

MODELING THE COMMON CRANE (Grus grus) POPULATION WINTERING
IN IBERIA

Juan C. Alonso

Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain

Javier A. Alonso

Facultad de Biología, Universidad Complutense, Madrid, Spain

Manuel Quintanilla

Instituto de Economía Agraria, CSIC, Madrid, Spain

Abstract. A field study carried out during the last seven years on a wintering population of Common Cranes (Grus grus) in Spain allowed us to gather accurate field data on certain relevant demographic parameters: (a) the size of the Western Palearctic population of this species is estimated to be around 40000 birds, and (b) the age composition in autumn is estimated for 1979-85 to be around 13.5% young. These data enabled us to develop and test a population dynamics model which combines the density- and age-dependent effects on productivity and survival rates. The parameters of the productivity and survival functions were varied within biologically reasonable limits. From the series of possible combinations we selected those that fitted our field data on population size and age structure best. Each variable was then varied to study their influence on the model.

INTRODUCTION

One of the fields in which mathematical models have been increasingly applied during the last years is wildlife ecology and management (e.g. Miller and Botkin 1974, Miller 1978, Johnson 1982). The complexity of animal population dynamics and the difficulty in measuring the many parameters involved, such as productivity and mortality rates, longevity, age of reproductive maturity and the effects of population density and age on them, make it very difficult to obtain a series of data long enough to detect and analyse the effects of natural or man-induced events that affect these animal populations. Mathematical models help understand the structure and function of the latter. This is particularly interesting in the case of vertebrate species that are K-strategists, i.e. have long maximum longevities, delayed reproductive maturities, low rates of increase and long generation times and, therefore, low replacement rates. This paper presents a first attempt to develop a population dynamic model for one of these species, the Common Crane (Grus grus), similar to those produced for the Sandhill Crane (Grus canadensis) (Miller et al. 1972, Johnson 1979) and the Whooping Crane (Grus americana) (Miller et al. 1974).

DEMOGRAPHIC PARAMETERS OF THE CRANE POPULATION

While some of the demographic parameters of the Common Crane

have been recorded quite accurately during the last years, others remain unknown, mainly due to the lack of individually marked birds.

Field data

Two of the parameters used were obtained by two of us (J.C.A., J.A.A.) during 1979-85 at Gallocanta, one of the most important wintering areas of the Western Common Crane population.

Population size. During the last decades some authors have tried to census the Western European Crane population. The results are diverse and confuse: some are only partial censuses in staging areas, reaching maximal figures between 25000 and 30000 birds (e.g. Keil 1970, Alerstam and Bauer 1973); others are estimations in more or less wide areas of the species' breeding range. Only recently has it been possible to count the migrants while leaving Iberia in spring, with a total of 31945 birds (Alonso *et al.* 1986). Assuming a certain error in minus, we estimate in around 40000 cranes the size of this population, which coincides with estimations recently made in Central Europe (Prange 1984, and in litt.).

Winter age composition. Only two age classes can be distinguished in the field by their plumage, here called adults and juveniles. In the "adult" category we included all cranes in nonjuvenile plumage, i.e. more than one year old. The birds less than one year old were included in the "juvenile" category. The adult:juvenile ratio was recorded at random, including 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 aged each season in the same area and time and under approximately equal conditions. The study area was surveyed regularly throughout the whole season. In total we aged over 125000 cranes, of which only the 105973 aged during autumn migration and early spring migration are used in this study. For a more detailed sample selection procedure see Alonso & Alonso (*in press*). The unweighted average for the seven years is 13.54% (Table 1).

Table 1. Age composition of the Western Common Crane population

Year	1979	1980	1981	1982	1983	1984	1985
% juveniles	12.48	12.95	14.17	12.12	11.67	12.34	19.02
No. cranes aged	5890	6508	20301	17991	20917	12898	21468

Data from other sources

Some of the data necessary to develop a population dynamics model are very poorly known or still unknown, like age of

first breeding, longevity and mortality. It would be very time-consuming to significantly increase the accuracy of these data. Therefore, as some acceptable data for these parameters are available of other crane species of the same genus, we have used them in the model.

Age of first breeding. Common Cranes have been reported to lay eggs at an age of three years, but on the basis of recent literature revisions (Walkinshaw 1973, Johnsgard 1983) and captive breeding experiences (Archibald pers. comm.) we assumed that they reach sexual maturity at an age of four years.

Longevity and mortality. Although there are some literature records of several species of cranes living more than 40 years in captivity, authors generally estimate maximum longevities of 20-25 years for natural populations (Walkinshaw 1973, Johnsgard 1983), and Binkley & Miller (1980) recently utilized 24 age-classes. We also assumed the existence of 24 age-classes.

