PEREGRINE FALCON POPULATION DYNAMICS DEDUCED FROM BAND RECOVERY DATA

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INTRODUCTION

North American Peregrine Falcons survived without difficulty until the late 1940's. *Falco peregrinus anatum* bred and wintered largely in the United States and the forested portions of mainland Canada. The Tundra Peregrine Falcon (*F. p. tundrius*) breeds in the arctic and winters as far south as Argentina. The Peale's Falcon (*F. p. pealei*) inhabits the islands off British Columbia and southern Alaska and the Aleutian Island chain. The race *anatum* has been greatly reduced in the United States and southern Canada, probably because of chlorinated hydrocarbon pesticides, and the other races may also be threatened.

In the forty years between 1924 and 1963, no more than about 1400 North American Peregrine Falcons were banded. Since the banding of Peregrines resident in the United States has nearly ceased, and few of the northern races are being banded, it is essential to obtain as much information as possible from the data already obtained. The following is an attempt to do so.

Most of this analysis of population dynamics is based on a list of Peregrines banded and recovered before 1964. This list was summarized by Enderson in 1966[1] and is divided almost equally between northern migrants and southern residents. More recently the lists of Peregrines banded as reported by most of the banders who obtained recoveries have been made available. In addition, computer listings of birds banded in the years 1955 through 1966 have been prepared. Although both lists of birds banded are incomplete, they aid considerably the understanding of the recovery data.

SURVIVAL RATE OF BREEDING AGE PEREGRINES

Seventy-four recoveries in the list are of resident Peregrines from the United States or southern Canada; 73 are of presumably arctic migrant Peregrines; and one is of a Peale's Falcon. Sixty-seven of the 74 resident falcons were banded as nestlings. Four were banded as adults, and there is no data on age when banded for the remaining three. Most of the 73 arctic migrant Peregrines recovered, on the other hand, were banded in the United States while on the southward migration in the fall. Fifty-two of the 73 were in immature plumage when banded, including three nestlings, and thirty-four of these were still immature when recovered. We wish to consider only birds of breeding age. Peregrines do not normally breed until the second spring after they are fledged. Therefore we must eliminate from our sample recoveries of birds banded while immature in the year after banding and the next year. We must also eliminate recoveries of birds banded as adults during the year after banding, not only to eliminate the birds banded as first-year adults but to eliminate possible bias from the relatively high recovery rate of some adults shortly after banding—three of the four *anatum* birds banded as adults were recovered within a month. Because this process reduces the size of the sample, it is desirable to add data from other populations. Data on Peregrines recovered in Great Britain is available[2], and as will be shown, it is very similar in pattern to that on North American adult Peregrines. It will therefore be used.

Eighteen recoveries are available for presumably arctic migrant Peregrines banded no later than the fall migration and recovered no sooner than the following fall, and there are twenty-two records of southern resident Peregrines recovered more than a year after banding. There are fifteen recoveries made in Great Britain more than a year after banding. Three of these birds were banded in Norway and Sweden, the remainder in Great Britain. The distribution of these fifty-five recoveries is shown sorted by population in Table 1 to illustrate how parallel the data are for all three groups. In this table, the second year starts one year after the date of banding for the southern residents and for those recovered in Great Britain, nearly all of which were banded as nestlings. For the arctic migrants the second year starts August 15 of the calendar year following banding.

Table 1. Peregrine Recoveries Sorted by Population

Year After Banding	2	3	4	5	6	7	8	9	10	11	12	13	14
Arctic Migrants	6	2	3	1	3	1	2	0	0	0	0	0	0
Southern Residents	6	4	2	3	3	1	1	0	0	0	0	1	1
Recovered in Great Britain	6	0	3	3	1	0	2	0	0	0	0	0	0
Totals	18	6	8	7	7	2	5	0	0	0	0	1	1

Because of their similarity in pattern, it seems reasonable to combine all three populations into a single larger group, and then redivide it into birds banded as nestlings or immatures, and birds banded as adults, as shown in Table 2.

Table 2. Peregrine Recoveries Sorted by Age When Banded

Year After Banding	2	3	4	5	6	7	8	9	10	11	12	13	14
Banded as Nestlings or Immatures	13	5	7	6	5	1	4	0	0	0	0	1	1
Banded as Adults	5	1	1	1	2	1	1	0	0	0	0	0	0

One can, in principle, begin life table computations at the end of the third year after banding just as well as at the second, assuming a model which is that of constant death rate for adults. Changes in band loss for the later years may make a slight difference in the results, but in this case this effect appears unimportant. When the third year after banding is accepted as the base year for the birds banded as nestlings or immatures, and the second year after banding used for the birds banded as adults, and the recoveries are combined, Table 3 results.

