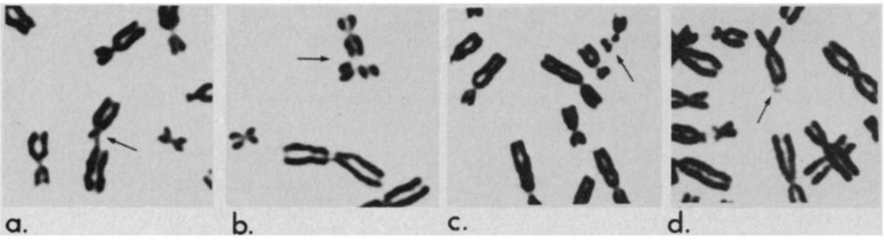

Fig. 1. Different appearances of lesions (arrowed) at fragile sites. (a) Breakage of a single chromatid at 2q1. (b) Triradial figure caused by duplication of chromatids distal to lesion at 10q23. (c) Unstained region of both chromatids at 20p11. (d) Unstained region of both chromatids at Xq27 or 8.

retardation, which has been estimated to account for one-fifth of males with an IQ in the 30 to 55 range (*4*). Most descriptions of X-linked mental retardation have included chromosome studies, but with few exceptions (*3*) these have shown nothing unusual. The fragile site on Xq, which is directly associated with at least one form of X-linked mental retardation, would probably have been missed if such studies were not carried out using medium 199; consequently, they should be repeated.

This association of the fragile site on Xq with one form of mental retardation could provide a means of prenatal diagnosis if the fragile site can be demonstrated in fibroblast cultures. Most reports of fragile sites do not include studies on fibroblast cultures, although Ferguson-Smith (*1*) found the frequency of lesions at a site at 2q to be much lower in these cultures than in lymphocyte cultures. I have been unable to demonstrate the fragile sites in fibroblast cultures from any of the cases in Table 1 regardless of the type of culture medium used.

Further studies of fragile sites are required to determine whether they all behave similarly, what exactly their phenotypic effects are, their frequency in the population, and their relationship to chromosome structure. Identification of the factors in medium 199 responsible for their induction would greatly facilitate this work.

GRANT R. SUTHERLAND

*Cytogenetics Unit,*
*Department of Histopathology,*
*Adelaide Children's Hospital Inc.,*
*North Adelaide, S.A. 5006*
*Australia*

**References and Notes**

1. M. A. Ferguson-Smith, *Ann. Genet.* **16**, 29 (1973).
2. F. Giraud, S. Ayme, J. F. Mattei, M. G. Mattei, *Hum. Genet.* **34**, 125 (1976).
3. H. A. Lubs, *Am. J. Hum. Genet.* **21**, 231 (1969); J. Harvey, C. Judge, S. Wiener, *J. Med. Genet.* **14**, 46 (1977); F. Giraud, S. Ayme, J. F. Mattei, M. G. Mattei; *Hum. Genet.* **34**, 125 (1976); G. R. Sutherland, unpublished data.
4. G. Turner and B. Turner, *J. Med. Genet.* **11**, 109 (1974).

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## Species Turnover Rates on Islands: Dependence on Census Interval

Abstract. *Measurements of species turnover in island bird communities demonstrate two trends with increasing census interval* t: *(i) Apparent turnover rates* T *decrease greatly with* t, *and (ii) the coefficient of variation of* T *decreases asymptotically to a constant value. These effects are predicted by a statistical model whose parameters are the immigration and extinction probabilities of each species. Available bird censuses at intervals of decades underestimate turnover rates by about an order of magnitude.*

A fundamental problem of population biology concerns population lifetimes: the species composition of any local community is subject to change with time as local populations of species die out and are reestablished by immigration. While this dynamic structure has received particular attention for island communities, because of the MacArthur-Wilson interpretation that species numbers on islands approach dynamic equilibriums (*1*), similar considerations are also relevant to mainland communities. Thus, censuses of all species present at a given locality at two successive times may reveal "turnover": some species present on the first census may be absent on the second because of local extinctions in the intervening time, and some species absent on the first census may be present on the second because of immigrations. For bird communities on several islands, species turnover rates at equilibrium have been estimated in this way, mainly from comparison of censuses spaced at intervals of several decades (*2–4*).

A major practical problem in turnover studies concerns an "uncertainty principle" associated with the choice of time interval $t$ between censuses. (The problem is analogous to that of an observer who wishes to determine the mean flickering rate of an array of light bulbs flickering at different individual rates, and who faces different types of difficulties depending on whether his frequency of observation exceeds or is less than the flickering frequencies.) The longer $t$ is, the more cases of turnover (either immigrations or extinctions) will be observed, hence the lower will be the coefficient of variation of the apparent turnover rate $T$. However, with increasing $t$, $T$ will underestimate the true turnover rate by an increasing factor because a species may repeatedly become extinct and then immigrate (or vice versa) in the time between censuses (the so-called in-and-out effect). This report has four purposes: (i) to illustrate the magnitude of this effect in island bird studies, (ii) to present a simplified statistical theory, (iii) to test the theory against observations, and (iv) to indicate refinements that should be incorporated in a second-generation theory.

