

SIMULATIONS ON A COMMON CRANE POPULATION MODEL

JAVIER A. ALONSO

Cátedra de Zoología de Vertebrados, Facultad de Biología, Universidad Complutense
28040 Madrid, Spain

JUAN C. ALONSO

Museo Nacional de Ciencias Naturales, José Gutierrez Abascal 2, 28006 Madrid, Spain

J. SILVIO MARTÍNEZ-VICENTE

Instituto de Economía y Geografía Aplicada, Consejo Superior de Investigaciones
Científicas, Pinar 25, 28006 Madrid, Spain

LUIS M. BAUTISTA

Cátedra de Zoología de Vertebrados, Facultad de Biología, Universidad Complutense
28040 Madrid, Spain

ABSTRACT

A simple deterministic model describing the population dynamics of Western European common cranes *Grus grus* has been developed. Here we present an updated version of the model and test the effects of various natural and man induced events. Low hunting rates (5% of total population or 1,000 birds annually) do not significantly reduce the size of the population, due to the density-dependence of survival assumed in the model. High decreases in annual productivity (50%), small decreases in survival (10%), and certain catastrophic events result in the extinction of the population.

INTRODUCTION

Simulation modeling has been increasingly applied during recent years to wildlife ecology and management (Miller and Botkin 1974, Miller 1978, Johnson 1982, Verner et al. 1986). This technique is especially useful for understanding population dynamics of long lived species, given the difficulty in obtaining long series of demographic data, as well as in detecting and analyzing the effects of natural or man-induced events that affect these populations. Most of the living crane species seem to be declining, and some of them are endangered. Despite present conservation efforts, it will hardly be possible to plan future management actions without a previous understanding of the dynamics of crane populations. The common crane is particularly suitable for such investigations, as its present status enables the gathering of relatively extensive demographic information.

In this paper we present a second version of a simple population model (Alonso et al. 1986a) similar to those produced for the sandhill crane *Grus canadensis* (Miller et al.

1972, Johnson 1979), and simulate the responses of the population to various events affecting the survival and reproduction of cranes.

DEMOGRAPHIC PARAMETERS

Two of the parameters used in the model — population size and percentage of juveniles — were obtained during the last eight years (1979-1986) at the wintering areas of the species in Spain. The size of the Western European population has been estimated at around 40,000-50,000 birds (Alonso et al. 1986b and unpublished data; Prange 1984 and pers. comm.).

The percentage of juveniles was recorded each autumn, with the unweighted average for the eight years being 13.5% (Table 1). The adult:juvenile ratio was obtained at random, by counting unselectively all flocks as they were found in the field. This age-ratio is only valid and representative of the whole population if a large number of birds can be assigned an age each season in the same area and

time, and under approximately equal conditions. For a more detailed sample selection procedure see Alonso and Alonso (1987).

Other demographic data — age of first breeding, longevity, and mortality — are still not well understood, due mainly to few individually marked birds. Therefore the data available for the sandhill crane and whooping crane *G. americana* have been used for the common crane in our model. On the basis of recent literature reviews (Walkinshaw 1973; Johnsgard 1983) and captive crane flocks (Archibald pers. comm.) the age at first breeding is assumed to be four years.

Although cranes can live more than 40 years in captivity, most authors estimate maximum longevity of 20-25 years for natural populations (Walkinshaw 1973; Binkley and Miller 1980; Johnsgard 1983). We have assumed the existence of 24 age-classes for the common crane.

The constant adult mortality rates assumed in classic bird population studies (Deevey 1947; Lack 1966) are not in accordance with current longevity data from recoveries of banded birds. This is probably due to the existence of an age-dependent mortality effect (Miller et al. 1972; Botkin

and Miller 1974). In this model we use the age-specific survivorship values estimated for the whooping crane (Binkley and Miller 1980), which are based on annual censuses and age-compositions of that population recorded since 1938. A density-dependent effect on mortality that affects birds of every age and reproductive condition has also been included.