Most classic bird population studies assumed constant adult mortality rates (Deevey 1947, Lack 1966). However, these are not in accordance with longevity data for certain species for which nowadays enough recoveries of banded birds are available. It seems more reasonable to assume an age-dependent mortality effect (Miller et al. 1972, Botkin & Miller 1974). A density-dependent effect on mortality is also generally accepted, which affects birds of every age and reproductive condition. Common Cranes have not yet been banded, for which there are no reliable data on the magnitude and causes of mortality. Some data are available for the Sandhill Cranes (Johnsgard 1983) although such values are surely overestimated due to the effect of hunting. Therefore we have used the age-specific survivorship values estimated for the non-hunted population of Whooping Cranes by Binkley & Miller (1980). These are based on annual censuses and age compositions of that population conducted since 1938.

MODEL DESCRIPTION

The model we have developed is a very simple one that describes the population dynamics of the species. The program was written in Basic Apple Soft and has been operated successfully by one of us (M.Q.) on an Apple II computer. Figure 1 presents a simplified causal diagram which accounts for the density-dependent effects of the population size on annual recruitment and survival rates. Figure 2 shows the complete flowchart of the model, including (a) the assumed 24 age-classes (see above, "Demographic parameters"), (b) the distinction between the first three nonreproductive age-classes and the rest of sexually mature cranes, and (c) the type of curves (=reverse logistic functions) that govern the density-dependent effects on recruitment and survival rates.

The crane population of level 1 (GOO, see Appendix) is determined by the following two equations:

$$\text{NAC} = \text{GTER} * \text{PRD}$$

where NAC = number of births; GTER = number of sexually

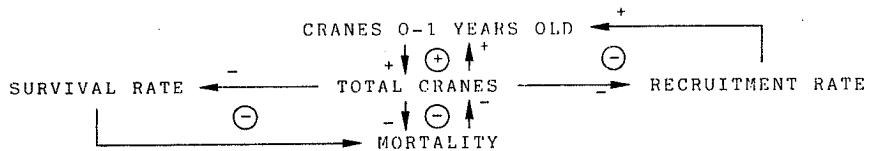


Figure 1. Simplified causal population model for the Common Crane.

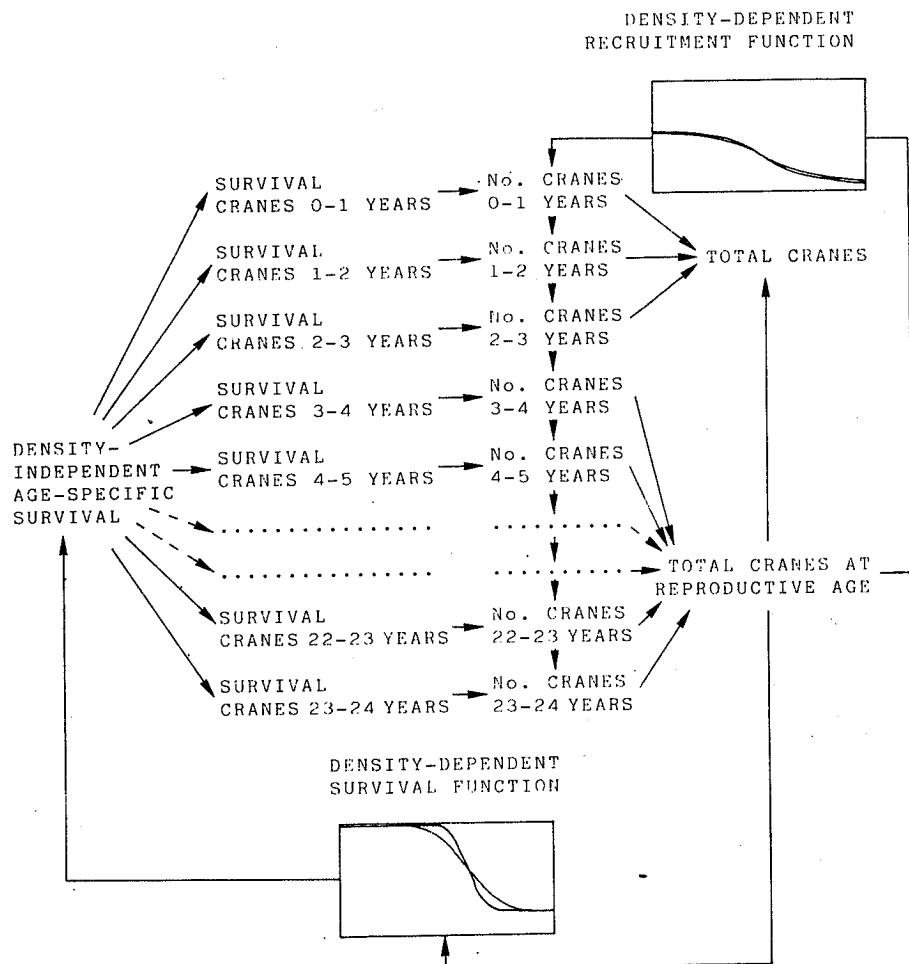


Figure 2. Flowchart of the Common Crane population model.

mature cranes; and PRD = productivity, or annual recruitment rate.

$$G00 = NAC$$

where G00 = number of cranes between 0 and 1 year old.

