

AN ANALYSIS OF BREEDING AND MORTALITY IN A MATURING KITTIWAKE COLONY

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ABSTRACT.—J. C. Coulson and other investigators have made an intensive study of the fecundity and mortality patterns of a kittiwake colony at North Shields, England, particularly with reference to differences between birds nesting at the center and at the edge of the colony. We have used the completeness of this data base to compute the intrinsic rates of increase (r) for center and edge birds, both during the colony's growth phase and after it has stabilized, and have used these values to quantify the roles of breeding and mortality in accounting for demographic change.

With center advantage defined as the difference between the r 's of center and edge populations, 67% of center advantage in the growth phase was due to high survivorship of center males. Likewise, transition to the lower growth rates of the stable phase was almost entirely due to increased mortality. During the stable phase, however, center advantage persisted and was entirely due to higher fledging rates among center birds. Although male survivorship was the reason for center advantage in the growth phase, in simulated stable-phase populations, where both sexes experienced female mortality rates, center advantage was twice as great as it was in populations with sex-specific mortality.

Although it is impossible to attribute center advantage exclusively to either sex or to breeding vs. mortality, analysis of variance disclosed that overall mortality had a significantly greater effect than breeding on the demographic patterns in the North Shields colony. *Received 29 September 1977, accepted 2 March 1979.*

SINCE 1954, J. C. Coulson and other investigators have been studying a colony of the Black-legged Kittiwake (*Rissa tridactyla*) at North Shields, Northumbria, England. They have individually marked all the breeding birds and all young reared in the colony. The colony grew almost continuously from 1949 to 1964 (the "growth phase") and since then has been in a "stable phase," oscillating around 90 breeding pairs (Coulson and Wooller 1976, Wooller and Coulson 1977). Population dynamics were very different in the two phases. In the growth phase, males nesting in the center of the colony showed significantly better survival than edge-nesting males, and center nesters had more young fledged per nest, despite the fact that there was no predation (Coulson 1968). As the colony stabilized, these center-edge differences weakened, and mortality for all groups in the population increased markedly (Coulson and Wooller 1976).

Although the center-edge phenomenon has been studied in other colonial seabirds (Patterson 1965, Tenaza 1971, Dexheimer and Southern 1974), the North Shields colony is unique in having a large body of data on both age-specific fecundity and mortality for center and edge birds. This allows computation of r , the instantaneous rate of increase, which determines both the growth rate and stable age structure of an exponentially growing population (Poole 1974). Using r as an index, we have summarized the growth differential between the center and edge birds of the North Shields colony, separated the roles of breeding and mortality in accounting for it, and tested the theory of Coulson (1968) that high mortality of edge males is the critical determinant of center advantage.

METHODS

We derived sex-specific fecundity and mortality schedules for birds in the growth phase, edge and center, and the stable phase, edge and center, from the literature on the North Shields colony. With the

aid of a computer we simulated the growth of populations with these fecundity-mortality schedules until the populations had attained a stable age structure. The rate of increase after this point allowed us to compute r for each population. This is merely a method of derivation (Poole 1974) and does not imply an assumption of unlimited or independent increase for the various parts of the colony. Our methods are a variation of those used by Kadlec and Drury (1968) for New England Herring Gulls (*Larus argentatus*). Some of the fecundity-mortality data were taken directly from the literature, but the rest had to be estimated with the use of various assumptions. These are detailed below.

We derived mortality from two sources. Coulson and Wooller (1976, Table 6) give age- and sex-specific survival rates for birds in both the growth and stable phases of the colony (here assumed to be 1954–1964 and 1969–1974, respectively) but do so without respect to center and edge. In their Table 3, however, they give average survival rates specific to sex, location in the colony, and colony development phase. As an example, the survival of growth-phase, edge males was 92% of the survival of growth-phase, center males. We assumed that this 8% differential was split, so that each colony-wide, age-specific rate for the growth phase in Table 6 would be 4% higher for center males and 4% lower for edge males. That is, we assumed that the colony-wide figures were derived from equal numbers of center and edge birds. This is approximately true (Coulson and Wooller 1976, Table 3). We followed a similar process for the other populations. As the recent literature had data only for breeding birds, we assumed that the first-year survival was 79% (Coulson and White 1959) and that survival from then until the first breeding year was the average survival given in Table 3 of Coulson and Wooller (1976) for male/female, center/edge, and growth phase/stable phase. Birds were assumed to have a maximum lifetime of 25 yr, although few lived that long.

