

A DEMOGRAPHIC MODEL OF NORTHERN GOSHAWKS

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Running head: DEMOGRAPHIC MODEL OF GOSHAWKS

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ABSTRACT.--Mueller et al. (1977) concluded their paper summarizing a 25-year study of Northern Goshawk (Accipiter gentilis) movements with the prediction that it would take several 10-year cycles for goshawks to recover from the crash of 1972-3. The large goshawk invasion of 1982 (Evans 1983) seems to have disproven this prediction.

In this paper, the model used by Mueller et al. is considered in detail in order to understand why their prediction proved incorrect. First, a general model is described. Then the model of Mueller et al. is considered as a special case of the general model. It will be suggested that two of the parameters assumed in their model were probably incorrect, and that the model itself was applied incorrectly to the data that were observed.

In their paper on the periodic invasions of Northern Goshawks (Accipiter gentilis), Mueller et al. (1977) used a simple demographic model to determine the rate of growth and the stable age distribution of a population of goshawks with given rates of survival and fertility. Then they compared the age distribution observed in birds captured at Cedar Grove, Wisconsin, during the autumn migration, with the age distribution of the model population in order to estimate the fertility rate during an invasion. They concluded that the population suffered a 70% reduction during the 1972-3 invasion and that this reduction was so severe that it would take several 10-year cycles for the population to recover.

There was a large invasion at Duluth, Minnesota, in the autumn of 1982, with 5819 Goshawks observed (Evans 1983), which suggests that the population had, in fact, recovered from the reduction of 1972-3. In this paper I will suggest that two of the parameters used by Mueller et al. in their model were wrong, and that these errors undervalued the goshawks' ability to recover from population declines. There were also two technical mistakes in the use of the model, and these exaggerated the magnitude of the population decline.

THE MODEL

First I will describe a general model for Goshawk populations, using an idea similar to Leslie's matrix

(Leslie 1945, 1948; the method was described in Krebs 1978; I will follow Pielou 1977, who gave a detailed discussion of the method). Then I will consider the model of Mueller et al. They did not describe their model explicitly, but I will reconstruct their model from their assumptions and consider the reconstruction as a special case of the general model.

The general model.--Goshawks show three distinguishable age classes, which Mueller et al. refer to as: juvenal, adult I, and adult II. We can think of these as birds of age 0, 1, and 2-or-more, respectively. Following Mueller et al. I will treat the adults II as members of a single age group (with the same annual survival and fertility). Then we can represent the goshawk population at time t by the column vector:

$$n(t) = \begin{pmatrix} n_0(t) \\ n_1(t) \\ n_2(t) \end{pmatrix},$$

where $n_i(t)$ = the number of female goshawks of age i at time t . Each year the population will change, and these annual changes can be interpreted by using a population projection matrix:

$$M = \begin{pmatrix} F_0 & F_1 & F_2 \\ P_0 & 0 & 0 \\ 0 & P_1 & P_2 \end{pmatrix},$$

where P_i = the probability that a goshawk aged i at time

t will survive to time t+1, and

F_i = the average number of daughters (aged 0) alive at time t+1 produced by a female goshawk aged i at time t.

Often in population modeling, females are considered alone, and, unless otherwise specified, I will consider only females. Notice that F_i includes survival implicitly, since if the population is considered at the time of fledging, the mother must have survived from the previous season in order to produce daughters in the present one.

The survival and fertility parameters in the population projection matrix M are written as constants, but they may be functions of time and population density. The important thing is to visualize a population changing from year to year according to some explicit rules. Matrix M is the same as the Leslie matrix except for the term P_2 , which is the probability that an adult II bird will survive another year. The population at time t+1 is determined by M and $n(t)$ as follows, using matrix multiplication:

$$(1) \quad n(t+1) = Mn(t).$$

Equation (1) is equivalent to the three linear equations:

$$(1a) \quad n_0(t+1) = F_0n_0(t) + F_1n_1(t) + F_2n_2(t)$$

$$(1b) \quad n_1(t+1) = P_0n_0(t)$$

$$(1c) \quad n_2(t+1) = P_1n_1(t) + P_2n_2(t).$$

Equations (1a-c) are useful in studying a population in detail, but it is more common to treat populations more generally, by assuming that the population has a stable age distribution and then calculating λ , the factor by which the population is multiplied each year, and then finding the stable age distribution. This is what Mueller et al. did. The finite rate of increase, λ , is found by considering the matrix $M - \lambda I$, where I is the identity matrix, and setting the determinant equal to zero:

$$(2) \quad |M - \lambda I| = 0.$$

This yields the equation:

$$(3) \quad \lambda^3 - (F_0 + P_2)\lambda^2 + (F_0P_2 - P_0F_1)\lambda + P_0F_1P_2 - P_0P_1F_2 = 0,$$

which can be solved numerically for λ in any particular case. Then the stable age distribution can be found by using:

$$(4a) \quad n_0 = 1 \quad (\text{to standardize}),$$

$$(4b) \quad n_1 = P_0/\lambda, \text{ and}$$

$$(4c) \quad n_2 = P_0P_1/(\lambda(\lambda - P_2)).$$

The survival and fertility rates (P_i 's and F_i 's) in the matrix M are convenient to use mathematically, but they are not the same values that are measured by biologists.

It is necessary to do some translation to change the observed values to the values needed in the model. For the survival probabilities there is no problem once one establishes the time of year at which the model is to be considered. I take this to be the time of fledging, not the time of autumn migration. The fertility values are more complicated to find. Since F_i is the average number of daughters produced at time $t+1$ by a female aged i at time t , the value of F_i is the probability of surviving the year (P_i), times the probability of successfully breeding (call it b_i), times the proportion of females among the offspring (call it s), times the clutch size (c_i). Thus, we might write:

$$(5) \quad F_i = P_i b_i s c_i.$$

The special case considered by Mueller et al.--Mueller et al. assumed that clutch size and the probability of successful breeding do not depend on age (i), and they assumed that $b_i = .75$ and $s = .5$. They assumed that $P_0 = .35$, $P_1 = P_2 = .70$ and considered various clutch sizes. Thus, using (5), we have: $F_0 = .13125c$ and $F_1 = F_2 = .2625c$, where c is the common clutch size. Under these assumptions, equation (3) reduces to:

$$(6) \quad \lambda = .7 + .13125c.$$

Using (6) and (4a-c) and assuming various clutch sizes,

Mueller et al. calculated the relative annual change, $\lambda - 1$, and the stable age distribution of a population that has achieved a stable age distribution. Their calculations depended on the assumption that the population was at its stable age distribution, that is, that the proportion of birds in each age class did not change from year to year. This is an important assumption and certainly is not true for a population that is crashing.

Table 1 shows the stable age distribution (the proportion of the population in each age class) and the annual rate of increase ($\lambda - 1$) for Mueller et al.'s model goshawk populations for various values of clutch size, c . Notice that the age distributions are weighted toward juveniles. This weighting will be heaviest when the population is viewed at the time of fledging, as is done here.

(Put Table 1 here.)

APPLICATION OF THE MODEL

Since the use of the model led to an incorrect prediction, we may look for a mistake in the model, either in the parameters used in the model, or in the way the model itself was used. It is possible that the population decline in 1972-3 was not as great as believed, or that the goshawks' ability to recover from a decline is greater

than believed, or both. I will argue that the life history parameters chosen by Mueller et al. led to an underestimate of the goshawks' ability to increase. Then I will argue that two mistakes in the application of the model led to an overestimate of the population decline during 1972-3.

The choice of parameters.---The parameters chosen by Mueller et al. probably erred in two ways. The fertility rate assumed for juveniles was probably too high, and the survival rate (for juveniles and adults) was probably too low.

