FLUCTUATIONS IN COLONY SIZE IN THE ROOK,
CORVUS FRUGILEGUS

BY S. C. RICHARDSON*, I. J. PATTERSON† AND G. M. DUNNET†

* Department of Social Statistics, The University, Southampton S09 5NH and † Culterty Field Station, Newburgh, Ellon, Aberdeenshire AB4 0AA

SUMMARY

(1) Capture-recapture data on rooks in two intensively studied colonies in north-east Scotland are used to obtain an estimate of 79.2% (S.E. 2.4%) for the annual survival-and-return rate for adult members of a colony.

(2) Such a high rate indicates that the observed large fluctuations in rookery sizes are due to fluctuations in the number of birds joining the breeding groups each year.

(3) It is shown how this arises in a simple model.

INTRODUCTION

Animal populations can often be regarded as aggregations of spatially separated sub-populations, perhaps because suitable habitat occurs only in discrete patches or because a clumped distribution has been adopted in a continuous habitat. In either case, each group may effectively be isolated from the others or there may be a significant degree of interaction including the possibility of exchange of individual animals between groups. It is clear that such interactions should be included in a proper assessment of population dynamics. An extreme but often-quoted example is provided by Huffaker's (1958) experiments on a predator-prey system established on an archipelago of habitat, in which it proved possible to produce overall persistence by manipulation of migration rates even though rapid extinction on a single island of habitat was certain. Unfortunately, exigencies of scale often restrict field studies to single sub-populations which may then have to be assumed closed. Theoretical approaches to population dynamics have also tended not to be concerned with spatial structure, although the 'island' and 'stepping-stone' models of geneticists (e.g. Kimura & Weiss 1964) and models developing from theories of island biogeography (MacArthur & Wilson 1967) are now familiar, while a discrete structure is essential for work on group selection (Wynne-Edwards, 1962).

The rook, Corvus frugilegus, is a species whose population has a conspicuously colonial structure. We shall use 'colony' to refer to the group of birds whose breeding site is the 'rookery'. Although colonies seem to be independent in so far as they have largely separate feeding areas and centre their activities on their own rookery through much of the year (Coombs 1961; Philipson 1933), different colonies join together to roost outside the breeding season. The likelihood of mixing through contact at the winter roost, observations of 'irregular and violent fluctuations' in the sizes of rookeries over the years and a high rate of desertion and founding of rookeries led Yapp (1951) to suggest that the colony may not be a stable unit. In his study area in west Gloucestershire, of fifty rookeries observed in 1933 as many as eighteen had been abandoned by 1939 while eighteen new ones had appeared, with three transients in the meantime. Throughout this period the
total population size was steady. Alexander (1933) noted a similarly high turnover in the Upper Thames Valley. Of 101 rookeries counted in 1928 and listed by Nicholson & Nicholson (1930), seventeen had disappeared by 1931 and all but two of fifteen newly discovered rookeries appeared to be new foundations. (These rates may be inflated by human interference: Alexander points out that five of the deserted sites were within the City of Oxford.) These data do not necessarily cast any light on Yapp’s suggestion since it is possible for the colony to have continuity whilst changing its breeding site frequently.

We now examine the stability of the colony on a subset of data collected at Aberdeen University on the rooks of the Ythan Valley and neighbouring areas of north-east Scotland. The original study is described in Dunnet & Patterson (1968).

ROOKS IN THE YTHAN VALLEY

The data include records of rookery sizes from nest counts in April for all rookeries in the Ythan Valley in the years from 1963. The definition of ‘rookery’ is that of Patterson, Dunnet & Fordham (1971), a ‘simple’ rookery being a distinct group of nests more than 100 m from any other group. Many birds, both adult and juvenile, have been trapped and tagged so as to be individually identifiable in the field and some of these have been found subsequently to be breeding in one of two intensively studied rookeries at South Artrochie and Macharmuir. These are about 1 km apart. The rookeries of the area are mapped in the original study and in Patterson, Dunnet & Fordham (1971).