Jones and Diamond have obtained annual censuses of breeding land bird populations on each of the California Channel Islands for the past 4 years and have studied results of similar censuses on islands elsewhere in the world (*5*, *6*). Table 1 lists the land bird species that bred on the Farne Islands off Great Britain in each of 29 consecutive years from 1946 to 1974. On these small islands (total area, 32 ha), which are protected as a bird sanctuary and owned by the National Trust, a resident warden and many visiting ornithologists determine the number of nesting pairs of each species each year; the chance that a breeding species would be overlooked is negligible. Of the 16 land bird species that bred on the Farnes in at least one of these 29 years, only four species bred in every year, and only two species "turned over" (immigrated or went extinct) only once. The remaining ten species turned over repeatedly. For instance, meadow pipit bred in the first two census years went extinct by the third year, then successively immigrated and went extinct five times, giving 11 cases of turnover in 29 years. Had only the censuses of 1946 and 1974 been available, one could have deduced only a single instance of turnover for meadow pipit, an extinction. Despite this considerable annual turnover of populations, the number of species breeding on the Farnes remained relatively constant [$\overline{X} = 6$, coefficient of variation (CV) = 0.20]. This finding confirms the basic hypothesis of MacArthur and Wilson (*1*), that species number on an island may be in dynamic equilibrium.

We used all pairwise combinations of census years for the Farnes to calculate the apparent turnover rate $T(t)$, defined (*2*) by

$$T(t) \equiv (I + E)/(S_1 + S_2)t \qquad (1)$$

where $I$ and $E$ are the minimum number of immigrations and extinctions deduced from comparison of the two censuses, and where $S_1$ and $S_2$ are the number of breeding species in the earlier and later census years, respectively. Figure 1 depicts, for each value of $t$ from 1 to 28 years, the average value of $T$ and its $\overline{CVT}$ as calculated from all pairs of censuses separated by the same interval $t$. Two main conclusions follow from Fig. 1. (i) As $t$ increases from 1 to 28 years, $T$ decreases by about an order of magnitude. The initial value at $t = 1$ year is 0.13 per year (that is, on average 13 percent of the breeding species turn over each year). At $t = 25$ to 28 years, $T$ is 0.013 per year. (ii) The $\overline{CVT}$ decreases with $t$, starting at approximately 1 at $t = 1$ year and approaching a constant value of approximately 0.35 after about 15 years (Fig. 1 actually shows $T(1 \pm \overline{CVT})$, that is $T \pm 1$ standard deviation, rather than $\overline{CVT}$ itself). These two conclusions also apply qualitatively to the turnover results for the California Channel Islands (*5, 6*) and other islands studied.

To formulate this problem theoretically, let $\lambda_i$ represent the probability per unit time that the $i$th species will immigrate to a particular island if the species is initially absent; and $\mu_i$, the corresponding probability per unit time that the $i$th species will go extinct on the same island if initially present. In general, $\lambda_i$ and $\mu_i$ will differ among species on the same island and will also differ among islands (depending, for example, on area and isolation) for a given species. For temperate-zone birds, the unit-time steps will correspond to successive breeding seasons 1 year apart, giving a discrete time series of presences and absences; the derivations of the functions $I_i(t)$ and $E_i(t)$ in Eqs. 2 then follow from difference equations involving $\lambda_i$ and $\mu_i$ (*7*).

Under these assumptions, the history of presences and absences of the $i$th species on a particular island will be a Markov process, akin to the sequences generated by tossing a loaded coin. If a species is initially absent, the probability $I_i(t)$ that it will be present after $t$ years is

$$I_i(t) = [\lambda_i/(\mu_i + \lambda_i)]\,[1 - (1 - \mu_i - \lambda_i)^t] \qquad (2a)$$

Similarly, if the species is initially present, the probability $E_i(t)$ that it will be absent after $t$ years is

$$E_i(t) = [\mu_i/(\mu_i + \lambda_i)]\,[1 - (1 - \mu_i - \lambda_i)^t] \qquad (2b)$$

The asymptotic probability $p_i$ of the species' being present at any random moment is

$$p_i = \lambda_i/(\mu_i + \lambda_i) \qquad (3)$$

This probability has been christened the "incidence" for the species. The dependence of $p_i$ on island area and species characteristics has been documented empirically by Diamond (*8*) and discussed theoretically by Gilpin and Diamond (*9*).