Mueller et al. assumed that the reproductive success of juvenile birds was the same as that of older birds. They gave evidence that juvenile birds do, in fact, breed, citing Looft (in Glutz et al. 1971) who reported that in all nesting pairs observed, 6.7% of the males and 9.7% of the females were juveniles. But, under the assumptions of Mueller et al., 30% of the breeding birds in a stationary population would be juveniles. Thus it is likely that juvenile fertility is much lower than that of older birds. However, changing this assumption would make it seem that goshawks have an even lower capacity for increase than Mueller et al. concluded.

The annual mortality rates assumed by Mueller et al. (65% for juveniles, 30% for adults I and II) were probably too high. These rates were based on recovery data for

banded European birds. In all the cases cited in Glutz et al. (1971) for which such data were given, a large majority of recovered birds were killed. Newton (1979) has pointed out that this is a source of bias and cites the study of Haukioja and Haukioja (1970) which showed that mortality estimates based on killed birds can be much higher than those based on birds found dead. Mueller et al. recognized this in their paper and they used values lower, but only slightly lower, than the averages of those found in Glutz et al. (1971). It might be more accurate to use substantially lower mortality estimates, such as the .5 for juveniles and .25 for adults suggested by Mueller and Berger (1967). Even with no juvenile reproduction, a population with these lower mortality rates could recover from a population decline faster than the population assumed by Mueller et al.

The use of the model.---Mueller et al. made two technical mistakes in the use of their model, each mistake leading to overestimation of the population decline. First, they did their calculations as if the population was at a stable age distribution, thus ignoring important changes in age distribution which take place during a decline. Second, they calculated the stable age distribution for the population at the time of fledging and then compared this calculated distribution with the distribution observed during the

autumn migration. This will lead to underestimation of fertility if fledglings suffer greater mortality between the time of fledging and the autumn migration than do older birds.

The importance of age distribution and reproductive value.--When a population reaches a peak and then declines, its age distribution will change. The declining population will have a greater proportion of older birds; these birds are of greater value in helping the population recover than are younger birds. This different value of birds of different ages is the basis of Fisher's (1930) idea of "reproductive value," which is defined as the relative contributions to the future population of individuals of different ages if the population continues to grow (or decline) with constant rates of survival and fertility. These rates are not constant for a fluctuating population, but if we assume with Mueller et al. that the population will continue to recover from a crash with rates that are constant for several years, then we can calculate the reproductive values of birds of different ages with respect to these rates. Using the usual notation, we write v_x to denote the reproductive value of a bird of age x , and we assume that survival and fertility are constant after the first year of life (that is, $P_1 = P_2$, $F_1 = F_2$) and we have

$$(7a) \quad v_0 = 1 \quad (\text{by definition}), \text{ and}$$

$$(7b) \quad v_1 = v_2 = F_1 / (\lambda - P_1) .$$

We may think about a population in terms of its total reproductive value (Fisher 1930), which will be

$$(8) \quad V = v_0 n_0 + v_1 n_1 + v_2 n_2 .$$

The reproductive value of a bird may be thought of as the number of fledglings that the bird is equivalent to. For the cases considered by Mueller et al.: $v_0 = 1$, and $v_1 = v_2 = 2$.

Reproductive value is important here because if a goshawk population increases to a peak and then crashes, the relative decrease in number of birds is greater than the relative decrease in total reproductive value. For a population to recover from a crash, it is the total reproductive value of the population, and not simply the total number of birds, that is important. Concentrating on the total population and ignoring reproductive value may have led Mueller et al. to exaggerate the magnitude of the population decline.

These ideas may be illustrated by considering a hypothetical goshawk population with the same parameters as Mueller et al. assumed ($P_0 = .35$, $P_1 = P_2 = .7$, 75% breeding success for all age classes, and an average clutch size of 3 during most years). Assume that a population of 10000 goshawks with these parameters was in a stable age distribution in 1971. Then assume that survival remained constant, but that there was no reproduction for two years.

Finally, assume that the population resumed reproduction at the old rate in 1974 and resumed growth. This hypothetical population would have recovered its 1971 numbers by 1981. This hypothetical population is illustrated in Table 2, which shows the number of birds in each of the three age classes, the total number of birds and the total reproductive value of the population for the years 1971-81.

(Put Table 2 here.)

