# AGE CORRELATIONS WITHIN PAIRS OF
# BREEDING BIRDS

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ABSTRACT.—I used simulation models to analyze the effect of different suites of life-history traits and mating rules on the correlation between ages of paired birds. If pair stability is high, the correlation between ages of mates may be strong even in the absence of active mate selection on the basis of age or experience. Even a low frequency of dissolved pairs substantially reduces the correlation between ages.

For 9 species with known life-history traits, I simulated the extent of active mate selection required to produce the observed patterns of ages of mates. In only 1 species could the pattern of ages be explained in the absence of any active mate selection on the basis of the experience of the mate. In 5 species the results suggested there was strong active selection of experienced breeders. With the exception of the Adélie Penguin (*Pygoscelis adeliae*) and the Blue-eyed Shag (*Phalacrocorax atriceps*), observed patterns of ages of mates could be reproduced by simulation models assuming only that birds can distinguish experienced from inexperienced breeders. *Received 20 April 1987, accepted 23 November 1987.*

THE members of pairs of breeding birds are frequently of similar age (Mills 1973, Coulson and Horobin 1976, Mills and Shaw 1980, Pugesek and Diem 1981, Ainley et al. 1983, Nisbet et al. 1984, Perrins and McCleery 1985, Shaw 1985). A common explanation for this similarity in age is nonrandom mate selection with respect to age or experience (Mills 1973, Nisbet et al. 1984, Shaw 1985). Because experienced breeders tend to have higher reproductive success (references given by Nisbet et al. 1984, Perrins and McCleery 1985, Shaw 1985), selection should exist for assortative mating.

While a correlation between ages can be produced by the choice of particular mates, several other factors also could produce this pattern in the absence of active selection on the basis of age or experience. For example, suppose that birds enter the breeding population at the same age and tend to choose mates at the same time or location. If mortality rates are low and the birds rarely change mates, then the initial similarity in ages of mates would be preserved and the correlation between ages would be strong (Mills and Shaw 1980, Nisbet et al. 1984, Shaw 1985).

Experimental tests of mate choice (e.g. Burley and Moran 1977) are the best means to assess the extent of assortative mating. When experimental tests are impractical, the statistical analysis of patterns can be used to infer causation. Specifically, the correlation between ages of mated birds may be used as evidence for assortative mating if it significantly exceeds that expected under the null hypothesis of random mate choice. For example, Perrins and McCleery (1985) compared observed frequencies of pairings of new and and experienced Great Tits (*Parus major*) with frequencies expected under conditions of random mating and found no evidence of assortative mating despite an apparent excess of pairs of experienced breeders.

In contrast, in studies of the Common Tern (*Sterna hirundo*; Nisbet et al. 1984), Blue-eyed Shag (*Phalacrocorax atriceps*; Shaw 1985), and Eurasian Sparrowhawk (*Accipter nisus*; Newton et al. 1981), the difference in the ages of mates differed significantly from patterns expected by random choice. The models used in these studies, however, assumed that birds were free to mate with any other bird; this assumption is false given the evidence for pair stability in these species. A different random model is needed as a null hypothesis against which to compare observed correlations. More generally, statistical studies of age correlations between mates would be strengthened by clarifying the influence of different life-history traits on the correlations expected under varying degrees of assortative mating. To address this issue I simulated the age correlations that result from dif-

The Auk 105: 278–285. April 1988

ferent suites of life-history traits and mating rules.

I used simulation models to analyze the effect of mortality rate, pair stability, and nonrandom mate choice on the correlation between ages of paired birds. The purpose was to demonstrate, for various values of survivorship and pair stability, the expected correlation between the ages of mated birds under various levels of assortative mating. I then determined the extent of nonrandom choice required to produce correlations observed in nine species for which field data are available. As a second test of the accuracy of the simulation model, I compared the distribution of age differences among older pairs in the simulation model with observed differences in field populations.

## METHODS

*Description of the model.*—Mate choice was simulated in a hypothetical population of 2,000 individuals (Fig. 1). I first examined the sensitivity of the age correlation to changes in survivorship, pair stability (the proportion of pairs with both birds surviving that did not change mates), and nonrandom choice (mate preference). After each breeding season a fixed percentage of the population continued to the next breeding season. Birds removed from the population were chosen randomly. Among pairs in which both birds survived, a percentage (equal to $1 -$ pair stability) changed mates. Birds that lost mates, either to mortality or through a change of mates, chose new mates from new recruits or from other experienced breeders that lost their mates.

