Appendix: Testing the strength of the pair bond

OLLI JÄRVINEN

Department of Genetics, University of Helsinki

The following communication shows how the hypothesis of random mating can be tested when the identity of the mates is known in two successive seasons.

Assume first that population dynamics (emigrations and immigrations, births and deaths) can be exluded. We can now calculate the probability of having a certain number of pairs in which the same male and female form a pair bond in two successive seasons (number of "right" pairs). The solution is based on the so-called *rencontre* problem in the theory of probability. One formulation (GNEDENKO, B., The theory of probability, 2nd printing, Progress, Moscow 1973, p. 68) is as follows:

"A person wrote letters to n addresses, one letter in each envelope, and then, at random, wrote one of the addresses on each envelope. What is the probability that at least one of the letters reached its destination?"

It is of interest to know more about letters and envelopes (males and females): the probability of having exactly k "right" pairs in a population of n pairs is

$$p_k = \frac{1}{k!}\left[1 - \frac{1}{1!} + \frac{1}{2!} - \ \ldots + (-1)^{n-k}\frac{1}{(n-k)!}\right]$$

If n approaches infinity, $p_k \to e^{-1}/k!$, which are terms in the well-known Poisson distribution (expectation and variance 1). In fact, if $n \geqq 10$, the Poisson terms can be used without appreciable error. Even if n is less than 10, the expectation and variance of the number of "right" pairs is 1, but the Poisson terms are not a satisfactory approximation.

To summarize, if there is no turnover of individuals, there will, *on average,* be one such pair of birds in which the same two individuals form a pair bond in two consecutive seasons. The number of "right" pairs has the variance of 1. Population size does not affect these conclusions; calculations are simple if $n \geqq 10$.

Example 1. There is a bird population with no turnover of individuals, $n = 20$ and observed $k = 5$. The probability of having at least 5 "right" pairs by chance is $1 - \sum_{k=0}^{4} p_k = 0.0037$. The birds thus favor their earlier mates (risk of false inference 0.0037).

Here emerge two practical difficulties. First, there is considerable turnover of individuals. Denote the probability of death and emigration by $1-s$; then both birds in a pair will survive the winter and return back with the probability s^2. The number of those pairs in which both pairs survive and return follows a binomial distribution. If there were t "right" pairs in a population without turnover, the probability of having k such pairs in a population with turnover is

$$P_t(k) = \binom{t}{k} s^{2k}(1-s^2)^{t-k}$$

The proper probability distribution is derived as follows: for a given p_t, calculate $P_t(k)$, $k = 0, 1, \ldots, t$, and repeat the procedure for all $t = 0, 1, \ldots, x$, where x is a number for which p_x is small enough to be neglected (depending on the accuracy required). The probabilities of having k pairs, taking into account turnover of individuals, is then obtained by summation

$$p_k^* = \sum_{t=k}^{x} P_t(k)\, p_t$$

Another problem is that all pairs can not be checked. Let us consider k "right" pairs. It is possible that 0 to k of them are included in the sample of the previous year. The probability of having exactly K "right" pairs in a sample of N pairs is, from the hypergeometric distribution,

$$P = \frac{\binom{k}{K}\binom{n-k}{N-K}}{\binom{n}{N}}$$

Here n and k denote numbers of pairs in the whole population, as above. If K of the "right" pairs have been checked in the previous year, it is possible that the sample of the present year includes 0 to K of these "right" pairs. The probability distribution can be calculated from these probabilities and p_k^*.

Example 2. Dr. O. HILDÉN estimates that $s = 15/25 = 0.6$ in a population of *Calidris temminckii.* None of the checked pairs was "right" except in 1968, when 5 such pairs were observed in a sample of 9 pairs (out of 18). Of course, it is possible that many "right" pairs escaped notice because of the incompleteness of the samples. From Example 1, we see that the observation is significant, even if both turnover of individuals and incomplete samples are neglected. When mortality and emigration are taken into account, we find that p_k^* is extremely small for $k \geqq 8$. For $5 \leqq k \leqq 7$ it is necessary to calculate the probability that at least 5 of these "right" pairs are included in the sample of 1967 (10/16 pairs), and, further, that these pairs, or at least five of them are included in the sample of 1968. As a result, the observation of 1968 has the probability of much less than 10^{-7}. Hence, there is a tendency to maintain an established pair bond in *Calidris temminckii*. The five years with zero "right" pairs do not refute this conclusion: such years will always be a majority unless the preference for the previous mate is very strong.

Note that it is incorrect to combine all the years in the above example to get an estimate of the proportion of "right" pairs, and compare this frequency with some theoretical frequency (e.g., by a binomial t test), because the probability of having twice t pairs is not identical with getting once $2t$.

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