-term wing survey program has been instituted for Mourning Doves.

MODEL CONSTRUCTION

Mourning Doves are habitat generalists (Aldrich and Duvall 1958, Sayre and Silvy 1993) and, therefore, efforts to develop large-scale predictive models of reproduction based on habitat or landscape metrics are unlikely to be successful. Lack of long-term datasets on reproductive success also precludes development of mechanistic or phenomenological models useful for prediction at large scales. I, therefore, chose to use a simple conceptual model that relied on basic parameters of the breeding cycle and to use the best available estimates of these parameters from the literature to construct a set of initial predictive models.

Predicted reproductive rates (P), defined as the number of fledglings produced per breeding pair, were made using the following construct:

$$P = (L/C) \times F,$$

where L = length of the breeding season, C = average duration of a nesting cycle, and F = number of fledglings produced per nesting attempt (fledging rate). This construct is consistent with Lack (1966), who stated that "the number of broods raised by a bird each year depends mainly on the length of time for which conditions are

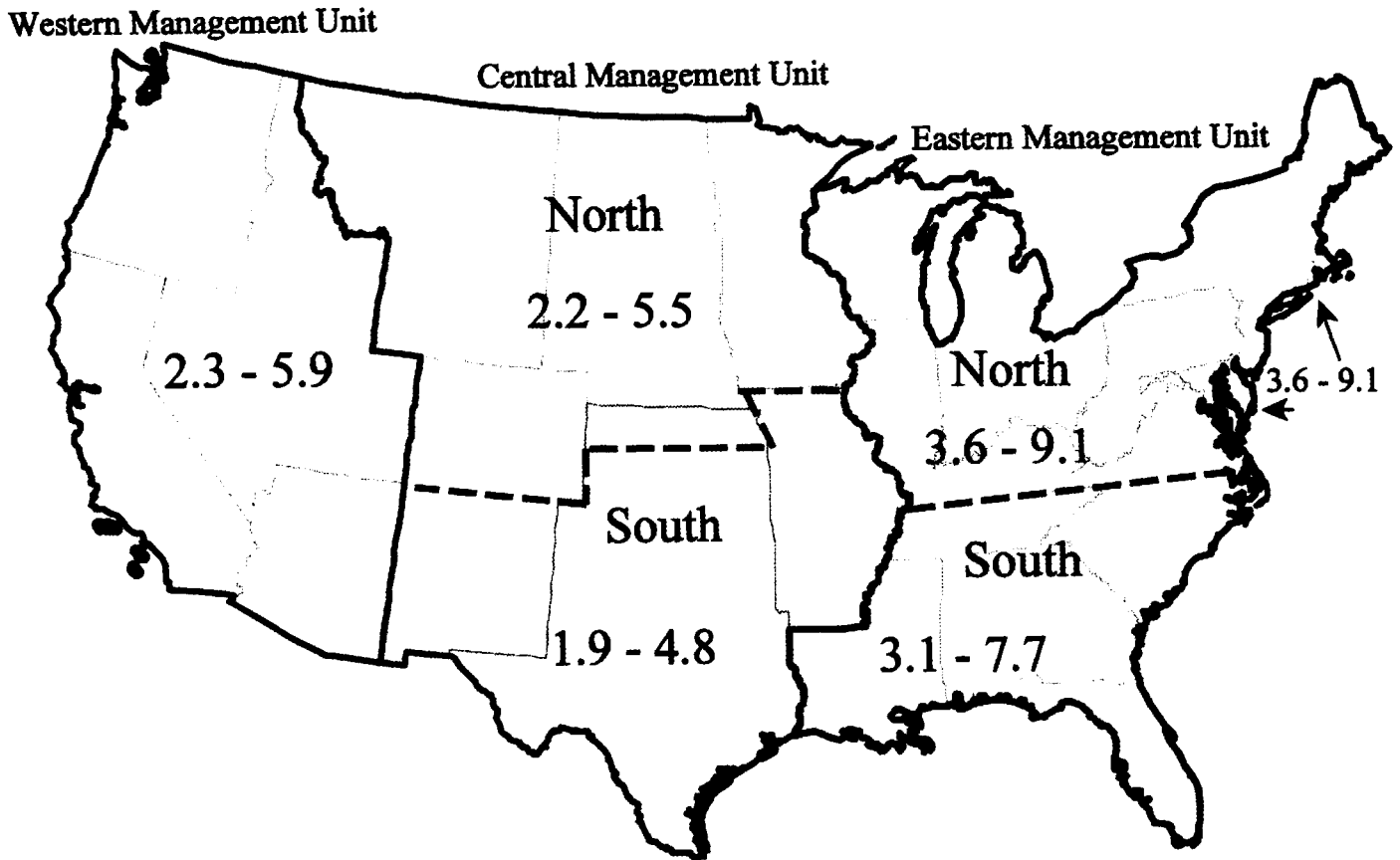


Fig. 1. Ninety-five percent confidence intervals for predicted annual Mourning Dove production per breeding pair within geographical regions of the U.S.

suitable for feeding young, and it may vary between populations of the same species.”

I assumed that L and F vary both spatially and annually, but that C is constant over time and space. The spatial scale was defined by the five regions used by Geissler et al. (1987) to summarize results of their national Mourning Dove nesting study (Fig. 1). The simplifying assumption of constant C was based on the premise that variation in this parameter was relatively small because of the physiological constraints of the species. Also, data in the published literature were inadequate for deriving estimates of variation for the parameters used in the calculation of C (see below). My objective was to produce a probability distribution for P for each region. The random variable P represents annual production, and, thus, a random observation from a regional probability distribution was a prediction for P in a given year. I assumed that P was normally distributed, and, therefore, two parameters, the mean and standard deviation (SD) were required to specify a given regional distribution.

I estimated C using the following parameters: duration of successful and unsuccessful nesting cycles, interval to the next nesting attempt following successful and unsuccessful attempts, and the nest success rate. Values from the literature for these parameters produced an estimate of 28 days for the expected length of a nesting attempt (Table 1).