The area is presumably very favourable for rooks since the density at 24 nests/km² is a good deal higher than densities recorded in many studies in other districts (see the list in Coombs 1960). Rookeries also tend to be larger than elsewhere, which may be due to conservatism in choice of nesting site implying that a general population increase produces larger rookeries rather than more rookeries; it does not seem to be caused by a lack of suitable sites (Patterson, Dunnet & Fordham 1971).

The total population of the area has been stable following a rapid increase from the 1963 level (Fig. 1) but the sizes of individual rookeries do fluctuate considerably. Thus the variance of the sum of rookery sizes is less than the sum of the variances of rookery sizes, which implies negative correlations, on average, between the sizes of different rookeries. In the absence of any model of inter-colonial competition predicting, for example, that high production in one colony tends to imply low production in its neighbours, we may take this as evidence for population interchange of some sort. The question of population exchange between colonies is investigated below using data from the intensively studied rookeries.

There is a low rate of abandonment of rookeries: of forty-five simple rookeries in the Ythan Valley over the years 1963–75 inclusive only six were ever recorded as being unoccupied (excluding sites where felling was known to have taken place). It is possible that this reflects the predominance of large rookeries for, on average, only six rookeries each year had less than thirty nests and it may be that the extinction rate for small rookeries is as high as it apparently is elsewhere. Four of the sites which became unoccupied fell into this category regularly: only one was known to have held a large population, seventy-five nests declining to zero over 6 years. The highest number of nests at a site the year before desertion was twenty-seven. Both South Artrochie and Macharmuir were well above this size, averaging 253 and 122 nests respectively over the first 10 years of the surveys. Thus the former was larger than the largest rookery recorded in five of the sixteen areas covered by the studies listed in Table 1 of Patterson, Dunnet & Fordham (1971).
Results from the intensively-studied rookeries

We first examine the fidelity of adult birds to the colony by calculating a 'survival and return' rate based on sightings of marked birds in the rookery in successive breeding seasons. These data are analysed by the method of Cormack (1964) for the stochastic capture-resighting experiment. Both South Artrochie and Macharmuir rookeries were occupied each year and thus it is assumed that fidelity to the rookery can be equated with fidelity to the colony.

It is necessary to assume that all birds in the marked sample from a particular colony have the same chance of being seen in a particular year. Given enough observation sessions, a bird that has lost one of the two tags it originally received should be effectively as detectable as a bird retaining both tags, while other possible exceptions, such as females remaining on nests unobservable from the hide, are not expected to be important. A further assumption is that the probability of death in a given year is the same for all members of the sample. Since loss of identifiable markings is equivalent to death in the experiment it is clear that the probability of 'dying' must be higher for birds with only one tag than for birds with two; there is also a suggestion that tags of different kinds may be lost at different rates. In principle there is no difficulty in incorporating extra parameters into the model to describe tag loss but there do not seem to be sufficient data to make this worthwhile. Hence tag loss is ignored and, as usual, the calculated survival and return rate may be interpreted as probably being an under-estimate of the true rate. If the estimated rate is to be taken as applying to the whole colony it must be assumed that all parameters are identical for marked and unmarked birds. A possible difference is inherent in the method of construction of the sample. Rooks were caught and tagged
mainly in the fields and not in the rookery but, in order to obtain as homogeneous a group as possible for the analysis, a ‘capture’—the admittance of a marked bird to the sample—is defined as occurring when a previously tagged bird is recorded as breeding in the rookery and hence definitely belonging to the colony. Since there is a number of non-breeding birds associated with a colony (about 10% of the adults according to Yapp, 1951) there is the possibility of birds that have never successfully bred in the colony being insecurely attached to it and having a low rate of return. ‘Resightings’ of marked birds in subsequent breeding seasons did not require evidence of breeding, presence alone being sufficient, justified by the infrequency of records (Table 1) of the presence of members of one of the intensively studied rookeries in the other in the same season.