It may be easier for birds to determine whether a potential mate is an experienced breeder than to determine the physical age of the potential mate. Consequently, I evaluated the effect of assortative mating by examining the effect of a preference for mating with experienced breeders. If a strong preference for mating with an experienced breeder does not produce age correlations equal to observed correlations, then birds must choose mates with a more exact decision rule (e.g. evaluating physical age). In contrast, if random selection of mates with respect to experience produces the observed correlations, then there is no need to assume that birds select mates on the basis of age or experience.

Among experienced birds choosing new mates, the preference of the birds to mate with experienced breeders was set by the variable termed "mate preference." Mate preference is the probability of choosing an experienced mate given the existing availability of experienced and inexperienced birds. The scale of mate preference (range 0–1) indicates an increasing preference for experienced birds, from 0 (only
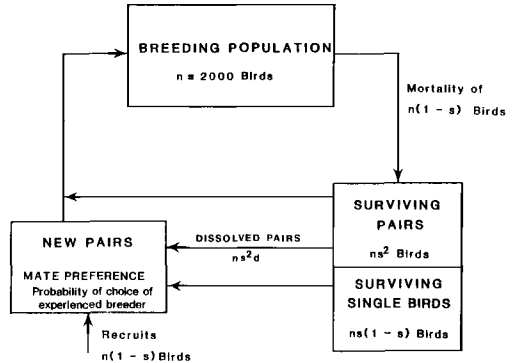


Fig. 1. Flow chart of simulation model. The age correlation is sampled each generation from the breeding population. The probability of survival is *s*, *n* is the population size, and *d* is the proportion of returning pairs that dissolve.

inexperienced birds chosen), to 0.5 (equal preference for experienced and inexperienced), to 1.0 (only experienced birds chosen). More precisely, a mate preference of 0 indicates that birds always choose mates from new recruits when recruits are available; 1.0 indicates birds always choose experienced breeders. A mate preference of 0.5 indicates the selection of mates is in direct proportion to the relative availability of inexperienced vs. experienced individuals. The exact meaning of other values of mate preference depends on the relative availability of experienced and inexperienced individuals. For example, if the ratio of experienced to inexperienced birds is 4:1 (as would occur if pair stability were low), then a mate preference of 0.5 indicates choice of experienced birds with probability 0.80, a mate preference of 0.25 indicates choice of experienced birds with probability 0.40 (i.e. [0.25/0.5] × 0.80), and a mate preference of 0.75 indicates choice of experienced breeders with probability 0.90 (i.e. 0.80 + [{1 − 0.75}/0.50] × [1 − 0.80]). Birds from pairs that dissolved chose mates from among the recruits and experienced breeders with the same mate preference as birds that lost mates through mortality. Because the population did not change in size, the number of recruits was equal to the number of birds that died each year. Consequently, under conditions of strong preference for inexperienced breeders (low values of mate preference), there were not enough inexperienced breeders to meet the demand. Under these conditions birds were allowed to mate with other old breeders after the allotment of inexperienced breeders was used. Pairs in which both birds died were replaced by new recruits. Under conditions of high preference for inexperienced breeders, the supply of recruits was exhausted before the formation of many new pairs.

For each set of parameters the simulation began with all birds of age 1 yr and ran for 25 breeding

seasons to allow the population to reach a stable age distribution. Correlations between ages of birds within pairs were then averaged over the following 75 breeding seasons. Because of the large sample size in the model population, the correlation between ages of mates reached a relatively constant value by generation 25. The intent of the simulation was to produce an expected value for the correlation, not to model variation around that value. Averaging over 75 seasons was sufficient to produce a repeatable value even with the additional variation introduced by including a probability distribution for age of first reproduction and pair stability as measured in natural populations (see below).

To make the simulation output comparable to the correlations that would be observed in field studies, pairs with birds older than age 20 were excluded from the correlation analysis of the simulation output. Birds older than age 20 are seldom observed in natural populations because of death or band loss (Kadlec 1975, Spear 1980). If these birds were included in the simulation model, the presence of a few very old birds with young mates would reduce the correlation between ages, and the resulting correlation could not be meaningfully compared with field data for which the age of mates of very old birds is not known. For all runs of the simulation model with parameters from field populations, the maximum age used in the calculation of correlations in the simulation output was the maximum age in the field sample for this same reason (see below).