Fledging rates were derived from data provided in Appendix C of Geissler et al. (1987, Table 2). Published estimates of fledging rates include 0.7 in Missouri (Drobney et al. 1998), 0.9 in California (Miller et al. 2001), 1.1 in Iowa (McClure 1943), and 1.2 in Illinois

(Hanson and Kossack 1963). Although Mourning Doves belong to the Order Columbiformes, it is interesting to note that these estimates are generally consistent with Lack's (1966:283) assertion that about 50% of eggs laid in open nests of passerines produced flying young. This generalization leads to an estimate of 1 fledgling/nest attempt, because Mourning Doves are determinate layers with a clutch size of two. Data are scarce for estimation of annual variation in F at any spatial scale. I derived a coefficient of variation ($CV = SD/mean$) from data reported in each of 3 multi-year studies of Mourning Dove reproduction (McClure 1943, Hanson and Kossack 1963, Miller et al. 2001), and used the resultant weighted average of $CV = 0.13$ to calculate an SD for F in each region.

Geissler et al. (1987) also provided nesting chronology data for their 5 geographic regions, and I used the middle 90% of the distribution of hatching dates to define a normal breeding season length (L). Although Mourning Doves have an extremely protracted nesting season, the extremes in nesting dates do not contribute significantly to overall production (Geissler et al. 1987). Again, data on annual variation in the range are nearly nonexistent. I used data from Hanson and Kossack's (1963) nine year study to estimate a $CV = 0.17$ for L and applied this estimate to all regions.

Using the parameter estimates described above, the average value of P and $SD(P)$ were calculated for each region, and 95% confidence bounds for an individual P were taken as $P \pm 2 \times SD(P)$. Because P is a function of L and F , both of which are random variables with associated variance, $SD(P)$ was derived using the delta method (Mood et al. 1974).

Table 1. Parameter values, citations, and calculation of average number of days in a nesting attempt (C) of Mourning Doves.

Parameter	Value	Citation
Length (days) of successful nesting cycle	32	Sayre and Silvey (1993)
Length (days) of unsuccessful nesting attempt ^a	16	—
Interval (days) until next nesting attempt if previous attempt successful	5	Swank (1955); Hanson and Kossack (1963); Westmoreland et al. (1986)
Interval (days) until next nesting attempt if previous attempt unsuccessful	6	Hanson and Kossack (1963)
Probability of nest success	0.40	Sayre and Silvey (1993); Drobney et al. (1998); Miller et al. (2001)
C ^b	28	

^aAssumed equal to 50% of the length of successful cycle

^b $C = 0.4 \times (32 + 5) + 0.6 \times (16 + 6)$

Table 2. Values of number of Mourning Dove fledglings per nest attempt (F) and the number of days in the breeding season (L) for regions of the U.S., derived from Geissler et al. (1987).