Table 3. Recoveries of Breeding Age Adults in Base Year and After

Year After Base Year	Base	1	2	3	4	5	6	7	8	9	10	11	12
Number Recovered	10	8	7	6	3	5	1	0	0	0	1	1	0

If we assume not only the death rate but the probability of recovery remains constant for an individual of breeding age as long as it is alive, then the theoretical curve for the number of recoveries as a function of years after banding is of the form

$$L_x = c_x L_0 e^{-rx}, \qquad \text{...Equation (1)}$$

where L_x is the expected value of the number of birds recovered in the xth year after the base year. The quantity c_x is a correction for the reduced numbers of banded birds available for recovery in a given age group because of the finite length of the observation interval and for band loss, with $c_0 = 1$. The quantity r is the probability of death within a year for a bird of breeding age.

Table 4 for the quantity c_x has been developed using the available records of birds banded each year during the interval of observation in North America, and using the assumption that serious band loss does not start until the fourteenth year after banding (x=11). The British pattern of banding and the interval of observation are much like the North American. The assumption on band loss is based only on the observation that Peregrines walk very little, and on the condition of two recovered bands. An actual band worn about five and one-half years shows very little wear, and a microfilm of a band worn eight years was reported by the Bird Banding Laboratory at Laurel, Maryland to be clear and the numbers easily legible.

Table 4. Values of the Parameter c_x

x	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
c_x	1	.96	.94	.89	.84	.79	.73	.68	.65	.60	.57	.45	.35	.23	.10	0

Using the recovery data of Table 3 and the values of c_x from Table 4, a maximum likelihood calculation produces the values $r = 0.25$ and $L_o = 10.9$ for the parameters of equation (1). The reciprocal of r is the life expectancy of a breeding age Peregrine—four years.

The value of 0.25 for r is compatible with the observed rate of decline of the Peregrines in the upper Mississippi River area[3] (r about 0.24 from 1955-62), and those migrating through Belgium[4] (r about 0.21 from 1951-59) during their respective population crashes, where breeding failure appears to have caused the population to die off at close to the normal adult mortality rate. The decline in Finland[5] was somewhat steeper (r about 0.4), perhaps because (as can be inferred from their greater band recovery rate) those Peregrines were under greater shooting pressure on their wintering ground than those in North America.

REQUIRED NESTING SUCCESS FOR A STABLE POPULATION

From the life expectancy of four years computed above for a bird of breeding age, and the fact that the Peregrine does not normally start breeding until it is two years old, it is a simple matter to determine the number of young birds which must be fledged and survive to breeding age if the population is to be maintained. Since it is probable that not all breeding age birds occupy nesting sites, several values for the per cent of breeding age birds nesting and for proportion of birds fledged surviving to breeding age are used to show the effect of these two variables on the required productivity of nesting pairs to maintain an equilibrium population (Table 5).

This table is correct only for a value of r = 0.25, that is an adult life expectancy of four years. The entry at the upper right-hand corner of the table, 0.68, corresponds to a survival rate for immature birds as high as for adults with all of the breeding age birds occupying nesting sites. Both are unlikely. Clearly, a productivity of less than 0.68 young per pair will result in decline. The actual productivity required must be higher.

Table 5. Average Number of Young Which Nesting Pairs Must Fledge as a Function of Per Cent of Breeding Age Birds Nesting and of Survival of Fledglings to Breeding Age

Per Cent of Breeding Age Birds Nesting	Proportion of Birds Fledged Surviving to Breeding Age 0.2	0.3	0.4	0.5	0.6
100	2.21	1.48	1.11	0.89	0.68
90	2.46	1.64	1.23	0.99	0.76
80	2.76	1.84	1.38	1.11	0.85
70	3.16	2.11	1.58	1.27	0.97

RECOVERY RATES OF BANDED PEREGRINES

A. *Recovery Rates for Principal Sub-Populations.* The recovery rates for banded birds can be determined from the banding data and the recovery data taken together if care is taken to eliminate bias which might result from the fact that only part of the banding data can be found. The original banding records in the files of the Bird Banding Laboratory have been located for most of the banders shown on the list of recoveries. They have not been located, however, for banders who banded Peregrines before about 1955 and obtained no recoveries. Banding records located by identifying all those banders who obtained recoveries have a very high probability of including all banders who banded many Peregrines, but they may not include a significant fraction of those who banded few. It follows that a recovery rate calculated as the ratio of the total number of recoveries reported to the total number of birds banded by those banders who obtained recoveries will certainly be an overestimate of the true band recovery rate.

One method which has a high probability of eliminating bias from this cause is to limit the sample to the birds banded by those few banders who obtained a relatively large number of recoveries. These banders must have banded enough birds so that there is only small probability that other banders who banded as many birds obtained no recoveries and so were not included on the list. Table 6 includes only birds listed in the banding data for banders who obtained five or more recoveries (or in the case of banders in Wisconsin, four or more recoveries). There is about 90 per cent probability that the entries in that table are not biased by the effect discussed above.