*Analysis of field data.*—I calculated the correlation between ages of members of pairs for field data from 9 species. When the sex of the birds is known, the assignment of ages of birds in the pair to the X and Y variate in the correlation analysis is unambiguous. To include data in which sex was not known, I calculated age correlations for all field samples disregarding the sex of the bird. Without knowledge of sex, the correlation calculated for a given set of data will vary, particularly when sample size is small, depending on which member of each pair is assigned to the X and Y variate. Consequently, I determined the average and standard deviation correlation between ages of members of pairs in the field data by averaging the correlations of 200 data sets generated by assigning the birds in each pair randomly to the X and Y variate.

I first tested this observed correlation against the correlation produced by the simulation model assuming random mate choice (mate preference = 0.5). The simulation model was run using measured or estimated values of survivorship, pair stability, and sex and age-specific recruitment (Table 1). Only age classes less than or equal to the oldest observed in the natural population were included in the calculation of correlations in the simulation model. For two species (Artic Tern, *Sterna paradisaea*; White-fronted Tern, *S. striata*) I present results under conditions of 95% and

80% pair stability because field measurements of pair stability are not available. If the correlation produced by the simulation model under these conditions of random choice was not significantly different from the observed correlation and if the frequency distribution of age differences in the simulated and field population did not differ (see below), then there was no need to assume assortative mating was a cause of the observed age correlation.

If the correlation produced by the simulation model under conditions of random mate choice did not match the observed correlation, I then used the simulation model to determine the value of (best-fit) mate preference required to produce age correlations equal to the observed correlation. Using measured or estimated values of survivorship, pair stability, and sex and age-specific recruitment (Table 1), the value of mate preference required to produce the observed correlation was calculated by iteration of the simulation model.

The correlation coefficient alone may not accurately reflect the relationship between the ages of birds in pairs because the correlation coefficient is weighted toward younger age classes by the greater abundance of young birds and by the length of time required to obtain samples of older birds. For example, if mate choice is random with respect to experience and if pair stability and survival are high, then young birds will show a strong correlation between ages (they begin breeding at the same age and remain mated) whereas older birds will show a weak correlation (when one bird dies it is replaced by a bird of any age). Consequently, as a second test of the fit of the simulation model to the field data, I tested the frequency distribution of age differences of mated birds among the oldest 50% of birds in the field sample against differences expected (1) under random mating and (2) using the best-fit mate preference. If the distribution of age differences among older birds in the simulation did not match the observed distribution, then the simulation was not a reasonable approximation of the dynamics of mate choice in the population. Frequency distributions for field and simulation data sets were constructed by totaling the number of pairs with a given difference in age in categories determined by the age of the oldest bird in the pair. Age classes in the simulation output were weighted to match the age classes present in the field sample. The distributions were compared with a Kolmogorov-Smirnov test of goodness-of-fit.

## RESULTS

Under conditions of perfect pair stability, high correlations between ages of birds within pairs are expected under conditions of random choice (Fig. 2). Typical correlations found among field populations ($r = 0.4$–$0.6$; Table 2) can be achieved

TABLE 1. Demographic parameters used in simulation models of assortative mating in natural populations. Estimates based on data from other species are in brackets; estimates calculated from data for the same species are in parentheses.