### Table 1. Sightings over the whole year of birds belonging to either of the intensively studied rookeries

<table>
<thead>
<tr>
<th>Year</th>
<th>No. of birds</th>
<th>Average no. of sightings in own rookery</th>
<th>No. of these birds seen in other rookery</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(a)</td>
<td>(b)</td>
</tr>
<tr>
<td>1966–67</td>
<td>42</td>
<td>27.0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>6.5</td>
<td>2</td>
</tr>
<tr>
<td>1967–68</td>
<td>63</td>
<td>10.2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>11.0</td>
<td>3</td>
</tr>
<tr>
<td>1968–69</td>
<td>53</td>
<td>7.1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>10.0</td>
<td>2</td>
</tr>
<tr>
<td>1969–70</td>
<td>44</td>
<td>11.9</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>34</td>
<td>17.9</td>
<td>3</td>
</tr>
<tr>
<td>1970–71</td>
<td>20</td>
<td>23.9</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>22</td>
<td>23.6</td>
<td>2</td>
</tr>
<tr>
<td>1971–72</td>
<td>20</td>
<td>21.3</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>19.4</td>
<td>1</td>
</tr>
</tbody>
</table>

In each year the upper and lower lines refer to South Artrochie and Macharmuir respectively. A bird is defined for the purpose of this table as belonging to the rookery in which it bred, was suspected of breeding or was seen nest-building in that year. Columns (a) and (b) refer to sightings at any time of the year and in the breeding season, respectively. Column (c) records birds seen more than once in the other rookery, all sightings being in autumn only.

The data for the estimation of the average survival and return rate for South Artrochie are presented in Table 2. A similar calculation for Macharmuir gives an average rate of 0.802 with a standard error of 0.037. These rates are not significantly different and are combined to give:

\[
0.791 \pm 0.024.
\]

An accurate estimate of adult survival does not seem to have been found before although Coombs (1960) suggests 84%.

It is apparent that, bearing tag loss in mind and taking the above estimate as applicable to the whole colony, the rate of survival and return is so high as to imply that the proportion of adult birds transferring allegiance from one colony to another is small. This stability appears at odds with the observations of previous studies mentioned above. If there is mixing through contact at the winter roost this may only affect small colonies: a
### Table 2. The rate of survival and return estimated from the South Artrochie data

<table>
<thead>
<tr>
<th>Year</th>
<th>Newly captured $u_i$</th>
<th>Birds captured in previous years $m_i$</th>
<th>Birds resighted $r_i$</th>
<th>Birds alive but not seen $z_i$</th>
<th>Rate of survival $\phi_i$</th>
<th>Standard error $\delta_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1965</td>
<td>32</td>
<td>32</td>
<td>29</td>
<td>0.906</td>
<td>0.052</td>
<td></td>
</tr>
<tr>
<td>1966</td>
<td>16</td>
<td>29</td>
<td>45</td>
<td>0.778</td>
<td>0.062</td>
<td></td>
</tr>
<tr>
<td>1967</td>
<td>6</td>
<td>35</td>
<td>41</td>
<td>0.702</td>
<td>0.092</td>
<td></td>
</tr>
<tr>
<td>1968</td>
<td>2</td>
<td>20</td>
<td>22</td>
<td>0.759</td>
<td>0.117</td>
<td></td>
</tr>
<tr>
<td>1969</td>
<td>22</td>
<td>13</td>
<td>35</td>
<td>0.817</td>
<td>0.074</td>
<td></td>
</tr>
<tr>
<td>1970</td>
<td>1</td>
<td>34</td>
<td>35</td>
<td>0.752</td>
<td>0.173</td>
<td></td>
</tr>
<tr>
<td>1971</td>
<td>—</td>
<td>22</td>
<td>10</td>
<td>—</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>1972</td>
<td>—</td>
<td>13</td>
<td>13</td>
<td>—</td>
<td>—</td>
<td></td>
</tr>
</tbody>
</table>

Average rate $\hat{\phi} = \left\{ \prod_{i=1}^{d} \hat{\phi}_i \right\} = 0.783$  
S.E. $\delta(\hat{\phi}) = 0.031$.