From Eq. 3 it follows that the equilibrium number of species on the island at a given time, $S^*$, is

$$S^* = \sum_{i=1}^{S_T} p_i \qquad (4)$$

Here $S_T$ is the total number of species in the pool of potential immigrants; henceforward all summations over $i$ will be understood to run from 1 to $S_T$. The variance about the mean probability for the $i$th species to be present is $p_i(1 - p_i)$, and therefore the overall coefficient of variation of $S^*$ is

$$\overline{CVS}^* = \left[\sum_i p_i(1 - p_i)\right]^{1/2} / S^* \qquad (5)$$

Similar expressions (*10*) pertain to the CV's for $I_i(t)$ and $E_i(t)$.

For the entire island community, the apparent rates of immigration or extinction of species, $\Lambda(t)$ or $\mathrm{M}(t)$, as calculated from two censuses spaced $t$ years apart, are

$$\Lambda(t) = \sum_i (1 - p_i)I_i(t) \qquad (6a)$$

$$\mathrm{M}(t) = \sum_i p_iE_i(t) \qquad (6b)$$

At equilibrium, these theoretical expressions for the average $\Lambda(t)$ and $\mathrm{M}(t)$ are identical; in practice, one would calculate $T(t)$ from censuses by averaging measurements of observed $I$ and $E$, as in Eq. 1.

Using Eq. 6 along with Eqs. 2 and 3 to estimate $I$ and $E$, and also using Eqs. 3 and 4 to estimate $S_1$ and $S_2$ in Eq. 1, we arrive at an expression for the expected turnover rate $T(t)$, as a function of census interval $t$:

$$T(t) = (1/tS^*) \sum_i \mu_i\lambda_i[\mu_i + \lambda_i]^{-2}\,[1 - (1 - \mu_i - \lambda_i)^t] \qquad (7)$$

The summation term is the number of differences expected to be found if one compared two censuses $t$ years apart. Equation 7 means that $T$ should decrease with time, as is actually observed. In the limits $t = 1$ and $t \rightarrow \infty$, Eq. 7 becomes

$$T(1) = (1/S^*) \sum_i \mu_i\lambda_i/(\mu_i + \lambda_i) \qquad (8)$$

$$\mathrm{Lim}_{t\rightarrow\infty}\, T(t) \equiv$$

$$T(\infty) \rightarrow (1/tS^*) \sum_i \mu_i\lambda_i/(\mu_i + \lambda_i)^2 \qquad (9)$$

The asymptotic relation Eq. 9 means that, for large $t$, a log-log plot of $T(t)$ versus $t$ yields a straight line of slope $-1$. This conclusion is not specific to our simple model, but necessarily follows from the defining Eq. 1 as an asymptotic (large $t$) result of any Markov process, so that it holds even if the $\lambda_i$ and $\mu_i$ exhibit short-term correlations either in time or between species. Note also that in our model there is a simple relation between the asymptotic turnover rate (Eq. 9) and the CV of the equilibrium species number (Eq. 5):

$$T(\infty) = S^*(\overline{CVS}^*)^2/t \qquad (10)$$

Finally, an expression may be found for the coefficient of variation of the expected turnover rate, $\overline{CVT}(t)$. This expression (reference *11*) means that, as actually observed, $\overline{CVT}$ decreases with time toward an asymptotic value

$$\mathrm{Lim}_{t\rightarrow\infty}\, \overline{CVT}(t) \equiv \overline{CVT}(\infty)$$

$$\rightarrow [\sqrt{2}S^*(\overline{CVS}^*)]^{-1} \qquad (11)$$

Eqs. 10 and 11 express interesting relations between the coefficient of variation of $S^*$ and the asymptotic values of the apparent turnover rate and its CV. For example, for a given $S^*$, an increase by a factor of 2 in the $\overline{CVS}^*$ implies a fourfold increase in $T(\infty)$ and a halving of $\overline{CVT}(\infty)$. These trends and relations between the various quantities are exhibited even by data sets that do not well fit the turnover equation (Eq. 7) as such.

This statistical theory accounts qualitatively for our observations on how $T$ and $\overline{CVT}$ depend on $t$. To assess the theory quantitatively for birds of the Farnes, we calculated the $\lambda_i$'s and $\mu_i$'s for each of the 16 breeding species. For each species, $\lambda_i$ was calculated as the total number of instances in which a year of breeding absence was followed by a year of breeding presence, divided by the total number of years of breeding absence (*12*). Each value of $\mu_i$ was calculated as the number of instances in which a year of breeding presence was followed by a year of breeding absence, divided by the total number of years of breeding presence. The last census year (1974) was ignored in evaluating the denominators, because the corresponding term of the numerators (the outcome of the 1974–1975 "trial") will not be known until the 1975 results are compiled. The resulting $\lambda_i$ and $\mu_i$ values (Table 1) have been used to make five predictions.