THE MODEL

The model we have developed is a very simple one, based on a sandhill crane model by Johnson (1979) but incorporating the age-dependent effect on survival rate. The program was written in Basic Apple Soft and has been operated successfully on an Apple II computer. Figure 1 shows the complete flowchart of the model, including (a) the assumed 24 age classes, (b) the distinction between the first three nonreproductive age classes and the other classes of sexually mature cranes, and (c) the type of curves (= reverse logistic functions) that govern the density-dependent effects on recruitment and survival rates.

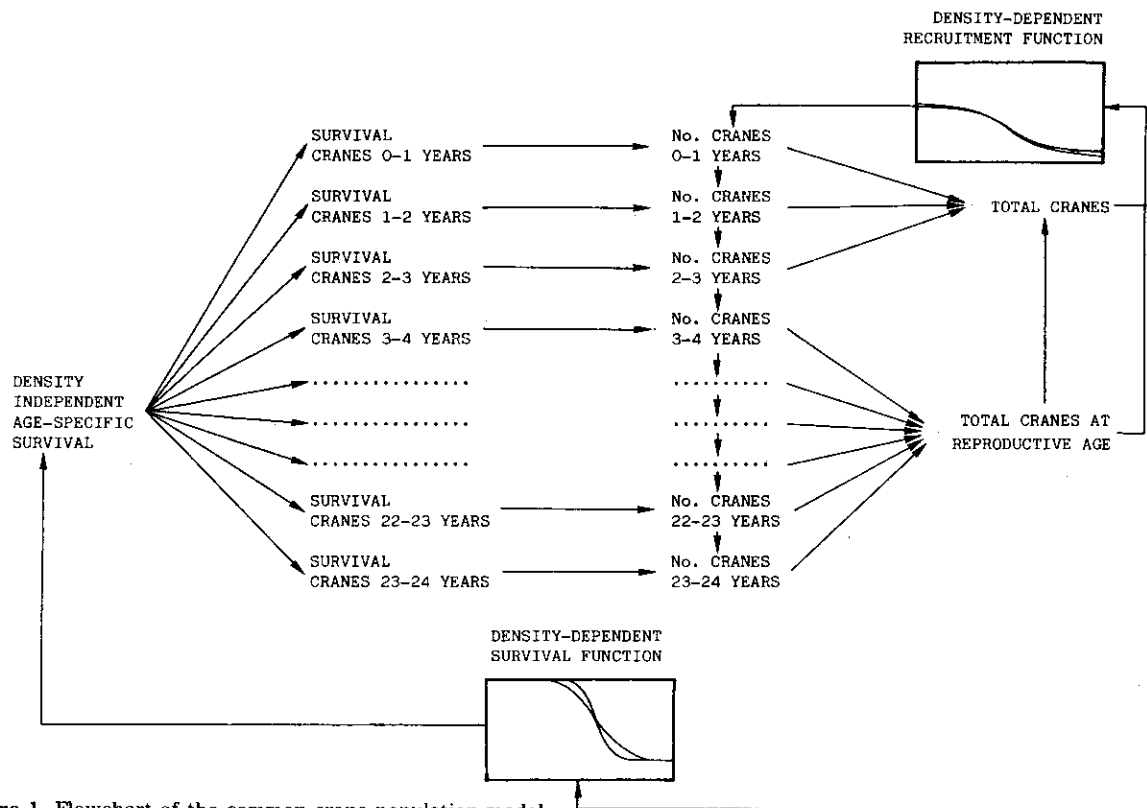


Figure 1. Flowchart of the common crane population model.

Year	1979	1980	1981	1982	1983	1984	1985	1986	Total
% Juveniles	12.48	12.95	14.17	12.12	11.67	12.34	19.02	13.27	13.50
Number of Cranes Aged	5,890	6,508	20,301	17,991	20,917	12,898	21,468	15,853	121,826

Table 1. Age composition of the western common crane population.

The crane population of level 1 (0-1 years old) is determined by the following equation:

$$\text{BIRTHS} = \text{BC} \times \text{P}$$

where BC = number of sexually mature cranes; and P = productivity, or annual recruitment rate.