| Species | Survival (%) | Pair stability[a] (%) | Sex | Age of first reproduction (%) | | | | | | | | Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| Adélie Penguin (Pygoscelis adeliae) | 89.4 | 50.6 | M | | | 3.9 | 18.2 | 32.5 | 42.6 | 2.9 | | Ainley et al. 1983 |
| | | | F | | | 7.1 | 33.3 | 25.3 | 25.3 | 9.1 | | |
| Yellow-eyed Penguin (Megadyptes antipodes) | 86.0 | 86.8 | M | | 8.0 | 47.0 | 33.0 | 12.0 | | | | Richdale 1957 |
| | | | F | | 48.0 | 42.0 | | | | | | |
| Blue-eyed Shag (Phalacrocorax atriceps) | [83.0][b] | 22.7 | M | | [100.0][b] | | | | | | | Shaw 1985 |
| | | | F | | [50.0] | 50.0][b] | | | | | | |
| Eurasian Sparrowhawk (Accipiter nisus) | 67.7[c] | 72.2[d] | | | (75.0 | 25.0)[e] | | | | | | Newton et al. 1981, 1983; Newton and Marquiss 1982 |
| Glaucous-winged Gull (Larus glaucescens) | 85.3 | 94.7 | | | | | 2.5 | 61.5 | 30.9 | 5.1 | | Reid unpubl. data |
| Red-billed Gull (Larus novaehollandiae) | [90.0][f] | 73.0 | M | | (23.0 | 25.0 | 16.0 | 36.0)[g] | | | | Mills 1973 |
| | | | F | | (8.0 | 42.0 | 13.0 | 23.0 | 14.0)[g] | | | |
| Black-legged Kittiwake (Rissa tridactyla) | 83.5 | 75.0 | | 100.0[h] | | | | | | | | Coulson 1966, Coulson and Wooller 1976 |
| Arctic Tern (Sterna paradisaea) | 86.7 | [80.0–95.0][i] | | | | (50.0) | 45.0 | 5.0)[j] | | | | Coulson and Horobin 1976 |
| White-fronted Tern (Sterna striata) | [86.7][k] | [80.0–95.0][i] | | | | (16.7 | 16.7 | 16.7 | 16.7 | 16.7 | 16.7)[l] | Mills and Shaw 1980 |

[a] The proportion of pairs in which both birds returned and remated with each other.

[b] Based on values for the Common Shag (Phalacrocorax aristotelis; Potts et al. 1980).

[c] Average of two estimates for male survival (excluding one low value) and four estimates for female survival (Newton et al. 1983).

[d] Calculated from data of Newton and Marquiss (1982), based only on pairs in which both birds were known to have returned (n = 18).

[e] Newton et al. (1981) indicated that many Eurasian Sparrowhawks did not breed as yearlings, but the exact distribution of age of first reproduction is unknown. If all birds first seen as second-year birds were breeding for the first time, the age of first reproduction would be approximately 50% 1-yr-olds and 50% 2-yr-olds. Because many 2-yr-old birds probably had bred as 1-yr-olds, the estimate used here probably is more realistic.

[f] Based on values for Herring Gull (Larus argentatus, 85–93%; references given by Chabrzyk and Coulson 1976), Dominican Gull (L. dominicanus, 93.4%; Fordham 1970), and Black-legged Kittiwake (83.5%; Coulson and Wooller 1976).

[g] Calculated from data of Mills (1973: fig. 1). Numbers of breeders in each age class estimated from figure, summed for the 4 yr, and corrected for survivorship. Age-specific recruitment then expressed as a percentage of the number of birds present at the age with the most known-age birds present (age 5 for males, age 6 for females).

[h] "Age" of birds in the study of Coulson and Thomas (1980; see Table 2) refers to the number of breeding seasons that the bird was present. Hence, actual values of age at first reproduction (age 2 and 3 yr) were not used in this analysis.

[i] Maximum estimate for pair stability in the Fairy Tern (Gygis alba) is 80% (Dorward 1963). Data for the Common Tern (Sterna hirundo; Austin 1947) indicate that 68 out of 73 pairs (93%) in which both birds returned remained paired. The analysis was performed at two values of pair stability (80%, 95%) in the absence of accurate estimates for the Arctic Tern and White-fronted Tern.

[j] Age 3 and age 4 calculated from Coulson and Horobin (1976: table 3) based on the increased number of breeding birds in successive years for the 1963 and 1964 cohorts. Age 5 recruitment was estimated by Coulson and Horobin (1976).

[k] Based on the survivorship of the Arctic Tern (Coulson and Horobin 1976).