Table 6. Recovery Rate by Sub-Population

Sub-Population	Per Cent Recovered	Standard Deviation (Per Cent)
Resident Peregrines from the U.S. and Southern Canada	12.1	2.0
Arctic Migrants Banded on Southward Migration in Wisconsin	15.0	3.0
Arctic Migrants Trapped on Southward Migration on Atlantic Beaches	6.3	1.6
Arctic Migrants Banded at the Nest in Alaska	1.9	1.9
Arctic Migrants Trapped in Texas During the Fall	23.0	7.1

B. *The Recovery Rate of Immature Peregrines as an Indicator of Death Rate.* When compared with that for adults, the recovery rate of immature birds is well known to be high for many species However, it does not necessarily follow that a high recovery rate implies a proportionately high death rate, and we must deduce from other indicators the relationship between the recovery rate and mortality rate of immature birds.

The population which nested in Massachusetts and was reported on by J. A. Hagar[6] provides much pertinent data. During the years 1935-42 the population was stable. Eighty-eight nestlings were banded. Of these, 14 were recovered. Only four of these had attained breeding age when they were recovered, and one might infer from this that only four in fourteen of all birds fledged, or 29 per cent, survived to breeding age. That this is incorrect follows from the known productivity of the breeding birds. During this period of stable population the observed productivity was only 1.14 birds fledged per occupied nesting site. Interpolating in Table 5 we find that if 90 per cent of the breeding age birds actually occupied nesting sites, then about 45 per cent of the fledglings must have survived to breeding age. We should have obtained only four or five recoveries of birds at less than breeding age, rather than the ten actually obtained, if the recovery rate had been proportional to the death rate of such birds. Furthermore, nine of the ten recoveries at less than breeding age were of birds less than one year old, and only three or four should have been if the recovery rate had been proportional to the death rate. Hence we find that the immature recovery rate probably exaggerates the immature death rate by at least a ratio of nine to four, or more than a factor of two.

A somewhat different approach has led to the same conclusion in the case of migrant Peregrines banded in Wisconsin and Texas, but not for those banded on the Atlantic beaches. In the case of the birds banded on the Atlantic beaches the shooting pressure is probably very low, and the recovery rate for immature birds roughly proportional to their death rate.

C. *High Vulnerability of Immature Arctic Migrants Banded in Texas*. The recovery rate of migrant Peregrines banded in Texas while in immature plumage is very high. Twenty-five immature birds and ten adults were banded in the fall migration by the one bander who obtained five or more recoveries. Seven of the immature birds banded were recovered by the next spring, and one in the following fall. All but one were recovered on or near the Gulf Coast, and all but one were shot. How many additional birds were shot and not reported is not known. However, investigations of the recovery rates for ducks and doves have disclosed that less than half of the bands recovered by hunters are reported under ordinary conditions[7,8]. With hawks the proportion may well be less. It seems possible that more than half of the immature Peregrines which reach Texas are shot before the following summer, especially since many of these birds winter in Texas where they are readily shot, as shown by the band recoveries there in winter and spring.

D. *Recovery Rate of Arctic Migrants Banded in Wisconsin*. The recovery rate of immature arctic migrants banded in Wisconsin is also high, although not as high as that of birds banded in Texas. Of 141 migrant Peregrines banded in Wisconsin, 21, mostly immature birds, were recovered, largely to the south in the same fall they were banded.

E. *Recovery Rate of migrant Peregrines Trapped on the Eastern Seaboard*. Not only is the overall recovery rate very low for migrants trapped on the beaches of the Eastern Seaboard, as can be seen in Table 6, but the recovery rate for immature birds is markedly lower than elsewhere during their first year of life. Only four of 142 immature birds banded on the fall migration were recovered before the following August 15. The very low recovery rate may be a consequence of low shooting pressure on the Atlantic Seaboard beaches. The records of recoveries show none of these birds which were released where they were trapped (*i.e.*, not transported inland) were recovered in the United States anywhere except the Atlantic Seaboard beaches and Key West.