In this way, reproduction is simplified in the present model to a single process that depends only on the breeding population and productivity expressed as recruitment of young birds to the winter population. The model ignores hatching and fledging success, for which no data are available. The subsequent age classes or levels are calculated as follows:

$$\text{For } I = 2 \text{ to } 24, C(I) = C(I-1) \times S(I-1)$$

where I = age class, or level; C(I) = number of cranes of age I; and S(I) = survival rate of cranes at age I.

These density-independent survival rates are assumed to be different for each age-class considered, due to the above mentioned age-dependent mortality effect. Each age-specific value is also affected by a reverse logistic function that accounts for the effect of population density. The survival rate declines at high population levels:

$$S(I) = \frac{S_m/S_M \times [1 - M(I)] + \frac{[1 - M(I)] \times (1 - S_m/S_M)}{1 + e^{[A \times (T - S_I / 1000)]}}}{1 + e^{[A \times (T - S_I / 1000)]}}$$

where S(I) = survival rate of cranes at age I; S_m/S_M = ratio between minimal and maximal assumed survival rates, i.e., lower and upper asymptotes of the logistic function; M(I) = density-independent mortality at age I, or natural rate of deaths due to accidents, predation, etc.; A = parameter that regulates the rate of decline of the logistic curve; T = total number of cranes in the population; and S_I = number of cranes at the inflection point of the curve.

Recruitment rates are also assumed to be density-dependent, varying from high values at low population densities to low values as the population grows:

$$P = \frac{R_M}{1 + e^{[B \times (T - R_I) / 1,000]}}$$

where p = recruitment rate of the population; R_M = maximal theoretical recruitment rate (see below); B = parameter that regulates the rate of decline; R_I = number of cranes at the inflection point of the curve and T as in the preceding equation.

This recruitment rate applies only to sexually mature birds, cranes at least four years old.

Each simulation starts with an initial population of 20,000 cranes. This initial population is assumed to have an age distribution identical to that calculated for the whooping crane by Binkley and Miller (1983). The model is then run for 50 years.

The initial values of the parameters A and B were estimated from the figures and equations given by Johnson (1979). Later, combinations of both parameters between 0.01 and 0.5 were tested. As these parameters govern the form of the logistic curve, it is virtually impossible to determine their values exactly with the data available at present.

S_m/S_M regulates the effect of population density on survival: high values of this parameter indicate low density-dependence of survivorship. We tested values of 0.5 to 0.9.

For S_I and R_I , various values around the real size of the crane population have been considered (35,000-60,000), with the assumption that the population is stable. The values for R_M were estimated in four different ways. (a) If we assume that each mature bird pairs in spring and each pair produces two chicks that survive until their first winter, then out of 100 cranes, 63.7 birds will be ≥ 4 years old (following Binkley and Miller 1983) and produce a maximum of 63.7 young, which will represent 39.1% of the next winter's population. (b) If instead of two young per reproductive pair we consider our field average of 1.35 young per pair (our own unpublished data), the maximum possible percentage of juveniles will be 30.1%, also assuming that all mature birds breed. (c) One may also assume that the annual recruitment observed for the whooping crane represents a maximal value, because the small population of this endangered species (18 birds in 1938, increasing to more than 100 at present) should stay at the left extreme of the density-dependent inverse logistic function of recruitment. The average for this species during the 43 years 1938-80 is 14.5% juveniles in the winter population. (d) We could also use the maximal percentage of juveniles observed for the whooping crane, which was 31.8% in 1939. We think, however, that possibility (d) may be influenced by the stochastic nature of the breeding process and should therefore be considered as an exceptionally high value, not representative for R_M in our deterministic model. Possibility (a) is also hardly representative, as it does not account for natural, density-independent losses of eggs and young up to the first winter when the simulation starts. Thus, we have tested as the most realistic values for R_M those values between 0.10 and 0.30.

RESULTS

We have tried a total of over 400 combinations of the parameters of the survival and recruitment functions, and have selected those (Table 2) that yield (a) stabilized populations between 40,000 and 50,000 cranes, and (b) percentages of juveniles of 13.50 ± 1.98 (= mean of the eight annual values measured in the field \pm 95% confidence interval).