[l] Based on data of Mills and Shaw (1980: table 2) indicating onset of breeding between age 3 and 8. I assumed constant age-specific recruitment during this period.
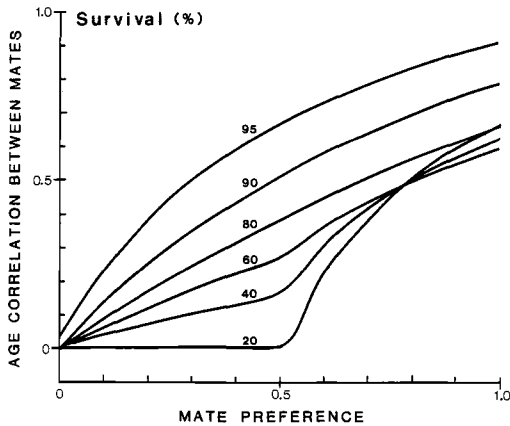
Fig. 2. Correlation between ages of birds within pairs as a function of the mate preference of mate selection. Separate curves are for different values of survival. Pair stability for all curves is 100%. The scale of mate preference indicates an increasing preference for experienced birds from 0 (only inexperienced birds chosen) to 1.0 (only experienced birds chosen).
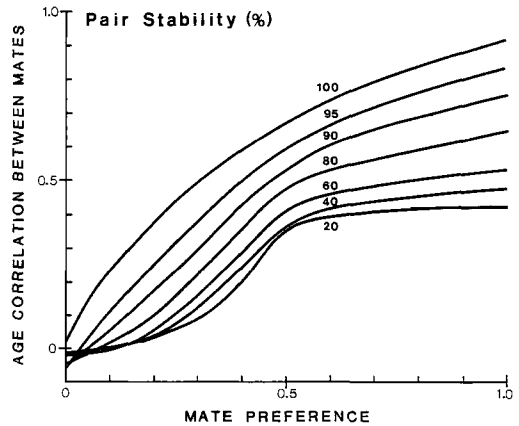
Fig. 3. Correlation between ages of birds within pairs as a function of the mate preference of mate selection. Separate curves are for different values of pair stability. Survival for all curves is 95%. The scale of mate preference indicates an increasing preference for experienced birds from 0 (only inexperienced birds chosen) to 1.0 (only experienced birds chosen).

under conditions of random choice (mate preference = 0.5) if survival rates are greater than 0.80. High age correlations are possible when survivorship is low (<0.60) as a result of the extremely short lifespan and the consequent reduction in the potential variation in ages of mates. Inclusion of low frequencies of dissolved pairs substantially reduced the age correlation (Fig. 3). For example, a decrease in pair stability to 90% reduced the correlation by nearly 0.15 under conditions of random choice. Even with low levels of pair stability, however, strong age correlations can be achieved if there is a preference for mating with experienced birds.

Eight of the nine species examined exhibited age correlations significantly different from the correlation expected under conditions of random mate choice (Table 2: Random mating). Only the age correlation for the Glaucous-winged Gull (*Larus glaucescens*) could be produced by a simulation model assuming random choice. The sample size for the Glaucous-winged Gull was one of the smallest used, however, and the test of observed to expected correlations was relatively weak. In the Yellow-eyed Penguin (*Megadyptes antipodes*) the observed and expected correlations differed by only 0.03, but the sample size was large and the difference was significant.

In 3 of the 8 species for which nonrandom choice was indicated (Yellow-eyed Penguin,

Eurasian Sparrowhawk, White-fronted Tern), only small mate preferences were required for the model to match the observed correlations (Table 2: Best fit). For these three species observed correlations could be matched by the simulation model using values of mate preference under 0.70. In the Yellow-eyed Penguin and the White-fronted Tern, a slight preference for mating with inexperienced breeders (that is, negative assortative mating) was necessary for the simulation model to match the observed correlations. In the Eurasian Sparrowhawk and the White-fronted Tern, the distribution of age differences among older birds predicted by the simulation of random mating did not differ from the actual pattern (Table 2: Random mating), although the White-fronted Tern sample size was small and the test was weak. The age differences among older Yellow-eyed Penguins did differ from the differences predicted by the simulation model under both the random-mating and best-fit conditions. The species with mate preferences near 0.50 (Yellow-eyed Penguin, Eurasian Sparrowhawk, Glaucous-winged Gull, White-fronted Tern) are 4 of the 5 species with the highest levels of pair stability (Table 1).