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

$$\text{For } I = 2 \text{ to } 24, \quad G(I) = G(I-1) * S(I-1)$$

where I = age-class, or level; $G(I)$ = 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 (see above, "Demographic parameters") and each age-specific value is also affected by a reverse logistic function that accounts for the effect of population density on it: the survival rate declines at high population levels:

$$S(I) = PTMM * (1-TM(I)) + \frac{(1 - TM(I)) * (1 - PTMM)}{1 + e^{(A * (GTOTAL - GPIX)/1000)}}$$

where $S(I)$ = survival rate of cranes at age I ; $PTMM$ = proportion between minimal and maximal assumed survival rates, i.e. lower and upper asymptotes of the logistic function; $TM(I)$ = 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; $GTOTAL$ = total number of cranes in the population; and $GPIX$ = 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:

$$PRD = \frac{TMP}{1 + e^{(B * (GTOTAL - GPIX)/1000)}}$$

where PRD = recruitment rate of the population; TMP = maximal theoretical recruitment rate (see above, "Demographic parameters"); B = parameter that regulates the rate of decline; and $GTOTAL$ and $GPIX$ as in the preceding equation.

This recruitment rate was applied only to sexually mature birds, i. e. ≥ 4 years old.

Each simulation was started with an initial population of 20000 cranes. This initial population was assumed to have an age-distribution identical to that calculated for the Whooping Crane by Binkley & Miller (1983). The model was 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 exactly their values with the data available at present.

$PTMM$ 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 GPIX, various values around the real size of the crane population have been considered (35000-60000), assuming that the latter is stable.

The values for TMP were estimated by four different ways:

(a) If we assume that each mature bird pairs in spring and each pair produces 2 chicks that would survive until their first winter, then from 100 cranes, 63.7 birds would be ≥ 4 years old (following Binkley & Miller 1983) and could produce a maximum of 63.7 young, that would represent 39.1% of the next winter population.

(b) If instead of 2 young per reproductive pair we consider our field average of 1.35 young per pair, the maximum possible percentage of juveniles would 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, provided that the small population of this endangered species (18 birds in 1938, increasing up to 78 in 1980) should stay at the left extreme of the density-dependent inverse logistic function of recruitment. The average for these 43 years (1938-80) and this species is 14.5 % juveniles in the winter population.

(d) We could also consider 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 be therefore considered as an exceptionally high value, not representative for TMP 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, moment of the simulation start. Therefore, we have used as the most realistic values for TMP those comprised between 0.15 and 0.30.

RESULTS

We have tried a total of 221 combinations of the parameters of the survival and recruitment functions, and have selected those that yield (a) stabilized populations between 35000 and 45000 cranes, and (b) with percentages of juveniles of 13.54 ± 2.27 (= mean of the seven annual values measured in the field $\pm 95\%$ confidence interval) (Table 2).

DISCUSSION

The model developed may seem mathematically too simple. This simplicity is mainly a consequence of the scarce data available on the demography of crane populations, particularly of the Common Crane. We are thus unable to narrow the variation margins of the multitude of possible combinations of these parameters sufficiently. Therefore, we must consider a relatively large series of plausible combinations of survival and recruitment curves that are consistent with the initially accepted conditions of population size and percentage of juveniles ((a) and (b), see Results).

A further limitation of the model is its deterministic nature.

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

Trial No.	PTMM	A	GPIX x1000	TMP	B	GTOTAL	% JUV
1	0.5	0.2	50	0.2	0.2	37200	13.20
2	0.5	0.2	50	0.2	0.15	36400	12.75
3	0.7	0.15	50	0.2	0.15	35875	12.86
4	0.7	0.15	50	0.2	0.2	36850	13.27
5	0.7	0.15	50	0.2	0.3	37780	13.72
6	0.7	0.2	50	0.2	0.15	38440	12.39
7	0.7	0.2	50	0.2	0.2	39400	12.87
8	0.7	0.2	50	0.2	0.3	40380	13.43
9	0.8	0.15	50	0.2	0.15	38000	12.50
10	0.8	0.15	50	0.2	0.2	39100	12.91
11	0.8	0.15	50	0.2	0.3	40380	13.43
12	0.8	0.2	50	0.2	0.15	39900	12.06
13	0.9	0.15	50	0.2	0.15	40900	11.79