The mathematical simplicity of the model is mainly a consequence of the few data available on the demography of the crane population and its deterministic nature is imposed by the scarcity of information on causal intercorrelations between environmental and population variables (see also Miller et al. 1972; Johnson 1979). The 12 combinations given in Table 2 represent only a selected sample of the series of plausible combinations that are consistent with the above mentioned conditions (a) and (b). Any of the 12 selected combinations of parameters (Table 2) can be used to simulate the behavior of the population in response to different environmental conditions or management situations. We have selected combination no. 12, which yields a total population and a percentage of juveniles closest to those observed in the field.

The main simulated scenarios (Figure 2) include the effects of hunting, variations in productivity, survival, and

age of first breeding, and a catastrophic decrease in the population size. All the experimental situations start after the twentieth year of the model unless otherwise stated.

1. Hunting Loss of 5% Cranes Annually (Figure 2A)¹

The 5% is assumed to be uniformly distributed among all age classes considered. The consequence will be a decrease in both the total number of cranes and percentage of juveniles by 2.4% and 3.1%, respectively, but both values will stabilize again in less than 10 years. These decreases are less than the 5% annual hunting harvest, due to the density dependent self-regulating capacity of the population.

2. Hunting Loss of 1,000 Cranes Annually (Figure 2B)¹

The 1,000 cranes are again uniformly harvested from all age classes. The effect is almost negligible: 0.4% decrease in the total number of birds and 1.6% in percentage of juveniles.

3. Productivity Reduced to 80% (Figure 2C)

A yearly reduction in the productivity due, for example, to human interferences in the breeding cycle (loss of breeding habitat through drainage or agricultural transformations, disturbances at nests, etc.) will cause an initial reduction followed by a slight recovery and stabilization at levels around 13% (for population size) and 11% (for percentage of juveniles) lower than those of the undisturbed population.

4. Productivity Reduced to 50% (Figure 2D)

The population could not stand such a yearly reduction and would therefore become virtually extinct (less than 150 birds) in about 20 years.

Trial No.	$S_m S_M$	A	S_I	R_M	B	R_I	Total Cranes	% Juv.
1	0.7	0.15	60,000	0.2	0.15	50,000	41,830	11.5
2	0.7	0.15	60,000	0.2	0.15	60,000	45,100	12.9
3	0.7	0.2	50,000	0.2	0.15	60,000	40,400	13.5
4	0.7	0.2	50,000	0.2	0.3	50,000	40,380	13.4
5	0.8	0.15	50,000	0.2	0.15	60,000	40,440	13.5
6	0.8	0.15	50,000	0.2	0.2	60,000	41,080	13.7
7	0.8	0.15	50,000	0.2	0.3	50,000	40,380	13.4
8	0.8	0.15	50,000	0.2	0.3	60,000	41,450	13.9
9	0.8	0.15	60,000	0.2	0.15	60,000	47,100	12.5
10	0.8	0.15	60,000	0.2	0.3	60,000	49,800	13.4
11	0.9	0.15	50,000	0.2	0.15	50,000	40,900	11.8
12	0.9	0.15	50,000	0.2	0.15	60,000	45,290	12.9

Table 2. Values of the model variables that yield stabilized population sizes and age ratios similar to those observed in the field.

¹Note: Simulations 1,2,6 and 7 do not consider negative influence of hunting on behavior, preferred areas, roosting routines, etc. Inclusion of these simulations does not imply endorsement of hunting of common cranes. The authors believe that hunting of cranes in Europe must remain strictly forbidden, and always subordinate to other cultural, scientific and aesthetic interests.