Region ^a	F	L
Eastern Management Unit (North)	1.02	175
Eastern Management Unit (South)	0.74	204
Central Management Unit (North)	0.81	134
Central Management Unit (South)	0.62	152
Western Management Unit	0.83	139

^aNational Mourning Dove harvest management is based on division of the U.S. into three management units: Eastern, Central, and Western (Reeves 1993).

Table 3. Expected values (P) and standard deviation (SD) of annual production per breeding pair for Mourning Doves in regions of the U.S.

Region	P	SD
Eastern Management Unit (North)	6.37	1.37
Eastern Management Unit (South)	5.39	1.16
Central Management Unit (North)	3.88	0.83
Central Management Unit (South)	3.37	0.72
Western Management Unit	4.12	0.89

RESULTS

The predicted average annual production was similar for regions in the Central Management Unit (CMU) and Western Management Unit (WMU), and considerably less than predicted production in the Eastern Management Unit (EMU, Table 3). Northern regions of the CMU and EMU had greater predicted average production than southern regions. Because CV estimates were used as the basis for calculating SD estimates, variation in P is necessarily greater for regions with greater expected production. This fact results in wider confidence limits for the EMU compared to the CMU and WMU. Average confidence interval width for the regional models was 3.98.

DISCUSSION

The collection of site and time specific studies of annual production of Mourning Doves produced estimates of P that varied greatly

due to a variety of factors, including environmental stochasticity, differences in methodology, and the inherent variation in parameters of the breeding ecology of a species that is a habitat generalist with a distributional range that includes much of North America. Thus, the wide confidence bounds for P in a given region and year produced by the models seem appropriate. Although comparison of the predicted expected values of the models to empirical estimates in the literature should be done cautiously due to the factors just mentioned, some coarse-level comparisons are useful for initial evaluation of the potential utility of the models. Sayre and Silvey (1993) presented a summary of production estimates from the literature, and their estimates of $P = 3.8$ for the CMU and $P = 4.4$ for the WMU coincide well with model predictions. However, model predictions for the EMU were much greater than their estimates of $P = 3.7$ for the northern EMU and $P = 1.8$ for the southern EMU. Any number of reasons could be proposed for these discrepancies, but it worthwhile noting that there were no sample sites in the northern tier of states in the EMU in the Geissler et al. study, which may have resulted in an overestimate of the length of the breeding season, and perhaps also biased fledging rate estimates for the northern EMU. Also, the summary estimates of Sayre and Silvey (1993) did not include an estimate of $P = 4.8$ derived by Martin and Sauer (1993) from a harvest wing survey in the EMU, or an estimate of $P = 5.7$ produced from a telemetry study in the southern EMU (G. Haas, unpublished data). These latter estimates are more consistent with model predictions, but discrepancies in these comparisons clearly suggest that special attention to refinement of model parameters in the EMU will be necessary.

The models presented here are intended to facilitate development of a long-term strategy for improvement of our understanding of the processes that influence Mourning Dove reproduction and the variation in the effects of those processes. The effects of large-scale land use and climatic change during the past 25 years on the magnitude and variation in Mourning Dove life history parameters are unknown. Research and monitoring studies that can provide contemporary estimates of these parameters are necessary to improve the validity of the models presented here and to modify their structure as appropriate. A large-scale program for collection of wings from hunters that provides data for harvest age ratio estimates is one obvious alternative for a monitoring program, although reliable quantitative relationships between harvest age ratio and production will require additional research effort.

The model presented can contribute in several ways to the greater goal of improving harvest management strategies for Mourning Doves. Confidence interval bounds for predicted production can be

coupled with regional survival models for purposes of comparing stochastic computer simulation estimates of population trends to available trend estimates from the national Call Count Survey (Dolton et al. 2002). In addition, the sensitivity of population models to factors such as breeding season length, perhaps modeled in turn as a function of weather parameters, can be evaluated. These exercises can be helpful in both improving our understanding of the population dynamics of the species and in prioritization of research initiatives in support of improved management.

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