

BREEDING SUCCESS IN AN ISOLATED POPULATION OF ROCK DOVES

DAVID E. PREBLE AND FRANK H. HEPPNER

There has been considerable discussion about actual or potential means by which some animal populations might maintain stability in the face of variable environmental pressures. This paper reports the results of a 2-year study of breeding success in an isolated population of Rock Doves (*Columba livia*, hereafter referred to as the pigeon) which suggests that an increase in egg predation is followed by a lowering of the adult nest desertion rate, thus maintaining the recruitment of new individuals into the population at a constant rate.

STUDY AREA AND METHODS

The study involved a breeding colony of 45-55 pigeons (depending on season) in the abandoned Plum Beach lighthouse in Narragansett Bay, Rhode Island. This structure is separated from land 0.8 km to the west and 1.2 km to the east. Food is readily available year around near habitation to the west and east from bird feeders and natural sources, but there is no food or water on the lighthouse itself. Severe storms and fog during the winter could cut off access to food and affect adult mortality. Great Cormorants (*Phalacrocorax carbo*) roosted on the upper outside portion of the structure. The Black-crowned Night Heron (*Nycticorax nycticorax*) was an occasional summertime visitor. No other vertebrates were known to be in the lighthouse. To minimize disturbance, we did not band individuals, and so do not have an accurate measure of the number of non-breeders or colony size. The number of active nests ranged from two during breeding lows to 25 at breeding peaks.

To determine the recruitment rate (total breeding success, or number of young fledged per eggs laid), we visited the lighthouse every 1-2 weeks in 1971 and 1972. On each visit, the location of every nest, egg and young was recorded on maps of each of the 5 levels of the 8-m-diameter lighthouse. The nests were scattered through each level, and were no closer than 1 m to each other. During the first full year of observation we left the nests untouched and in the second year we removed a fraction of eggs laid, simulating the action of an egg predator. The objective was to see if egg desertion would drop by an amount corresponding to the number removed, thus maintaining a constant recruitment rate. This artificial predation was performed by counting the number of eggs laid since the last visit. Twenty percent of this number were then removed from the total number present.

The removed eggs were checked for fertility and stage of development. Egg replacement by the birds would have biased the results, but the pigeon is a determinate layer with a 2-egg clutch-size (Sturkie 1954). At the end of another full year, the results were tabulated and compared both with the data from the first year, and with breeding data from Murton and Clarke (1968).

RESULTS

Breeding season.—The Plum Beach light pigeons are year-round breeders, but demonstrate a different annual pattern than seen in the British

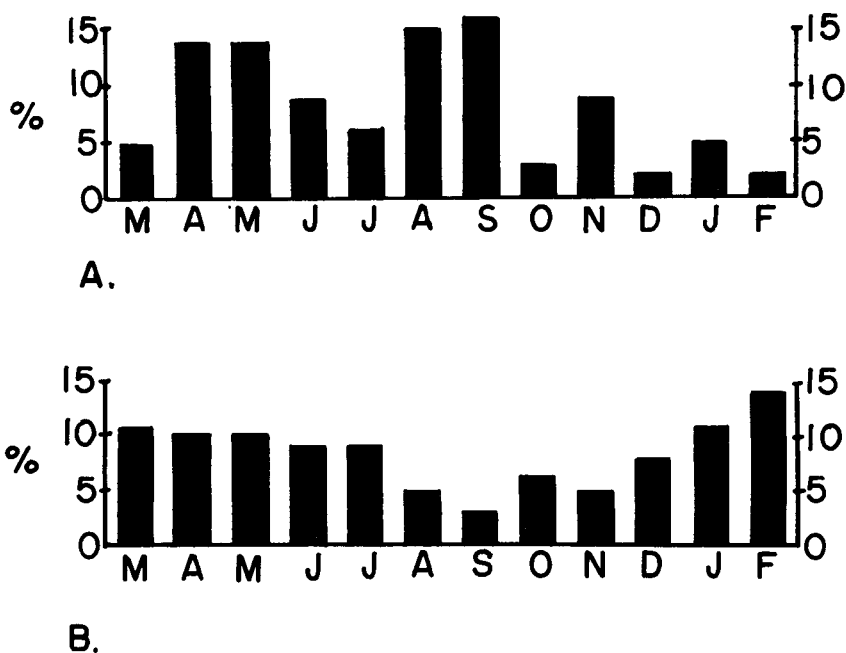


FIG. 1. Number of eggs (expressed as a monthly percent of the year's total) laid in each month by pigeons (A) in Yorkshire, England (Murton and Clarke 1968); composite of 2 years, 1965-66; (B) in Narragansett Bay, Rhode Island; monthly average for the years 1971-72 and 1972-73.

Isles (Fig. 1) by Murton and Clarke (1968) or Lees (1946). Lees found a constant low level of breeding in northern Scotland, with high activity at 4 periods; April, August, November and January. Murton and Clarke (1968) found the same pattern in England, with the spring and summer periods accounting for 60% of the total annual breeding. At the Plum Beach light, however, there was a marked low in August and September, followed by a rather steady rise to a high point in February and March, which was then followed by a steady drop through the spring until the August low point was reached again.