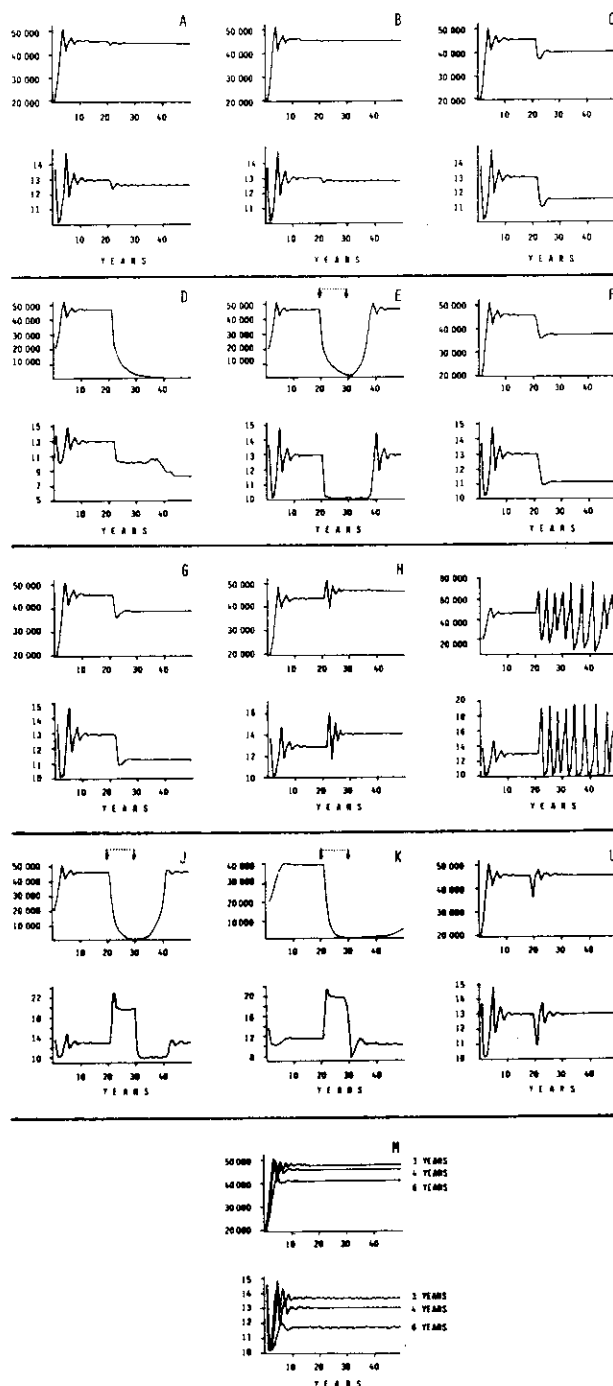


Figure 2. Experimental simulations on the model; trial no. 12 (from Table 2) has been used in all simulations. Each simulation represents a period of 50 years. Perturbations of the original model, representing various environmental disturbances, act from year 21 on, except in E, J, and K, in which the disturbance is maintained only between years 20 and 30 (arrows and dotted lines on top of graphs). Each pair of graphs is the result of one simulated scenario: the upper graph of each pair represents the population size, and the lower, the percentage of juveniles. Simulation M shows together the results for the three ages of first breeding considered.

5. Productivity Reduced to 50% for 10 Years (Figure 2E)

In the case of a 50% decrease in productivity in effect only for 10 years, the population would theoretically recover, according to the model. We think, however, that it might be impossible for a natural crane population to recover after decreasing to such a low number of individuals.

6. Hunting Loss of 5% Cranes Annually Plus Reducing the Productivity to 80% (Figure 2F)¹

This simulation combines the effect of simulations 1 and 3. The resulting reduction in the population size (-18%) is slightly higher than the sum of the isolated effects of 1 and 3 (-16%).

7. Hunting Loss of 1,000 Cranes Annually Plus Reducing the Productivity to 80% (Figure 2G)¹

Here the combined disturbances result in a decrease equivalent to the sum of both isolated effects.

8. Productivity Increased to 120% (Figure 2H)

If a management effort could succeed in increasing productivity each year by 20%, the benefit for the population would be an increase of only around 8%. This result is again due to the density-dependent regulating capacity of our population model. Interestingly, prior to stabilization of the population, there is a period of around 5 to 10 years of high oscillations — both in percentage of juveniles and in population size — which was almost absent in the case of an equivalent reduction (simulation 3 and Figure 2C).