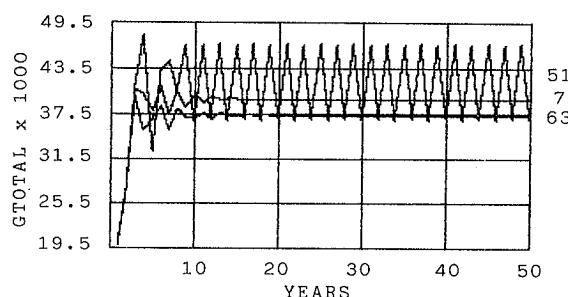
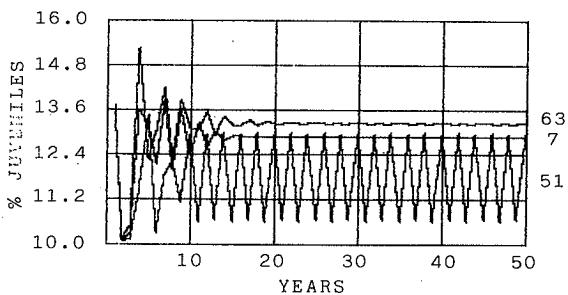
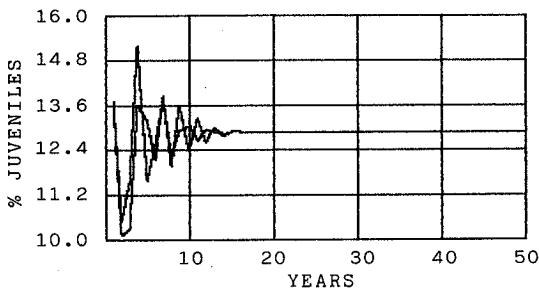
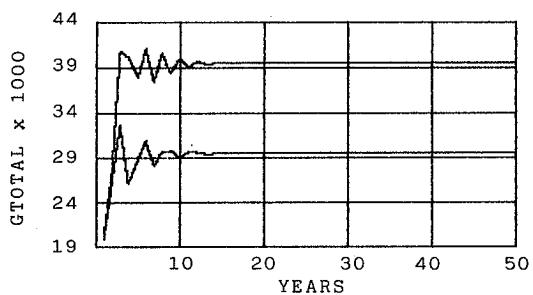
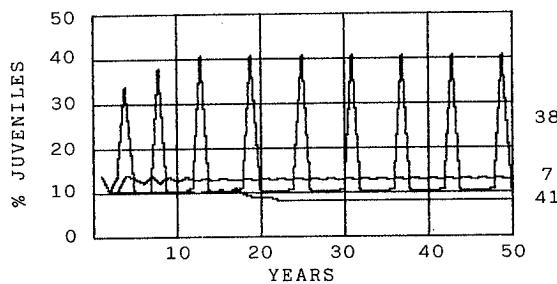
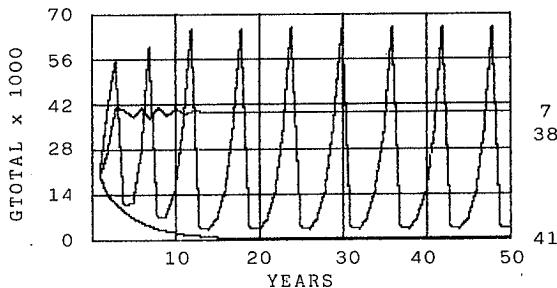


Fig. 3. Examples of simulations (trial number at right side of the diagrams) showing the effect of changing parameter PTMM from 0.7 (trial no. 7, accepted as one of the best simulations tested, see Table 2) to 0.5 (trial no. 63) or (trial no. 51) in the size of the crane population (left diagram), and the percentage of juveniles (right diagram).





As claimed by Miller *et al.* (1972) and Johnson (1979), stochastic variability of biological processes related with crane demography cannot be modeled due to the lack of information on causal intercorrelations between environmental and population variables.

Nevertheless, the model remains interesting and valid as a description of the population dynamics of this potentially threatened species, provided the difficulty of significantly improving the accuracy of most demographic parameters in a near future. It helps, as well, discover the kind of data that need further study most urgently, in order to try to manage the species properly. Although a sensitivity analysis remains to be done, the study of varying the model parameters already suggests some interesting preliminary conclusions. The value given to parameter PTMM, that governs the density-dependence effect on survival, depends entirely on the author criterion. So, the models of Miller *et al.* (1972) and Johnson (1979) differ in the relative importance of this parameter. In our model, as the value of PTMM increases, the population (GTOTAL) and the % juveniles present higher oscillations, the first around higher than normal values and the second around lower values (Fig. 3). Thus, a decrease in the relative importance of the density-dependence (= increase of PTMM) reduces, as expected, the self-regulating ability of the population. The best value of PTMM is 0.7 (Table 2 and Fig. 3), and 20% changes around this value determine changes of only approximately 5% in the size of the population and 3% in the percentage of juveniles.

Values of TMP lower than 0.10 determine the extinction of the population in less than 20 years, for every numerical combination of the other four parameters (Fig. 4). On the contrary, values higher than 0.20 determine high oscillations of the population size and percentage of juveniles. It is interesting to observe that all values of annual recruitment measured in the field in the crane population and the most realistic values inferred from our species as well as from other crane species fall within these limits. This suggests similar demographic structures in the various crane species for which populational data are available. Also interestingly, the annual recruitment values measured are closer to the lower limit than to the higher of those inferred, perhaps suggesting a conservative behaviour of the crane population in the selection of the optimal productivity rate.