Breeding success.—The observations recorded at each visit to the lighthouse are shown in Table 1. The difference between the years in total egg and total juvenile observations is the result of more visits in the second year, since the total egg and juvenile observation figures are the sum of the total number of eggs or juveniles present at each visit. The total number of new eggs and total number of new juveniles was unaffected by the number and frequency of visits, since visits were close enough together

TABLE 1
COMPARISON OF BREEDING SUCCESS OF PIGEONS IN NON-ISOLATED (MURTON AND CLARKE 1968) AND ISOLATED (PREBLE 1973) LIGHTHOUSES

	Murton and Clarke		Preble	
	1965	1966	1971-72	1972-73
Total egg observations	—	—	948	1295
Total juvenile observations	—	—	547	860
Total eggs laid	346	409	562	672
Total no. hatched	211	286	312	388
% hatched	61	70	56	58
% egg predation	25	15	1 (8) ^a	22 (145)
% infertile	5	5	5 ^b	4 (6)
% deserted	9	10	38 (218)	16 (106)
% fledged of eggs hatched	70	71	77 ^c	83 ^c
% fledged of eggs laid	43	49	42 ^c	48 ^c

^a Numbers in parentheses are actual numbers of eggs.

^b Approximation, see text.

^c Calculated value, see text.

that no eggs could be laid or juveniles hatched between visits without being counted. The lower new egg and new juvenile production for the first year is, in part, due to the termination of the first year's data acquisition, due to adverse weather, 1 full week before the end of a complete year, in February 1972. Inflating the production of the second year was the high number of eggs laid in January and February 1973, probably due to an unusually mild and snowless winter which resulted in a large number of adults in breeding condition.

The parameters involved in breeding success for the 2 years at Plum Beach light and, for comparison, the 2 years that Murton and Clarke (1968) worked on the beacon tower at Flamborough Head, are also shown in Table 1. On the Plum Beach light, 1971-72, total egg predation consisted of 8 eggs (1%) pecked open or removed between 10 June and 3 August 1971. During 1972-73 natural predation consisted of 9 eggs pecked open or removed, and was supplemented by the experimental removal of an additional 136 eggs to bring the total "predation" level for that year to 22%.

The number of infertile eggs (Table 1) was determined in 1972-73 by opening and examining the eggs removed. The number of infertile eggs was six, which is 4.4% of the total, or 1.8-9.4% at 95% confidence limits. This value is in the same range ($\chi^2_{(2)} = 0.01$, $P > 0.99$, NS) as the 5% (3.6-6.8% at 95% confidence limits) reported by Murton and Clarke (1968). Since there was no nest disturbance in 1971-72, it was impossible to check

directly for infertility by opening and examining the eggs, although it was indirectly determined that there was little or no change in egg fertility between the years of the study (Preble 1973). Since there was a constant level of infertility in the 2 years, and there was no significant difference in fertility between the British and American populations, Murton and Clarke's (1968) 5% figure is used in all calculations (Table 1).

Egg desertion (Table 1) was determined on the assumption that a fertile egg which is not destroyed by predation will hatch if incubated. Failure to incubate then constitutes desertion of the egg. Desertion may be caused by adult mortality or abandonment. We determined the number deserted by subtracting the number removed by predation and infertility from the number that failed to hatch. In 1971–72, desertion accounted for 38% of the total number of eggs laid, while in 1972–73 it accounted for 16%.

The young fledged per young hatched (juvenile success) and the young fledged per eggs laid (total success, Table 1), were determined indirectly. If there was no mortality at any state of the reproductive cycle, then we expected that a ratio of the total number of eggs present and juveniles present on each visit would equal the ratio of the amount of time an individual spent in the egg compared to the amount of time spent as a juvenile: 17.5 and 24 days, respectively (Whitman 1919, Goodwin 1967, Murton and Clarke 1968). Taking the total number of egg observations for 1971–72, and the known time individuals spent in the egg as a juvenile, and assuming no mortality of eggs or juveniles, the expected number of observations of juveniles would reflect the following ratio: $17.5 \text{ days}/24 \text{ days} = 948 \text{ egg observations}/X$. The expected number of observations of juveniles assuming neither egg nor juvenile mortality (X) then equals 1300. The juvenile mortality was determined as follows. Since the number hatched (Table 1) shows that the actual egg survival was 56% (egg mortality 44%), then the expected number of observations of juveniles if there had been no juvenile mortality, but with the observed egg mortality is: $0.56 \times 1300 = 728 = \text{expected number of observations of juveniles with the observed egg mortality}$. Since there were only 547 actual observations of juveniles (Table 1) then the level of juvenile success must be: $547 \text{ actual observations}/728 \text{ expected observations} = 75\% \text{ fledged of eggs hatched}$, or a juvenile mortality of 25% of the eggs hatched. Since 312 eggs hatched (Table 1), and inferentially 75% were successfully fledged, then the number that fledged of all the eggs laid equals: $0.75 \times 312 = 234 \text{ eggs fledged of } 562 \text{ eggs laid}$. The total success (fraction of eggs laid) then becomes: $234 \text{ eggs fledged}/562 \text{ eggs laid} = 42\%$. The same procedure applied to the data from 1972–73 yields a fraction fledged of eggs hatched of 83% and a fraction fledged of eggs laid of 48%.