Derivation of the number of young fledged per nest was slightly more complex. Wooller and Coulson (1977, Table 4) give the age distribution of center and edge males breeding for the first time. Their Table 7 shows the average number of young fledged per breeding pair during the first and subsequent breeding seasons, again for both center and edge. We combined these data in the following way. If the data indicated that center nesters 4 yr or less of age and breeding for the first time fledged 1.17 young/pair and that only 18% of 3-yr-old birds bred at all (Wooller and Coulson 1977, Table 4), we assumed that each 3-yr-old bird contributed, on the average, $0.5 \times 1.17 \times 0.18 = 0.11$ fledged young. We used the number of young fledged/pair in Wooller and Coulson (1977) for the stable phase populations, but for the growth phase we went back to the fledging data in Coulson (1968). Because Coulson (1968) reported an 11% depression in the edge fledging rate relative to the center, we assumed that, during the growth phase, all the age-specific fledging rates for the growth-phase edge would be depressed by this same amount. These rates were then combined with the data for age at first breeding in the same way as above to give a growth-phase fecundity schedule. In both our simulations and in reality females were usually in excess at North Shields (Coulson and Wooller 1976, Table 2), so we allowed the number of mature males to determine the potential number of breeding pairs.

We believe the assumptions we made in developing the breeding and mortality schedules were the most reasonable ones possible. To test the sensitivity of our conclusions to them, however, we also used a much more extreme set of assumptions. For mortality, we tested the effect of assuming that survivorship, instead of being evenly high for center birds and low for edge ones, fluctuated wildly from low values to 100% in alternate years. The only constraint was that the low values and the high ones had to average together to give the age-specific rates in Table 6 and the center-edge survival differential in Table 3 of Coulson and Wooller (1976). We also tested our greatest assumption about breeding, that at all ages the growth-phase edge birds would experience the average 11% depression in fledging rates relative to the center birds, as reported by Coulson (1968). The highest average fledging rate reported in the North Shields literature is 1.50 young/pair (Wooller and Coulson 1977, Table 9). We assumed that the age-specific fledging rates, instead of constantly remaining 11% lower for edge than for center birds, would fluctuate in alternate years between a high of 1.50 young/pair and a low value. This low value was the rate that, when averaged with 1.50, produced the average fledging success reported in Coulson (1968). In other words, for both breeding and mortality we tested the most extreme assumptions still consistent with Coulson's data.

Once the fecundity and mortality schedules were complete, we simulated the growth of each population for 25 yr, at which time a stable age structure had been attained. We computed the yearly instantaneous rate of increase (r) by taking the natural log of the ratio of each population to that population in the preceding year. These r 's and their associated doubling times are shown in Table 1. To separate the effects of breeding and mortality on r , we simulated all possible combinations of breeding and mortality schedules (e.g. center, growth-phase breeding with center, growth-phase mortality; center, growth-phase breeding with edge, stable-phase mortality; etc.). Because each r value in Table 1 was the sum of a

TABLE 1. Annual r values and doubling times in years (in parentheses) for the tested populations. C stands for center, E for edge, G for growth phase, and S for stable phase.

Breeding schedule	Mortality regimes			
	CG	EG	CS	ES
CG	0.149 (4.7)	0.079 (8.7)	0.035 (19.7)	0.035 (19.7)
EG	0.118 (5.9)	0.047 (14.8)	0.004 (188.0)	0.004 (184.7)
CS	0.137 (5.0)	0.069 (10.1)	0.026 (27.0)	0.026 (26.9)
ES	0.129 (5.4)	0.060 (11.6)	0.016 (43.3)	0.016 (43.1)

breeding effect and a mortality effect, we were able to extract these by finding the difference between the average r of Table 1 and each row and column mean r . These differences are presented in Table 2. Each entry in Table 2 is the factor attributable solely to breeding or mortality that must be added to the mean r of Table 1 (0.059) to give the observed r of that breeding-mortality combination. For instance, for growth-phase, edge birds, the mortality effect is 0.005, and the breeding effect is -0.016 , and $0.059 + 0.005 - 0.016 = 0.048$, within rounding error of the 0.047 presented for the growth-phase, edge birds in Table 1. Table 2 is particularly useful because it summarizes mortality and breeding effects independently of each other and allows a precise breakdown of change in r into the portions due to breeding and mortality.

Because a low male survival has been cited as a critical factor in colony dynamics (Coulson 1968, Wooller and Coulson 1977), we then repeated the process for populations where both males and females experienced the female mortality rate appropriate to their age, location in the colony, and colony development phase. These results are in Tables 3 and 4.

RESULTS

In the following discussion, we let C stand for center, E for edge, G for growth phase, and S for stable phase. Then, because each population is a combination of breeding and mortality, we designate them in the form CS_b-ES_m , where CS_b means the breeding schedule of center, stable-phase birds and ES_m the mortality experience of edge, stable-phase birds.