9. Productivity Increased to 150% (Figure 2I)

This increase is too high for the population to reach stabilization, either in number of birds or in percentage of juveniles, given the relatively small self-regulating capacity imposed by the survival equation in our model (i.e., $S_m/S_M = 0.9$). Values of S_m/S_M smaller than 0.9 (i.e., a higher self-regulating capacity for the population) would allow a more rapid stabilization.

10. Survival Reduced to 90% for 10 Years (Figure 2J)

The population would become virtually extinct, as in simulation 5. Interestingly, the result of this simulation is not similar to that of simulations 1 and 2 (hunting). In the hunted population, survival increases — as a consequence of the density-dependence of both survival and productivity — as the total number of birds decreases, while in the present case the possibility of survival rates to compensate for the simulated situation is suppressed by the very terms of this simulation.

11. Survival Reduced to 90% Plus Productivity Reduced to 80%, for 10 Years (Figure 2K)

This is a combination of simulations 3 and 10, representing a general deterioration of environmental conditions,

during breeding and also through the rest of the annual cycle of the birds. Again, the result would probably be the extinction of the population.

12. Catastrophe: 10,000 Cranes Killed (Figure 2L)

If a portion of the crane population were killed as a consequence of an accident, this model predicts a rapid recovery and stabilization at the original population level. This recovery, however, appears too fast to be true in a natural crane population, for which the most realistic result of such an event would be the virtual extinction of the population. As the rapid recovery of the population after a perturbation results from the high stability of the model, being closely dependent on the density-dependence survival function, the parameters defining this function should be reexamined.

13. Influence of Age of First Breeding (Figure 2M)

If the age of first breeding were six years, instead of the assumed four years, the change would only be a stabilization of both the population size and the percentage of juveniles at lower levels (around 10% lower). In the case of first breeding at three years the stabilization levels would be about 5% higher.

DISCUSSION

The simple model developed should be considered, together with a previous draft (Alonso et al. 1986a), as a first attempt to describe the common crane population dynamics. The series of combinations of values presented in this paper (Table 2) do not exclude the possibility that other equally valid parameter combinations exist. The main limitations of the model derive from the difficulty in obtaining demographic data in the field. This limitation is not only due to the difficulty of accurately measuring demographic variables in wild populations, but also because of the long series of annual data necessary. This problem is especially true in the case of mortality rates, for which only crude estimates are available from recoveries of banded sandhill and whooping cranes, as well as for other long-lived bird species.

In our opinion, one of the short-comings of our model is the rapid response of the population to perturbations affecting the total number of birds, i.e., its high stability. Wild crane populations probably have a lower ability to recover from perturbations increasing mortality, and the effects of such perturbations last for a longer time than our model predicts. The rapid recovery is probably a consequence of the high sensitivity of the density-dependent survival function, determined by the high magnitude of the difference between upper and lower asymptotes of the inverse logistic curve. Indeed, the models developed for sandhill cranes differ mainly in the relative importance given by their authors to the density-dependent regulation of survival rates. While some authors have proposed models that are highly sensitive to alterations in the density of birds, with

survival increases of up to 30% at lower population densities (Johnson 1979), others use such low values (2×10^{-5}) that the effect is almost negligible (Miller et al. 1972; Miller 1974; Miller and Botkin 1974). The importance of both features of the model — the magnitude of the density-dependent effect on survival, and the form of the function (linear, logistic) — is evident when the model is perturbed: a high density-dependent regulation ability enables the population to recover quickly from hunting, while a low density-dependent regulation ability prevents such a quick recovery at even the lowest hunting rates. This variability makes it difficult to predict accurately the effects of human disturbances like hunting. The almost negligible effect of hunting on the population presented in this paper should therefore be interpreted with extreme care.

In the case of the function regulating the density-dependent response of productivity rate, the critical values are much better known. The series of annual recruitment values recorded, together with the data from other bird species, help us model this effect more realistically. In our

model, values for R_M (= maximal theoretical recruitment rate, or upper asymptote of the density-dependent inverse logistic function) below 0.1 (i.e., less than 10% juveniles produced yearly) result in the extinction of the crane population for every numerical combination of the other five parameters (see also Alonso et al. 1986a). Values higher than 0.2 cause high oscillations in population size and percentage of juveniles. It is interesting to observe that all values of annual recruitment measured in the field in our crane population, and the most realistic values inferred for our species as well as for other crane species, fall within these limits. This not only supports the validity of the model but also suggests similar demographic structures in the various crane species for which population data are available.