AGE RATIOS OBSERVED AMONG MIGRATING PEREGRINES

The west shore of Lake Michigan and the barrier beaches of the Atlantic Coast are two of the most important places from which the fall migration of Peregrines can be observed. In both places, far more immature birds than adults were observed over the period from 1938 to 1967. Berger reported to Enderson[9] that his observations in Wisconsin over many years added up, in those cases where age and sex was determined, to 114 immature birds and 17 adults—a ratio of over 13 immature birds to each two adults. Rice and Berry[10] reported that 368 immature birds and 69 adults were caught at Assateague Island, Maryland during the years 1954-65—a ratio of 10.7 immature birds for each two adults. However, even at the time of the fall migration the adults must exceed the immature birds in numbers. If we assume that on the average 1.5 birds are fledged from each occupied nest, as reported by Hickey[11] for 67 British and American sites, there will be no more than about 1.17 fledglings produced for each two adults because about two adults in nine will be non-breeding first-year adults. When we allow for the fact that some breeding age birds also do not nest, and for losses from the time of fledging until the birds are seen on the migration, we cannot count on much more than about one immature bird for every two adults by the time the birds reach the United States. It follows that a large part (of the order of ninety per cent) of the adult birds are not seen in migration. If, also, as seems likely, only a fraction of the immature birds are seen, then only about a tenth that fraction of the adults are seen.

GEOGRAPHICAL SEPARATION OF ARCTIC MIGRANT PEREGRINES FROM SOUTHERN RESIDENTS

The banding returns show a distinct separation in locations of band recoveries along the Eastern Seaboard between the arctic migrants and the southern residents. None of the 74 banding returns from the Peregrines which nested in the United States and Southern Canada are from the Atlantic beaches. On the other hand, no Peregrine Falcon banded and released on Assateague Island, Maryland through 1963 was recovered inland in the United States, although they were found on the Atlantic beaches of the eastern United States, south through the Caribbean into South America and north to the west coast of Greenland.

POPULATION ESTIMATES FROM THE BANDING DATA

The available lists of birds banded on the Atlantic beaches show that an average of about five adults and seven immature birds were banded annually during the period from 1939 through 1962. No recoveries of the birds on these lists were made by banders in subsequent migrations. It is possible to show from this that the probability is at least 0.95 that the population from which the birds migrating along these beaches was drawn consisted of at least 1000 adults, and that the probability is at least 0.5 that the population consisted of at least 4500 adults. The situation is analogous to that of drawing balls from an urn: if a ball is drawn from an urn containing only a few balls, marked and returned, then the chance of drawing it again if the contents of the urn are well mixed is high; if, on the other hand, the urn contains many balls, the chance of drawing the marked ball again is small.

Using the same productivity as was assumed in the discussion of age ratios observed among migrating Peregrines, a population consisting of 1000 adults can be expected to produce on the order of 400 or 500 immatures at the time of the fall migration.

SOME DEDUCTIONS FROM THE RESULTS

Certain conclusions may be drawn from the data presented in this paper which may be helpful in considering the interaction of man with the Peregrine Falcon population.

A. *Effect of Trapping on the Migrant Peregrine Falcon Population.* Ten per cent or less of the adults migrate on the Atlantic and Lake Michigan beaches with the immatures. Therefore shooting or trapping pressure on adults on these beaches is unlikely to have a large direct effect on the adult segment of the migrant population.

B. *Protection of Southern Residents While Trapping Migrant Peregrines.* Because of the behavioral separation of races, trapping of migrant Peregrines on the Atlantic beaches, on the Gulf Coast, and in Florida could be expected to have no effect on the population resident in the United States and southern Canada even if it were to recover.

C. *Potential Indicator of Declining Tundra Peregrine Population.* The most sensitive indicator of an impending decline would be the disappearance of the immature birds from the migration routes while the adults continued to be observed. If a ratio of the order of five or more immature birds to each adult continues, this can probably be taken as evidence that the birds are continuing to breed, and that any decline will be slow. If the ratio falls off sharply and stays low, it will probably signal a population crash. In the fall of 1969, the ratio of immatures to adults remained high in over 200 birds sighted on the beaches of the Eastern Seaboard, but had fallen to half of its value five years previously in Texas[12].

D. *Effect of Harvest of Immature Peregrines from the Population.* It will be recalled that the population which migrates through Wisconsin withstood far more gunning pressure than was imposed on the population migrating along the Atlantic beaches and seems to have done so without measurable effect. In view of the apparent continuing lack of gunning pressure on the Atlantic beaches, the population which migrates down them can almost certainly withstand some trapping of immature birds without difficulty so long as it continues to breed successfully. The size of the harvest needs to be determined. However, based on the calculations of this paper, there appear to be at least the order of 500 immature birds produced each year. In fact, observations of about 200 Peregrine Falcons, mostly immature, on the Atlantic beaches in the fall of 1969 as reported by qualified observers to R. B. Berry[13] and to the author indicate that the production must still be considerably greater than 500 birds, since it is not conceivable that as many as a third of the total immature population were sighted. Regulating the harvest of these birds on the basis of an assumed production of 500 immature birds per year should be a conservative approach.

ACKNOWLEDGEMENTS

The author is indebted to Mr. Earl B. Baysinger, Chief of the Bird Banding Laboratory, Laurel, Maryland for providing copies of the original lists of birds banded from the files of the Laboratory, and to Dr. J. H. Enderson for his continuing encouragement and valuable suggestions.

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