Notation (Seber 1973): in year $i$, $u_i$ birds are newly 'captured' (see text) and $m_i$ birds captured in previous years are resighted; $z_i$ birds are not seen but are known to have been alive by virtue of being seen in later years. $R_i = m_i + u_i$ is the total 'released' in year $i$, of which $r_i$ are seen in some subsequent year. $\phi_i$ estimates the rate of survival between years $i$ and $i + 1$ with return to the same rookery. The table is not extended beyond 1972 because the low numbers involved make estimation too imprecise.

Larger group may be better able to maintain its integrity in contact with others. But even large rookeries undergo fluctuations far greater than is consistent with the high estimate of adult fidelity obtained here unless there are large fluctuations in the number of birds joining the colony each year. The term 'recruitment' will be used for the annual addition to the breeding group.

#### Recruitment

It is clear that young rooks do not necessarily come to breed in their natal colony. Dunnet & Patterson (1968) present data that show considerable population increase in rookeries suffering heavy losses through shooting of fledglings, increases that could not be accounted for by local production. The rookery of birth was known for very few birds breeding in the intensively studied rookeries but of ten pulli ringed in South Artrochie in various years and later identified as breeding, four were doing so in Macharmuir and six in South Artrochie.

Grace (1973) observed young marked rooks visiting both South Artrochie and Machar-muir and attempted to relate subsequent recruitment to the behaviour shown on such visits. Whatever behavioural mechanisms are involved, the probability of a potential recruit joining a particular colony must depend on perceived qualities of that colony which could be termed 'attractiveness'. The operation of natural selection should ensure a close relation between 'attractiveness' and the expected breeding success on joining that colony. As the simplest model, we suppose that 'attractiveness' is a function only of the current size of the colony, possibly involving parameters determined by physical conditions such as limitations of space at the rookery occupied by the colony. Since a young rook is a potential recruit to several colonies, it is the relative attractiveness of the alternative colonies that matters. The proportion of recruits going to colony X amongst those going to X or Y will be a function of $n_x$ and $n_y$, the current sizes of these two colonies, and independent of the sizes of other colonies. Holding $n_y$ constant, how do we expect the proportion $p_{xy}$ to vary as a function of $n_x$?
Size of rook colonies

For a social species it is reasonable to assume that attractiveness initially increases with group size, so that $p_{xy}$ is an increasing function of $n_x$ for small $n_x$. This effect of aggregation is sometimes termed an Allee Effect. Ultimately as attractiveness eventually falls to zero (through overcrowding or other factors) $p_{xy}$ must do likewise. Hence the simplest model is a unimodal curve for $p_{xy}$ against $n_x$ at constant $n_y$.

In lieu of sufficient data on any one pair of rookeries, we attempt to demonstrate that $p_{xy}$ does indeed have this form by combining data from several pairs, assuming that recruitment to similar pairs of rookeries will be described by similar curves. The forty-five simple rookeries whose sizes were recorded over the years 1963 to 1975 inclusive provide twenty-one pairs of neighbours (which are presumably alternative breeding sites for a potential recruit) of which one had between 200 and 220 nests in the year in question while the other was smaller. We estimate the proportion of recruits to both going to the smaller of the pair by supposing that 82% of the previous year’s population remains to breed at each rookery, this figure being the estimate of 79% for survival and return given above, augmented by a crudely estimated 3% allowance for tag loss. Of the twenty-one points, plotted in Fig. 2, three pairs refer to the same pair of rookeries in different years.

The points in Fig. 2 clearly do follow a curve of the suggested shape. An analysis of variance indicates a highly significant quadratic term in the regression ($F$-ratio of 10-32, 1 and 18 d. f.).