Simulations using the "extreme" assumptions previously mentioned never produced r 's varying by more than 10% from the values shown in Table 1. Such small differences would not change the patterns discussed below, so the rest of our analysis is based on the premise that our conclusions are not artifacts of our assumptions.

Table 1 is consistent with the kittiwake literature in several respects. First, the absolute values of our rates are realistic. For example, although the growth of the North Shields colony was partly caused by immigration, if an exponential curve is fitted to the 1954-1965 population data in Table 2 of Coulson and Wooller (1976), the r values for males (0.145) and for females (0.147) compare very well with the predicted CG_b-CG_m value (0.149) in our Table 1. The corresponding annual percentage increase (16%) is in the mid-range of values reported for English *Larus* gull colonies by Harris (1970) but is far above the average 3% annual increase of English

TABLE 2. Breeding and mortality components computed from Table 1. These are the factors that are added to the average r in Table 1 (0.059) to obtain the observed r for any breeding-mortality combination. Abbreviations as in Table 1.

	Mortality	Breeding
CG	0.074	0.016
EG	0.005	-0.016
CS	-0.039	0.005
ES	-0.039	-0.005

TABLE 3. Annual r values and doubling times for populations where both sexes experience the group-specific female mortality rates.

Breeding schedule	Mortality regimes			
	CG	EG	CS	ES
CG	0.189 (3.7)	0.174 (4.0)	0.105 (6.6)	0.094 (7.4)
EG	0.160 (4.3)	0.144 (4.8)	0.074 (9.4)	0.061 (11.4)
CS	0.177 (3.9)	0.163 (4.3)	0.095 (7.3)	0.084 (8.3)
ES	0.170 (4.1)	0.155 (4.5)	0.085 (8.1)	0.074 (9.4)

and Welsh kittiwakes reported by Coulson (1963). The North Shields population apparently grew at an exceptional pace for a kittiwake colony.

Second, the relative magnitudes of the rates show that the rate of increase drops dramatically from the growth phase to the stable phase but that the decline is more severe for center birds. Center nesters experience a 5.74-fold increase in their doubling time as they move from the growth to the stable phase; for edge birds the increase is only 2.90-fold. Center advantage still exists in the stable phase (doubling time of 27.0 vs. 43.1 yr for the edge) but is weakened. These trends have been previously reported (Wooller and Coulson 1977).

In addition to conforming with the data, the simulations disentangle the roles of breeding and mortality in accounting for center advantage and demographic change as the colony matures. Casual inspection of Table 1 shows that populations with either CG or EG mortality (the first two columns) can be given any breeding schedule without substantial effect on their rate of increase. In the last two columns (CS and ES mortality), however, changing the breeding schedule makes a very great difference in doubling times.

Table 2 becomes useful here. Taking the growth phase first, Table 1 shows that CG_b - CG_m birds had an r of 0.149, and EG_b - EG_m birds an r of 0.047. The difference, 0.102, is broken down in Table 2. The effect of going from a CG mortality to a EG mortality is $0.074 - 0.005 = 0.069$. Likewise, there is a difference of 0.032 between CG and EG breeding. These add up to the observed difference (within rounding error) and show that center advantage in the growth phase is almost precisely 67% due to the survivorship difference and 33% due to a higher center-breeding rate.

Using similar reasoning, center birds making the transition to the stable phase suffer a drop in r from 0.149 to 0.026, of which 91% is accounted for by the drop in survivorship. For edge birds, mortality accounts for more than 100% of the drop in r , because breeding becomes more successful for edge birds as they move into the stable phase.

Once in the stable phase, the situation is changed. Table 2 shows identical mortality factors for the center and edge populations, and so any difference must be due to breeding. During the growth-phase to stable-phase transition, the center breeding

TABLE 4. Breeding and mortality components computed from Table 3. See Table 2 for explanation.

	Mortality	Breeding
CG	0.049	0.015
EG	0.034	-0.016
CS	-0.036	0.005
ES	-0.047	-0.004

factor has dropped from 0.016 to 0.005 and the edge's factor has risen from -0.016 to -0.004 , but a gap remains, which causes a slight center advantage to persist.

To evaluate the statistical significance of these observations, we did analysis of variance on the r values in the upper left quadrant of Table 1 (representing purely growth-phase populations) and another on the lower right quadrant (representing stable phase). Each quadrant was treated as a 2×2 factorial, and the object was to test for homogeneity of the breeding and mortality main effect mean squares. In the growth phase, mortality was the larger mean square ($F = 5.0$ with 1 and 1 degrees of freedom), and in the stable phase, breeding was more important ($F = 27.6$ with 1,1 df). Both of these missed significance because 1,1 df F -tests are very insensitive (significance would have required an F of 647.8), but the trend for mortality to cause center-edge effects in the growth phase and for fledging success to assume importance in the stable phase was clear.