The parameter GPIX directly affects the stabilization level of the population size. Changes in the parameter between 40000 and 50000 change GTOTAL in the same sense and by identical magnitudes, but do not alter the % juveniles (Fig. 5). Higher values of GPIX determine very high oscillations of GTOTAL and % juveniles. Although we have used the same GPIX for both survival and recruitment functions, if different points are used in the same simulation, the results are different.

Changes in parameters A and B change GTOTAL and % juveniles in the same sense, although by lower magnitude.

CONCLUSIONS

We have developed a simple model that serves as an appropriate instrument for the description of the Common Crane population

dynamics. The series of curves obtained do not exclude the possibility that other combinations exist. This model may be considered as a first attempt, with only preliminary results. The main limitations derive from the difficulty of obtaining certain demographic parameters. The main advantage is the possibility of generating hypothesis and undertaking "natural experiments" on this basic model (determination of optimal population size depending on carrying capacity of breeding and wintering areas, predicting future trends of the population, etc.) and readjusting it to new data. A sensitivity analysis is necessary to determine the relative importance of the parameters used. The possibility remains of future incorporation of submodels that account for the stochastic variability due to natural events or human activities. The model presented could provide a basis for future research as well as guidelines for the management and conservation of the Common Crane in W-Europe.

ACKNOWLEDGEMENTS

We sincerely thank J.S. Martínez-Vicente for writing the program and discussing the results, significantly contributing at different stages of the work. Financial support while in the field was obtained from ICBP^W, the MOPU, and CAYCIT Project No. 22107-01.

REFERENCES

- Alerstam, T. & Bauer, C.A. (1973). A radar study on Crane (*Grus grus*) spring migration over the Southern Baltic area. *Vogelwarte* 27:1-16.
- Alonso, J.A. & Alonso, J.C. (in press). Demographic parameters of the Common Crane *Grus g. grus* population wintering in Iberia. *Aquila*.
- Alonso, J.C., Alonso, J.A. & Cantos, F.J. (1986). On the size of the Common Crane *Grus grus* population migrating through Western Europe. *Ornis Fennica* 63.
- Binkley, C.S. & Miller, R.S. (1980). Survivorship of the Whooping Crane, *Grus americana*. *Ecology* 61: 434-437.
- Binkley, C.S. & Miller, R.S. (1983). Population characteristics of the Whooping Crane, *Grus americana*. *Can. J. Zool.* 61: 2768-2776.
- Botkin, D.B. & Miller, R.S. (1974). Mortality rates and survival of birds. *Amer. Nat.* 108: 181-192.
- Deevey, E.S. Jr. (1947). Life tables for natural populations of animals. *Quart. Rev. Biol.* 22: 238-314.
- Johnsgard, P.A. (1983). Cranes of the World. Croom Helm. London.
- Johnson, D.H. (1979). Modeling Sandhill Crane population dynamics. U.S. Fish Widl. Serv., Spec. Sci. Rep. Wildl. 222 (10 pp.).
- Johnson, D.H. (1982). Population Modeling for Furbearer Management. In G.C. Sanderson (Ed.), Midwest Furbearer Management. North Central Section, Central Mountains and Plains Section, and Kansas Chapter of the Wildlife Society, pp 25-37.

- 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. In S.A. Temple (Ed.), *Endangered Birds: Management Techniques for Preserving Threatened Species*. The Univ. of Wisconsin Press, Madison, pp.413-417.
- Miller, R.S. & Botkin, D.B. (1974). Endangered species: models and predictions. *Amer. Sci.* 62: 172-181.
- Miller, R.S., Botkin, D.B. & Mendelsson, R. (1974). The Whooping Crane (*Grus americana*) population of America. *Biol. Conserv.* 6: 106-111.
- Miller, R.S. Hochbaum, G.S. & Botkin, D.B. (1972). A simulation model for the management of Sandhill Cranes. *Yale Univ. Sch. For. Environ. Bull.* 80: 49 pp.
- Prange, H. (1984). Der Kranichzug in Thüringen und seine Einordnung in die Mitteleuropäische Flugroute. *Thür. Orn. Mitt.* 32: 1-16.
- Walkinshaw, L.H. (1973). Cranes of the World. Winchester Press, New York.