Two further points which could have been added to Fig. 2 were omitted as referring to different cases. In each pair, the smaller rookery held a low number of nests only in 1963, the year of generally low population, and then increased considerably, maintaining large populations thereafter.

DISCUSSION

In order to indicate some of the implications of this pattern of recruitment we suppose that, in a particular year, colony $C_i$ has a share $s_i$ of the total population and a share $r_i$ of
total recruitment. If the mortality rate $\mu$ and the birth rate $\lambda$ (including survival to recruitment) are taken as the same for all colonies then $C_t$ will be larger in the following year if

$$r_t > s_t \mu / \lambda.$$  

(1)

If $s_t$ is small then this inequality is satisfied by small values of $r_t$ so it should be noted that the model need not predict rapid extinction of small colonies, as Fig. 2 might suggest at first sight.

The percentage change in size in the following year is

$$\left( \lambda r_t / s_t - \mu \right) \times 100\%$$  

(2)

from which we may see how relatively large fluctuations in colony size arise. Taking $\mu$ as 0-18 and supposing firstly that there is no change in total population ($\lambda = 0.18$), we find that a colony holding 5% of the population will increase by almost 11% of its own size if its share of total recruitment is no more than 8%. Secondly, the same share of recruitment would lead to the colony increasing by almost 19% of its own size if the net population increase was 5% ($\lambda = 0.23$).

The effect of large changes in total population may be surmised by crudely dividing colonies into those occupying small and large rookeries, where ‘small’ and ‘large’ are to be understood as applying to the upper size at which the ‘attractiveness’ of the occupying colony has effectively declined to zero. This may be a function of physical limitations at the rookery, as suggested before, of the size of the feeding areas available to the colony and of other factors. A year of major population decline will probably be characterized by a high value of $\mu$ and a low value of $\lambda$. Thus eqn (2) suggests that the effect of variations in the ratio $r_t/s_t$ is small, so that all colonies decrease by much the same percentage. An effect of this is that large rookeries will tend to be much more attractive than small rookeries in the following year, so that a general population increase would then tend to be concentrated on the large rookeries. These predictions can be tested only partly on our data. It has been suggested (Dunnet & Patterson, 1968) that the low total population of the Ythan Valley area in 1963 may have been an outcome of the severe winter of 1962–63 and that the greatly increased population in 1964 was a movement towards the previous level. Unfortunately figures are not available for 1962 so only the population increase between 1963 and 1964 can be examined. Of twenty-seven simple rookeries whose sizes are recorded for both these years, the largest not showing an increase declined from 166 to 158 nests. The twelve rookeries larger than this all increased, as against only eight of the fourteen smaller ones, so that an overall population increase did indeed correspond to an increase mainly in the larger rookeries.

The recruitment pattern discussed here bears obvious similarities to a theory of habitat selection put forward by Fretwell (1972). He considers birds faced with the choice of alternative habitats for breeding and predicts that the distribution over the habitats will be such as to equalize ‘suitability’, a measure of expected breeding success, if the birds possess some means of assessing suitability. When an Allee Effect is operating, he demonstrates (pp. 89–90) how small changes in total population may result in drastic changes in distribution over habitats. However the full theory cannot be applied to a colonially-structured population by substituting ‘colony’ for ‘habitat’ unless it is assumed that all birds move freely from colony to colony. It has been demonstrated here that established breeding adults do not do this. One would expect this of course to be a general result: the better strategy for breeding members of a colonially-breeding species will usually be to remain in the present colony rather than competing for a place elsewhere.
ACKNOWLEDGMENTS

We are happy to reiterate our gratitude to all those involved in gathering the data and to landowners who allowed access to rookeries. I.J.P. and G.M.D. thank the Agricultural Research Council for financial support. S.C.R. thanks the Science Research Council for a Research Studentship and the staff at Culterty Field Station for their hospitality during his visit.

REFERENCES


(Received 10 March 1978)