The remaining 5 species were distinctive for the strong active selection of experienced breeders suggested by comparisons of actual age correlations with simulation results. For example, the Adélie Penguin (*Pygoscelis adeliae*),

TABLE 2. Correlations between ages of birds within breeding pairs and estimates of the value of mate preference required to fit the simulation model to observed correlations.[a] The simulation was performed under two conditions. First, with mate preference = 0.5 (Random mating) there was no selection on the basis of experience. The correlation produced under this condition (Expected age correlation) was tested against the mean correlation of the field sample (and the significance of the test listed under: Observed r different from expected r?). The frequency distribution of age differences among older pairs in the simulation model was then tested against the observed frequency distribution. Second, the best-fit age preference (Best fit) required to make the simulation model match the Observed age correlation was determined, and the frequency distribution of age differences was again tested.

| | Field data | | | Simulation model | | | | |
| | | | | Random mating | | | Best fit | |
| Species | No. of pairs | Max-imum age | Observed correlation between ages (r)[b] | Expected correlation between ages (r) | Observed r different from expected r?[c] | Frequency distribution of age differences[d] | Mate preference | Frequency distribution of age differences[d] |
|---|---|---|---|---|---|---|---|---|
| Adélie Penguin | 59 | 10 | 0.60*** | 0.26 | Yes*** | 0.172 (36) | 1.00+[e] | 0.223 (36) |
| Yellow-eyed Penguin | 193[f] | 16 | 0.15*[g] | 0.18 | Yes*** | 0.325 (98)*** | 0.46 | 0.342 (98)*** |
| Blue-eyed Shag | 127 | 12 | 0.49*** | 0.31 | Yes*** | 0.201 (64)** | 1.00+[e] | 0.191 (64)** |
| Eurasian Sparrowhawk | 67 | 9 | 0.44*** | 0.33 | Yes*** | 0.122 (35) | 0.66 | 0.132 (35) |
| Glaucous-winged Gull | 21 | 17 | 0.44*** | 0.43 | No | 0.263 (11) | 0.51 | 0.302 (11) |
| Red-billed Gull | 212 | 10 | 0.54*** | 0.38 | Yes*** | 0.102 (94) | 0.97 | 0.102 (94) |
| Black-legged Kittiwake[i] | 1,440[j] | 18 | 0.47*** | 0.31 | Yes*** | 0.083 (607)*** | 0.88 | 0.070 (607)** |
| Arctic Tern | 29 | 18 | 0.56*** | | | | | |
|   Divorce = 0.05 | | | | 0.40 | Yes*** | 0.358 (14)* | 0.77 | 0.179 (14) |
|   Divorce = 0.20 | | | | 0.34 | Yes*** | 0.321 (14) | 0.97 | 0.216 (14) |
| White-fronted Tern | 11 | 17 | 0.23 | | | | | |
|   Divorce = 0.05 | | | | 0.33 | Yes*** | 0.440 (7) | 0.34 | 0.493 (7)* |
|   Divorce = 0.20 | | | | 0.32 | Yes*** | 0.446 (7) | 0.41 | 0.453 (7) |

[a] References as in Table 1 except Black-legged Kittiwake (Coulson and Thomas 1980). * = *P* < 0.05, ** = *P* < 0.01, *** = *P* < 0.001.

[b] Two-tailed test of significance of correlation.

[c] Expected correlation tested against observed correlation; two-tailed *t*-test.

[d] Kolmogorov-Smirnov *D*; sample size in parentheses.

[e] Mate preference of 1.0 was not sufficient to match observed correlation.

[f] Data refer to ages of birds at time of initial pair formation. Simulation analysis performed accordingly.

[g] Maximum estimate; ages of birds in grouped catagories assigned to minimum age of group.

[h] Unpublished data. Ages of birds (male-female): 7-6, 7-7, 7-7, 7-10, 7-14, 8-7, 9-8, 10-5, 10-12, 10-14, 11-6, 11-13, 11-14, 12-12, 12-14, 13-9, 13-11, 13-17, 14-8, 14-11, 16-15.

[i] "Age" refers to the number of breeding seasons.

[j] Includes birds seen in more than one breeding season. Thus, a known-age pair seen in two seasons is present twice in the correlation (and sample size).