APPENDIX I. PROGRAM

```

5000 REM ***MODELO GRULLAS-5***  

5010 REM  

5020 REM ***CODIGO DE VARIABLES***  

5030 REM  

5040 REM G00=NUMERO DE GRULLAS ENTRE 0 Y 1 ANOS(INDIVIDUOS),N,#01  

5050 REM G01=NUMERO DE GRULLAS ENTRE 1 Y 2 ANOS(INDIVIDUOS),N,#02  

5060 REM G02=NUMERO DE GRULLAS ENTRE 2 Y 3 ANOS(INDIVIDUOS),N,#03  

5070 REM G03=NUMERO DE GRULLAS ENTRE 3 Y 4 ANOS(INDIVIDUOS),N,#04  

5080 REM G04=NUMERO DE GRULLAS ENTRE 4 Y 5 ANOS(INDIVIDUOS),N,#05  

5090 REM G05=NUMERO DE GRULLAS ENTRE 5 Y 6 ANOS(INDIVIDUOS),N,#06  

5100 REM G06=NUMERO DE GRULLAS ENTRE 6 Y 7 ANOS(INDIVIDUOS),N,#07  

5110 REM G07=NUMERO DE GRULLAS ENTRE 7 Y 8 ANOS(INDIVIDUOS),N,#08  

5120 REM G08=NUMERO DE GRULLAS ENTRE 8 Y 9 ANOS(INDIVIDUOS),N,#09  

5130 REM G09=NUMERO DE GRULLAS ENTRE 9 Y 10 ANOS(INDIVIDUOS),N,#10  

5140 REM G10=NUMERO DE GRULLAS ENTRE 10 Y 11 ANOS(INDIVIDUOS),N,#11  

5150 REM G11=NUMERO DE GRULLAS ENTRE 11 Y 12 ANOS(INDIVIDUOS),N,#12  

5160 REM G12=NUMERO DE GRULLAS ENTRE 12 Y 13 ANOS(INDIVIDUOS),N,#13  

5170 REM G13=NUMERO DE GRULLAS ENTRE 13 Y 14 ANOS(INDIVIDUOS),N,#14  

5180 REM G14=NUMERO DE GRULLAS ENTRE 14 Y 15 ANOS(INDIVIDUOS),N,#15  

5190 REM G15=NUMERO DE GRULLAS ENTRE 15 Y 16 ANOS(INDIVIDUOS),N,#16  

5200 REM G16=NUMERO DE GRULLAS ENTRE 16 Y 17 ANOS(INDIVIDUOS),N,#17  

5210 REM G17=NUMERO DE GRULLAS ENTRE 17 Y 18 ANOS(INDIVIDUOS),N,#18  

5220 REM G18=NUMERO DE GRULLAS ENTRE 18 Y 19 ANOS(INDIVIDUOS),N,#19  

5230 REM G19=NUMERO DE GRULLAS ENTRE 19 Y 20 ANOS(INDIVIDUOS),N,#20  

5240 REM G20=NUMERO DE GRULLAS ENTRE 20 Y 21 ANOS(INDIVIDUOS),N,#21  

5250 REM G21=NUMERO DE GRULLAS ENTRE 21 Y 22 ANOS(INDIVIDUOS),N,#22  

5260 REM G22=NUMERO DE GRULLAS ENTRE 22 Y 23 ANOS(INDIVIDUOS),N,#23  

5270 REM G23=NUMERO DE GRULLAS ENTRE 23 Y 24 ANOS(INDIVIDUOS),N,#24  

5280 REM S00=TASA DE SUPERVIVENCIA DE G00(TANTO POR 1),F,#25  

5290 REM S01=TASA DE SUPERVIVENCIA DE G01(TANTO POR 1),F,#26  

5300 REM S02=TASA DE SUPERVIVENCIA DE G02(TANTO POR 1),F,#27  

5310 REM S03=TASA DE SUPERVIVENCIA DE G03(TANTO POR 1),F,#28  

5320 REM S04=TASA DE SUPERVIVENCIA DE G04(TANTO POR 1),F,#29  

5330 REM S05=TASA DE SUPERVIVENCIA DE G05(TANTO POR 1),F,#30  

5340 REM S06=TASA DE SUPERVIVENCIA DE G06(TANTO POR 1),F,#31  

5350 REM S07=TASA DE SUPERVIVENCIA DE G07(TANTO POR 1),F,#32  

5360 REM S08=TASA DE SUPERVIVENCIA DE G08(TANTO POR 1),F,#33  

5370 REM S09=TASA DE SUPERVIVENCIA DE G09(TANTO POR 1),F,#34  

5380 REM S10=TASA DE SUPERVIVENCIA DE G10(TANTO POR 1),F,#35  

5390 REM S11=TASA DE SUPERVIVENCIA DE G11(TANTO POR 1),F,#36  

5400 REM S12=TASA DE SUPERVIVENCIA DE G12(TANTO POR 1),F,#37  

5410 REM S13=TASA DE SUPERVIVENCIA DE G13(TANTO POR 1),F,#38  

5420 REM S14=TASA DE SUPERVIVENCIA DE G14(TANTO POR 1),F,#39  

5430 REM S15=TASA DE SUPERVIVENCIA DE G15(TANTO POR 1),F,#40  

5440 REM S16=TASA DE SUPERVIVENCIA DE G16(TANTO POR 1),F,#41  

5450 REM S17=TASA DE SUPERVIVENCIA DE G17(TANTO POR 1),F,#42  

5460 REM S18=TASA DE SUPERVIVENCIA DE G18(TANTO POR 1),F,#43  

5470 REM S19=TASA DE SUPERVIVENCIA DE G19(TANTO POR 1),F,#44  

5480 REM S20=TASA DE SUPERVIVENCIA DE G20(TANTO POR 1),F,#45  

5490 REM S21=TASA DE SUPERVIVENCIA DE G21(TANTO POR 1),F,#46  

5500 REM S22=TASA DE SUPERVIVENCIA DE G22(TANTO POR 1),F,#47