Notice that while I have assumed that there was no reproduction at all during 1972-3, my calculations show that the hypothetical goshawk population could have recovered within eight years (by 1981) if it grew at the rate assumed by Mueller et al. They concluded that the recovery would take more than 12 years. Part of the reason for this difference is seen by comparing the decrease in total numbers with the decrease in total reproductive value during the 1972-3 crash. From 1971 to 1973, the hypothetical population declined by 64%, from 10000 to 3603, while the total reproductive value declined by only 51%, from 14706 to 7206. By considering numbers alone and not the age distribution and reproductive value of the declining population, Mueller et al. exaggerated the magnitude of the population decline. This error alone can account for almost all the discrepancy between Mueller et al.'s prediction that the goshawk population would require more than 12 years to recover

from the 1972-3 decline and the fact that the population seems to have recovered by 1982.

Although a goshawk population with the high mortality rates assumed by Mueller et al. could recover within 8 years from a two-year decline with no reproduction if they had an average clutch size of 3, a population with the lower mortality rates assumed by Mueller and Berger (1967) could recover from such a decline within four years, even if juveniles did not reproduce during the recovery. If juveniles could reproduce during the recovery, but only at half the rate of adults, a population with the lower mortality rates could recover from a crash in three years.

The importance of the time at which the population is viewed.--A second technical point about the use of a demographic model is that the age distribution should be calculated for the same time as that at which the real population is observed. Mueller et al. did not do this. They calculated the stable age distribution for a population at the time of fledging and made their observations during the autumn migration. Comparing the age distributions in this way will produce an underestimate of fertility. This can be illustrated by considering a hypothetical example which satisfies the assumptions of Mueller et al.'s model.

Consider a hypothetical stationary population ($\lambda = 1$)

having the survival rates ($P_0 = .35$, $P_1 = P_2 = .7$) assumed by Mueller et al. Assume that there are 1000 young fledged each year. At the time of fledging, there will be 1000 fledglings and 350 adult I birds (since $P_0 = .35$). The ratio of juveniles to adults I is 20:7. Now, consider the same population the next year, just before fledging. Now the 1000 fledglings will be reduced to about 350 birds, while the 350 adults I will be reduced to about 245 birds, and the resulting ratio will be 10:7. If such a population were observed during the autumn migration, the ratio of juvenile to adult I birds would be somewhere between 20:7 and 10:7. The difference between these ratios is due to the fact that juveniles suffer greater mortality than adults I. If most of the additional mortality suffered by juveniles occurs between the times of fledging and migration, the expected ratio of juveniles to adults I would be closer to 10:7. Haukioja and Haukioja (1970) looked at the number of banded goshawks killed each month, starting at the time at which young became independent (1 August). They found that mortality occurred earlier for juveniles than for adults I and II. Forty-two percent of the juveniles killed were killed in the first two months after independence, and 67% were killed in the first three months. These data based on killed birds are subject to the criticism given earlier, but even so, it is likely that a large part of the additional mortality suffered by young

birds occurs before the autumn migration.

If the juvenile: adult I ratio is substantially lower during the autumn migration than at fledging, then it is misleading to compare the juvenile: adult I ratio during migration to the theoretical ratio calculated at fledging. If, in the example considered above, the juvenile: adult I ratio was observed to be 5:7 during migration, comparing this with the theoretical ratio at fledging of 20:7 would suggest that reproduction had been only 1/4 of that needed for a stationary population. If the 5:7 ratio was compared with the 10:7 ratio expected later, it would suggest that reproduction had been 1/2 of that needed for a stationary population. The evidence presented by Mueller et al. did show that reproduction was very low in 1972-3, but their method of comparison made it look even lower than it actually was.

DISCUSSION

The observations of field biologists are seldom used with demographic theory to make predictions about populations. Making such predictions is risky, but the attempt to do so is very valuable, because it throws light on the theory and the observations. Mueller et al. predicted that the Northern Goshawk population would take more than 12 years to recover from the decline of 1972-3. The large goshawk invasion in 1982 suggests that the population recovered

sooner than predicted. The model was incorrect, both because it assumed that goshawk mortality was higher than it probably was, and because it ignored the reproductive value and changing age distribution of the population.