Blue-eyed Shag, Red-billed Gull (*Larus novaehollandiae*), Black-legged Kittiwake (*Rissa tridactyla*), and Arctic Tern (under the low-pair-stability condition) required values of mate preference greater than 0.85 for the model to match the observed correlation between ages of mated birds (Table 2: Best fit). In the Adélie Penguin and Blue-eyed Shag even a 100% preference for experienced breeders was insufficient to produce the observed correlation. In the Adélie Penguin, Blue-eyed Shag, and Red-billed Gull there was an excess of pairs with small age differences in the natural populations when compared with the best-fit model popu-

lation (significant in the Blue-eyed Shag; Table 2: Best fit). This suggests that a choice mechanism more exact than the modeled experienced vs. inexperienced choice is necessary to explain the pattern of age correlation. Such a mechanism may involve choice on the basis of actual age or choice on the basis of a variable highly correlated with age (i.e. for some species, the timing or location of mating). Shaw (1985) was unable to account for the high age correlation in the Blue-eyed Shag by temporal or spatial patterns of pair formation and suggested that the birds may use physical or behavioral cues to estimate the age of potential mates.

WALTER V. REID

## DISCUSSION

For all nine species (Table 2) there was evidence that reproductive performance increased with the age or experience of the adult (references given in Table 1), yet only the species with low levels of pair stability appear to exhibit strong age preferences. It is not clear why species with high levels of pair stability should not exhibit equally strong preferences given the apparent advantage of mating with experienced birds.

Three factors may help explain the low values of mate preference in some species. First, the simulation model may not reveal existing age preferences. Some patterns of nonrandom mating with respect to age could decrease the correlation between ages of mates. For example, the preference of young females for old males found in the Yellow-eyed Penguin (Richdale 1957) produced a low correlation between ages and, thus, a low value for mate preference despite obvious age-specific mate choice. In several species there is also evidence for a decrease in reproductive performance among very old breeders (references given by Mills and Shaw 1980, Newton et al. 1981), suggesting that mate preference may vary across age classes. Some age classes, in species with low average values of mate preference, may exhibit strong age preferences not detected in this simulation. In this situation a strong correlation between ages would be observed only among pairs with both birds less than the age of decline in performance.

Second, although there may be selection for choice of experienced breeders, not all species may be able to assess the age or experience of potential mates. The Adélie Penguin, faced with an extremely short breeding season, exhibits a pronounced age-specific pattern of arrival times at the colony, with older birds arriving first (Ainley et al. 1983). Pairs that dissolve tend to be composed of birds with the least synchrony in arrival times (as also found in the Black-legged Kittiwake; Coulson and Thomas 1980) and, because of the age-specific pattern of arrival, the new mates of birds from dissolved pairs tend to be chosen from a similar age class. Among species in which pair stability is less dependent on the synchrony of arrival, colony occupation times may not be as clearly age specific. In the Glaucous-winged Gull, for example, the colony is occupied by the majority of breeders for over

one month before the initiation of laying (pers. obs.), and there is no evidence of age-related patterns of colony occupation. In March 1984 the age distribution of 26 birds observed on the colony (2 months before laying) did not differ from the age distribution of 160 breeding birds in June (Kolmogorov-Smirnov $D = 0.087$, $P > 0.20$). In species with high pair stability the advantage of mating with experienced birds may be as great as in species with low pair stability, but the birds may be less capable of determining the age or experience of potential mates.

Finally, the higher reproductive success of older birds is only one component of the costs and benefits of assortative mating. For example, among species with high pair stability the "cost" of mating with an inexperienced bird may be relatively low because of the high probability of remating with the bird in subsequent years when it is more experienced. Thus, although the initial breeding success of a bird mating with an inexperienced individual may be low, the lifetime reproductive success may exceed that of an individual mating with a series of older birds. Moreover, if birds can evaluate the quality of potential mates rather than just the experience or age, then the correlation between ages of mates would be only as strong as the correlation between quality and age. A pair composed of an old and a young bird may be very successful if the young bird is of high quality.

In only one of the nine species examined can random mating with respect to experience account for observed correlations in ages between mated birds. With the exception of the Adélie Penguin and the Blue-eyed Shag, the observed correlations can be reproduced by simulation models that assume only that birds can distinguish experienced from inexperienced breeders. Among species with high pair stability, only a small preference for mating with experienced birds is needed to account for significant age correlations between mates. Only in the Blue-eyed Shag did it appear that mate choice was made directly on the basis of age rather than on the basis of timing or location of breeding.

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