```

```

5510 REM !LA TASA DE SUPERVIVENCIA DE G23 ES 0!
5520 REM GTER=TOTAL DE GRULLAS EN EDAD DE REPRODUCIRSE(INDIVIDUOS),A,#4
8
5530 REM PRD=PRODUCTIVIDAD,A,#49
5540 REM GTOTAL=NUMERO TOTAL DE GRULLAS(INDIVIDUOS),A,#50
5550 REM J%=PORCENTAJE DE GRULLAS JOVENES(TANTO POR 1),A,#51
5560 REM
5570 REM ***CODIGO DE PARAMETROS O TASAS***
5580 REM
5590 REM PTMM=PROPORCION DE LA FUNCION DE SUPERVIVENCIA,#01
5600 REM A=PARAMETRO DE LA FUNCION DE SUPERVIVENCIA(..),#02
5610 REM GPIX=TAMANO DE LA POBLACION EN EL PUNTO DE INFLEXION(INDIVIDUO
S),#03
5620 REM TMP=TASA MAXIMA DE PRODUCTIVIDAD(TANTO POR 1),#04
5630 REM B=PARAMETRO DE LA FUNCION DE PRODUCTIVIDAD(..),#05
5640 REM TM00=TASA DE MORTALIDAD DE G00(TANTO POR 1),#06
5650 REM TM01=TASA DE MORTALIDAD DE G01(TANTO POR 1),#07
5660 REM TM02=TASA DE MORTALIDAD DE G02(TANTO POR 1),#08
5670 REM TM03=TASA DE MORTALIDAD DE G03(TANTO POR 1),#09
5680 REM TM04=TASA DE MORTALIDAD DE G04(TANTO POR 1),#10
5690 REM TM05=TASA DE MORTALIDAD DE G05(TANTO POR 1),#11
5700 REM TM06=TASA DE MORTALIDAD DE G06(TANTO POR 1),#12
5710 REM TM07=TASA DE MORTALIDAD DE G07(TANTO POR 1),#13
5720 REM TM08=TASA DE MORTALIDAD DE G08(TANTO POR 1),#14
5730 REM TM09=TASA DE MORTALIDAD DE G09(TANTO POR 1),#15
5740 REM TM10=TASA DE MORTALIDAD DE G10(TANTO POR 1),#16
5750 REM TM11=TASA DE MORTALIDAD DE G11(TANTO POR 1),#17
5760 REM TM12=TASA DE MORTALIDAD DE G12(TANTO POR 1),#18
5770 REM TM13=TASA DE MORTALIDAD DE G13(TANTO POR 1),#19
5780 REM TM14=TASA DE MORTALIDAD DE G14(TANTO POR 1),#20
5790 REM TM15=TASA DE MORTALIDAD DE G15(TANTO POR 1),#21
5800 REM TM16=TASA DE MORTALIDAD DE G16(TANTO POR 1),#22
5810 REM TM17=TASA DE MORTALIDAD DE G17(TANTO POR 1),#23
5820 REM TM18=TASA DE MORTALIDAD DE G18(TANTO POR 1),#24
5830 REM TM19=TASA DE MORTALIDAD DE G19(TANTO POR 1),#25
5840 REM TM20=TASA DE MORTALIDAD DE G20(TANTO POR 1),#26
5850 REM TM21=TASA DE MORTALIDAD DE G21(TANTO POR 1),#27
5860 REM TM22=TASA DE MORTALIDAD DE G22(TANTO POR 1),#28
5870 REM
5880 REM ***SISTEMA DE ECUACIONES ANALITICAS***
5890 REM
5900 REM G00=GTER*PRD
5910 REM G01=G00*S00
5920 REM G02=G01*S01
5930 REM G03=G02*S02
5940 REM G04=G03*S03
5950 REM G05=G04*S04
5960 REM G06=G05*S05
5970 REM G07=G06*S06
5980 REM G08=G07*S07
5990 REM G09=G08*S08
6000 REM G10=G09*S09
6010 REM G11=G10*S10
6020 REM G12=G11*S11
6030 REM G13=G12*S12
6040 REM G14=G13*S13
6050 REM G15=G14*S14