In spite of the difficulties, the model presented enables future incorporation of submodels and variables that better represent demographic features or account for new effects, thus providing a basis for future research as well as guidelines for the management and conservation of the European population of the species.

ACKNOWLEDGMENTS

We thank M. Quintanilla for assisting us with the computer programming. This project was financed by ICONA. Additional financial aid while in the field was obtained from ICBP, the Dirección General de Medio Ambiente (MOPU), and CAICYT Project No. 22107-01. Travel costs to China were in part covered by the Ministerio de Asuntos Exteriores, the Ministerio de Educacion and the C.S.I.C.

REFERENCES CITED

- Alonso, J. C., J. A. Alonso, and M. Quintanilla. 1986. Modeling the common crane (*Grus grus*) population wintering in Iberia. Pages 303-318 in J. Aracil, J. A. D. Machuca, and M. Karsky, eds., System dynamics: on the move. The 1986 International Conference of the System Dynamics Society, Sevilla, Spain.
- Alonso, J. A., J. C. Alonso, and F. J. Cantos. 1986. On the size of the common crane *Grus grus* population migrating through Western Europe. *Ornis Fennica* 63: 58-59.
- Alonso, J. A., and J. C. Alonso. 1987. Demographic parameter of the common crane *Grus g. grus* population wintering in Iberia. *Aquila* 93: 137-143.
- Binkley, C. S., and R. S. Miller. 1980. Survivorship of the whooping crane, *Grus americana*. *Ecology* 61: 434-437.
- Binkley, C. S., and R. S. Miller. 1983. Population characteristics of the whooping crane, *Grus americana*. *Canadian Journal of Zoology* 61: 2768-2776.
- Botkin, D. B., and R. S. Miller. 1974. Mortality rates and survival of birds. *American Naturalist* 108: 181-192.
- Deevey, E. S., Jr. 1947. Life tables for natural populations of animals. *Quarterly Review of Biology* 22: 238-314.
- Johnsgard, P. A. 1983. *Cranes of the world*. Croom Helm. London. 258 pp.
- Johnson, D. H. 1979. Modeling sandhill crane population dynamics. U.S. Fish and Wildlife Service, Special Scientific Report, Wildlife 222. 10 pp.
- Johnson, D. H. 1982. Population modeling for furbearer management. Pages 25-37 in G. C. Sanderson, ed., Midwest furbearer management. North Central Section, Central Mountains and Plains Section, and Kansas Chapter of the Wildlife Society.

- Keil, W. 1970. Untersuchungen über den Zug des Kranichs von Herbst 1966 bis Frühjahr 1970. *Emberiza* 2: 49-60.
- Lack, D. 1966. Population studies of birds. Clarendon, Oxford. 341 pp.
- Miller, R. S. 1978. Population modeling as an aid to designing management programs. Pages 413-417 in S. A. Temple, ed., *Endangered birds: management techniques for preserving threatened species*. University of Wisconsin Press, Madison.
- Miller, R. S., and D. B. Botkin. 1974. Endangered species: models and predictions. *American Scientist* 62: 172-181.
- Miller, R. S., D. B. Botkin, and R. Mendelsshon. 1974. The whooping crane (*Grus americana*) population of America. *Biological Conservation* 6: 106-111.
- Miller, R. S., G. S. Hochbaum, and D. B. Botkin. 1972. A simulation model for the management of sandhill cranes. *Yale University School of Forestry and Environmental Studies Bulletin* 80. 49 pp.
- Prange, H. 1984. Der Kranichzug in Thüringen und seine Einordnung in die Mitteleuropäische Flugroute. *Thür. Ornithologische Mitteilungen* 32: 1-16.
- Verner, J., M. L. Morrison, and C. J. Ralph, eds. 1986. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison. 480 pp.
- Walkinshaw, L. H. 1973. *Cranes of the world*. Winchester Press, New York. 370 pp.