Continuing the analysis, we treated all of Table 1 as a 4×4 factorial and again tested for the homogeneity of the breeding and mortality mean squares. Overall, mortality was the larger mean square and the F ratio was 15.6 with 3 df, which allows a more sensitive test than the 1,1 df case above. This was significant at the 2.5% level, appropriate for a 2-tailed variance homogeneity test (Ostle 1963).

Finally, we tested breeding and mortality effects in a population where both males and females suffered female mortality rates (Tables 3 and 4). The patterns in Table 1 were weakened, but did not disappear. Center-edge effects in the growth phase decreased and were 67% attributable to breeding. In the stable phase the longest doubling time decreased from 188.0 to 16.4 yr, and the role of mortality in center advantage increased from none to 58%. As before, transition to the stable phase was almost entirely due to a mortality increase. Analysis of variance on Table 2 showed no significant difference between breeding and mortality, overall.

DISCUSSION

Understanding trends in birth rates and death rates is basic to an understanding of a population's history. Careful investigation of these rates has revealed that the kittiwake colony at North Shields has both a definite structure (center/edge) and has experienced different phases of development (growth/stable). We have taken advantage of this unusually complete data base and used the intrinsic rate of increase (r) to summarize mortality, breeding effort with age, and fecundity into a single statistic. We have then broken down center/edge and growth-phase/stable-phase differences in r into the portions due to breeding and mortality changes. The analysis confirms some previous theories and suggests new ones.

Wooller and Coulson (1977) emphasize the intense effort that male kittiwakes put into defending a nest site and give evidence for a consequent decreased survival. Coulson (1968) noted the low survival of edge males during the growth phase and said that it was an important source of center advantage. Our analysis confirms the pivotal role of male mortality, which accounted for 67% of the growth-phase center to growth-phase edge drop in r and more than 90% of the growth-phase to stable-phase drop. The dramatic drop in growth rates in the stable phase is much less in hypothetical populations where males and females both suffer female mortality rates. This would seem to indicate that discovering the causes of heavy male mortality is the key to understanding the dynamics of the North Shields colony.

Tables 2 and 4, however, indicate that caution in making such deductions is

advisable. Center advantage in the stable phase, quantified as the difference in r between center and edge populations, is only 10% of its growth phase magnitude, but mortality of males accounts for none of this. Superior center breeding explains center advantage in the stable phase, in spite of the fact that the breeding component of r for center birds (Table 2) has fallen and the component for edge birds has risen since the growth phase. On the other hand, if male mortality were not a factor (Tables 3 and 4) and center advantage were again defined as the difference in r between center and edge, stable-phase center advantage would be twice as great as it was during the growth phase, and female mortality would account for 58% of it. In the growth phase, 67% of center advantage would be accounted for by breeding. To say that center advantage is rooted in differential male mortality is therefore mostly true for the growth phase but not at all true for the stable phase, and in the absence of differential male mortality, center advantage would persist and in some cases become even larger.

Wooller and Coulson (1977) offer evidence that nest site defense and early breeding cause increased mortality among males. Because the site defense must be most vigorous in the center of the colony, this theory would predict that the increase in mortality as the colony stabilizes in size would be felt more strongly by the center population. Tables 2 and 4 confirm these predictions. The drop in r for center populations entering the stable phase is 30% greater for simulations including male mortality than for simulations including only female mortality. For edge populations, on the other hand, the drop in r is only 44% as great with males as without them. In fact, the mortality increase in the stable phase is felt more strongly by center populations with males, center all-female populations, and even edge all female populations than it is by edge populations with males included. It would seem that the question of why edge male mortality increases so little in the stable phase is just as interesting as the question, addressed in Wooller and Coulson (1977), of why center male mortality increases so much.

The separation of breeding and mortality effects by the analytical methods used here is only as reliable as the fecundity and mortality schedules, which generate the initial intrinsic rates of increase. These in turn depend on extensive field work of the kind done at North Shields. If more such studies are performed, it may be possible to determine whether the demographic trends seen in this work are peculiar to North Shields or more nearly universal among colonial seabirds.

ACKNOWLEDGMENTS

We would like to acknowledge helpful criticism by Charles Leck, Bertram Murray, Edmund Stiles, and Steven Brown. Also, we thank Joan Borski, who typed the several revisions of the manuscript.

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