```

```
6060 REM G16=G15*S15
6070 REM G17=G16*S16
6080 REM G18=G17*S17
6090 REM G19=G18*S18
6100 REM G20=G19*S19
6110 REM G21=G20*S20
6120 REM G22=G21*S21
6130 REM G23=G22*S22
6140 REM S00=PTMM*(1-TM00)+((1-PTMM)*(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6150 REM S01=PTMM*(1-TM01)+((1-TM01)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6160 REM S02=PTMM*(1-TM02)+((1-TM02)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6170 REM S03=PTMM*(1-TM03)+((1-TM03)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6180 REM S04=PTMM*(1-TM04)+((1-TM04)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6190 REM S05=PTMM*(1-TM05)+((1-TM05)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6200 REM S06=PTMM*(1-TM06)+((1-TM06)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6210 REM S07=PTMM*(1-TM07)+((1-TM07)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6220 REM S08=PTMM*(1-TM08)+((1-TM08)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6230 REM S09=PTMM*(1-TM09)+((1-TM09)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6240 REM S10=PTMM*(1-TM10)+((1-TM10)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6250 REM S11=PTMM*(1-TM11)+((1-TM11)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6260 REM S12=PTMM*(1-TM12)+((1-TM12)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6270 REM S13=PTMM*(1-TM13)+((1-TM13)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6280 REM S14=PTMM*(1-TM14)+((1-TM14)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6290 REM S15=PTMM*(1-TM15)+((1-TM15)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6300 REM S16=PTMM*(1-TM16)+((1-TM16)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6310 REM S17=PTMM*(1-TM17)+((1-TM17)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6320 REM S18=PTMM*(1-TM18)+((1-TM18)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6330 REM S19=PTMM*(1-TM19)+((1-TM19)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6340 REM S20=PTMM*(1-TM20)+((1-TM20)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6350 REM S21=PTMM*(1-TM21)+((1-TM21)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
6360 REM S22=PTMM*(1-TM22)+((1-TM22)*(1-PTMM)/(1+EXP(A*(GTOTAL-GPIX)/1
000)))
```

```
6370 REM PRD=(TMP/(1+EXP(B*(GTOTAL-GPIX)/1000)))
6380 REM GTOTAL=GTER+G00+G01+G02
6390 REM
7000 REM ***SISTEMA DE ECUACIONES MDS***
7010 IF T < > TI THEN 7030
7020 GOTO 7070
7030 VN(1) = INT (VN(48) * VN(49) + .5)
7040 FOR I = 1 TO 23
7050 VN(I + 1) = INT (VN(I) * VN(24 + I) + .5)
7060 NEXT I
7070 VN(48) = 0
7080 FOR I = 4 TO 24
7090 VN(48) = VN(48) + VN(I)
7100 NEXT
7105 VN(50) = VN(48) + VN(1) + VN(2) + VN(3)
7110 FOR I = 1 TO 23
7120 VN(I + 24) = TA(1) * (1 - TA(I + 5)) + (1 - TA(I + 5)) * (1 - TA(1))
    / (1 + EXP (TA(2) * ((VN(50) - TA(3)) / 1000)))
7130 NEXT I
7140 VN(49) = TA(4) / (1 + EXP (TA(5) * ((VN(50) - TA(3)) / 1000)))
7160 VN(51) = INT ((VN(1) / VN(50) + .00005) * 10000) / 100
8000 RETURN
30000 REM
30010 REM ***DATOS ESTRUCTURALES***
30020 REM
30030 DATA 0001,0050,1,1
30040 DATA 24,28,51
30050 REM
30060 REM ***CONDICIONES INICIALES***
30070 REM
30080 DATA 2700,1620,1520,1420
30090 DATA 1340,1240,1160,1080
30100 DATA 1000,0920,0840,0760
30110 DATA 0680,0620,0540,0480
30120 DATA 0420,0360,0300,0240
30130 DATA 0200,0140,0092,0044
30140 REM
30150 REM ***VALORES DE PARAMETROS O TASAS***
30160 REM
30170 DATA .7
30180 DATA .2
30190 DATA 40000
30200 DATA .20
30210 DATA .2
30220 DATA .3750,.0183,.0210,.0238
30230 DATA .0222,.0347,.0344,.0376
30240 DATA .0416,.0464,.0517,.0576
30250 DATA .0647,.0725,.0826,.0939
30260 DATA .1090,.1270,.1510,.1860
30270 DATA .2370,.3220,.4910
```

```
31000 REM
31010 REM ***SÍMBOLOS DE VARIABLES***
31020 REM
31030 DATA G00,G01,G02,G03,G04
31040 DATA G05,G06,G07,G08,G09
31050 DATA G10,G11,G12,G13,G14
31060 DATA G15,G16,G17,G18,G19
31070 DATA G20,G21,G22,G23
31080 DATA S00,S01,S02,S03,S04
31090 DATA S05,S06,S07,S08,S09
31100 DATA S10,S11,S12,S13,S14
31110 DATA S15,S16,S17,S18,S19
31120 DATA S20,S21,S22
31130 DATA GTER,PRD,GTOTAL
31135 DATA JX
31140 DATA PTMM,A,GPIX,TMP,B
31150 DATA TM00,TM01,TM02,TM03,TM04
31160 DATA TM05,TM06,TM07,TM08,TM09
31170 DATA TM10,TM11,TM12,TM13,TM14
31180 DATA TM15,TM16,TM17,TM18,TM19
31190 DATA TM20,TM21,TM22
```