During the 1972-3 goshawk invasion Mueller et al. observed a large majority of females among the adult birds captured. They took this as evidence of increased mortality among males at this time, and they added this inferred mortality to that already inferred by comparing observed and theoretical age distributions. While such a large sex difference in mortality may have occurred, it is also possible that adult females are more likely to emigrate than adult males during some invasion years. The 1972-3 goshawk invasion coincided with a crash in the population of snowshoe hares (McGowan 1975, Keith and Windberg 1978). Storer (1966) concluded that female goshawks take larger prey than do males, and gave evidence that females take relatively more mammals as prey than do males. Female goshawks may have been affected more by the snowshoe hare crash than were males and therefore emigrated in greater numbers.

Some of the parameters needed in a realistic model of goshawk populations (such as annual mortality) are difficult or impossible to measure. It is understandable when a model based on such values produces an incorrect prediction. Furthermore, if a model based on incorrect theory is used,

it can also lead to an incorrect prediction.

However, the model itself is not subject to experimental error, and the model used should follow correctly from the theory used. In the treatment of their model, Mueller et al. ignored the effect of changing population age structure. This, in itself, can account for almost the entire difference between their prediction that the goshawk population would take more than 12 years to recover from the 1972-3 decline and the observed fact that it recovered within 9 years.

Assuming lower mortality rates and considering the changing age structure and reproductive value give a more realistic picture of goshawk populations. Adults have good survival and high reproductive values. When prey are plentiful, reproduction is high and the population increases rapidly, mainly due to an increase in young birds. When the prey population crashes, goshawk reproduction slows down and the population decreases, mainly due to a decrease in young birds. While the entire goshawk population fluctuates, the fluctuation in the number of young birds is much greater than that of older birds.

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TABLE 1. Stable age distribution and annual rate of population change for a model goshawk population.^a

Clutch size ^c	Proportion in each age class ^b			Population change ^d
	Juvenile	Adult I	Adult II	
4.0	.600	.171	.229	.225
3.5	.568	.171	.261	.159
3.0	.529	.169	.301	.094
2.5	.484	.165	.351	.028
2.0	.429	.156	.416	-.038
1.5	.360	.140	.500	-.103
1.0	.273	.115	.612	-.169
0.5	.158	.072	.770	-.234

^a The population is assumed to be in a stable age distribution, and have $P_0 = .35$, $P_1 = P_2 = .70$. The values are obtained using equations (6) and (4a-c). (After Mueller et al. Table 4)

^b These values are rounded. Otherwise, they would sum to one..

^c This is actually the average number of young fledged per successful breeding pair.

^d These values equal $\lambda - 1$.

TABLE 2. Hypothetical goshawk population which undergoes a crash in 1972-3 and otherwise grows at the rate assumed by Mueller et al.^a

Year	Number of goshawks ^b			Total	Total Reproductive Value
	Juveniles	Adult I	Adult II		
1971	5294	1694	3012	10000	14706
1972	0000	1853	3294	5147	9313
1973	0000	0000	3603	3603	7206
1974	2837	0000	2522	5359	7882
1975	3103	993	1765	5861	8620
1976	3394	1086	1931	6411	9429
1977	3713	1188	2112	7013	10313
1978	4061	1299	2310	7670	11279
1979	4441	1421	2526	8388	12337
1980	4858	1554	2764	9176	13493
1981	5312	1700	3023	10035	14758

^a The population is assumed to start in 1971 in a stable age distribution for the parameters assumed by Mueller et al. ($P_0 = .35$, $P_1 = P_2 = .70$; clutch size, $c = 3$, and all age classes having the same reproductive success, $b = .75$). In 1972-3 no reproduction occurs, but survival remains unchanged. Then, in 1974, reproduction resumes at the original rate and continues until 1981.

^b These values are rounded to the nearest whole number, and the total is the sum of the rounded values.