It thus appears that net recruitment, measured by total nest success,

remained at approximately the same level (42% in 1971–72, and 48% in 1972–73; $t_s = 1.29$, $P < 0.90$) although egg “predation” significantly differed, from 1% in the first year to 21% in the second year ($t_s = 8.03$, $P > 0.001$). The fraction fledged of eggs hatched (Table 1) is somewhat higher at Plum Beach light than in England, and somewhat higher at Plum Beach light in 1972–73 than in 1971–72, probably reflecting the milder winter.

DISCUSSION

Population homeostasis in the pigeon could be maintained through a mechanism which regulates the recruitment rate of young adults by means of a variable rate of egg desertion. Lack (1966, 1968) suggested that each species produces as many young as it can successfully rear in a food-limited environment and that adult mortality through starvation is the variable factor that controls population size. Skutch (1967) has argued that some species could produce more young than they do, and that the rate of egg-laying may be a factor. Fretwell (1969) has attempted to mediate this dispute by suggesting that there may be a dominance hierarchy which extends to nestlings, the lower ones being most subject to selective mortality in hard times.

In prior work on the breeding biology of the pigeon, egg predation was sufficiently high to mask the effects of egg desertion (Murton and Clarke 1968). On the Plum Beach lighthouse, where the rate of natural egg predation is very low and suitable nest-sites are readily available, the results of this study suggest that the population has a breeding reserve which enables it to remain stable through selective desertion of eggs. Although there is insufficient evidence to do more than speculate, this desertion appears to be a behavioral mechanism, rather than the result of starvation of adults. If the latter was the case, then one would expect to see a high rate of desertion of juveniles as well as eggs. The desertion, however, is suffered primarily by eggs, and only when predation of eggs is low.

There are several mechanisms that might account for this differential desertion. Wynne-Edwards' (1963) model of group selection is not incompatible with the observations reported here, but the more recent concept of kin selection (Eberhard 1975) requires fewer assumptions about conditions existing in the colony. The observations here do support the idea of population regulation based on behavior, but cannot help to differentiate between the competing models of behavioral regulation.

SUMMARY

Breeding success (number fledged/eggs laid) and nest desertion were determined in a flock of Rock Doves (*Columba livia*) breeding in an isolated, abandoned lighthouse in Narragansett

Bay, Rhode Island, over a 1-year period. Breeding success was 42% in that year and 38% of nests with eggs were deserted. In the following year, 20% of eggs laid were removed. Nest desertion dropped to 16%, while breeding success was 48%, suggesting that recruitment might be related to nest desertion.

ACKNOWLEDGMENTS

Our thanks to the Rhode Island Department of Natural Resources for permission to visit the lighthouse, and C. Robert Shoop for critically reading the manuscript.

LITERATURE CITED

- EBERHARD, M. J. W. 1975. The evolution of social behavior by kin selection. *Quart. Rev. Biol.* 50:1-33.
- FRETWELL, S. D. 1969. The adjustment of birth rate to mortality in birds. *Ibis* 111:624-627.
- GOODWIN, D. 1967. Pigeons and doves of the world. British Museum (Nat. Hist.), London, England.
- LACK, D. 1966. Population studies of birds. Clarendon Press, Oxford, England.
- . 1968. Ecological adaptations for breeding in birds. Methuen and Co., London, England.
- LEES, J. R. 1946. All the year breeding of the Rock Dove. *Br. Birds* 39:136-141.
- MURTON, R. K. AND S. P. CLARKE. 1968. Breeding biology of Rock Doves. *Br. Birds* 61:429-448.
- PREBLE, D. E. 1973. Breeding homeostasis in the feral Rock Dove (*Columba livia*). M.S. thesis, Univ. Rhode Island, Kingston, Rhode Island.
- SKUTCH, A. F. 1967. Adaptive limitation of the reproductive rate of birds. *Ibis* 109:579-599.
- STURKIE, P. D. 1954. Avian physiology. Comstock Publishing Assoc., Ithaca, New York.
- WHITMAN, C. O. 1919. Posthumous works, Vol. 3. The behavior of pigeons (H. A. Carr, ed.). Carnegie Inst., Publ. 257. Washington, D.C.
- WYNNE-EDWARDS, V. C. 1963. Intergroup selection in the evolution of social systems. *Nature* 200:623-626.

DEPT. ZOOLOGY, UNIV. RHODE ISLAND, KINGSTON, RHODE ISLAND 02881.

ACCEPTED 22 OCT. 1980.