1) The equilibrium species number $S^*$ is predicted from Eqs. 3 and 4 to be 5.9 species. This is identical to the actual value of the average number of breeding species in the 29 census years.

2) The $\overline{\mathrm{CV}S}{}^*$ is predicted from Eqs. 3 and 5 to be 0.19. The actual value is 0.20 (Table 1).

3) The $T(t)$ was calculated as a function of census interval $t$ from Eq. 7. The predicted curve closely parallels the actual $T$ values but falls slightly below them (Fig. 1).

4) The dependence of $\log T$ on $\log t$ for large $t$ is predicted from Eqs. 4, 5, and 10 to approach a straight line with slope $-1$ and ordinate intercept of

$$\log T = \log \{[\Sigma p_i(1 - p_i)]/(\Sigma p_i)\} = -0.84$$

On the basis of fitting a straight line through actual $(T,t)$ values for $t = 10$ to 24 years, the actual slope is $-0.82$, and the intercept $\log T = -0.84$.

5) The predicted statistical fluctuations in apparent turnover rate are calculated from (*10*). The predicted time-dependent fluctuations are qualitatively similar to, but somewhat larger than, the observed ones (Fig. 1).

Let us now examine errors in the fit of our theory to the data and correlations among the errors. The data base of Diamond and Jones includes 16 islands whose breeding birds were surveyed in at least 13 consecutive years, in the best case 39 consecutive years. We have tested these 16 turnover studies against our theory as described for the Farnes. The resulting fits are instructive in suggesting what biological effects should be incorporated into a "second-generation" theory of turnover. (i) The predicted $S^*$ is always close to the observed value, is equally often too high or too low, and deviates on the average by 3 percent. (ii) The predicted $\overline{\mathrm{CV}S}{}^*$ is too low in 15 of 16 cases, on the average by 32 percent. (iii) The predicted $T(1)$ value is usually slightly too low, on the average by 10 percent. With increasing $t$, the predicted $T(t)$ always becomes increasingly too low. (iv) The predicted asymptotic value of $\overline{\mathrm{CV}T}(t)$ at large $t$ values is always too high, on the average by 145 percent. (v) With increasing $t$, the product $Tt$ was predicted to approach an asymptote, and a graph of $\log T$ versus $\log t$ to approach a slope of $-1$. Some islands, as the Farnes, approximately fulfill this prediction, but for other islands, $Tt$ is still creeping upward after $t = 10$ or 20 years, and the slope of $\log T$ versus $\log t$ is less than $-1$.

As predicted by our theory, some of these errors prove to be correlated. The five islands with the largest negative errors in predicted $\overline{\mathrm{CV}S}{}^*$ (predicted value too low) also have the largest negative errors in $T(t)$ at large $t$ and large positive errors in $\overline{\mathrm{CV}T}(\infty)$. These islands also have the largest positive errors in $S^*$ and largest negative errors in $T(1)$, a correlation suggested but not strictly required by our theory. What distinguishes these five islands is that $S^*$ gradually rises with time, whereas it shows no secular trend for the other islands. The reasons for the trends in these five cases are various: progressively increased moisture, growth of taller vegetation, recovery from a harsh winter near the start of the census period, and reduced human disturbance. It is especially instructive that two islands, Skokholm and Helgoland, whose breeding birds were repeatedly censused both before and after World War II, show a more marked trend in $S^*$ as well as more marked deviations from our theory for the postwar than the prewar period. This indicates that the trend in $S^*$ is related to the main cause of the misfits to our simplified theory.

Three characteristics of turnover that are neglected in our simplified theory may warrant inclusion in the next, more refined theory.

1) Our theory neglects possible correlations between species in their records of presence and absence. Negative correlations due to interspecific competition would make $\lambda_i$ and $\mu_i$ respectively decreasing and increasing functions of $S^*$ and would reduce $\overline{\mathrm{CV}S}{}^*$. In the extreme case of species that replaced each other strictly in random temporal sequence, $\overline{\mathrm{CV}S}{}^*$ would be zero despite high turnover. On the other hand, $\overline{\mathrm{CV}S}{}^*$ higher than that predicted by our theory could reflect interspecific facilitation (unlikely for birds) or else correlated environmental fluctuations in carrying capacity. Numerous examples of the latter effect are obvious from Diamond and Jones's data base (*6*) and may contribute to the fact that the observed $\overline{\mathrm{CV}S}{}^*$ was higher than predicted: for instance, the harsh

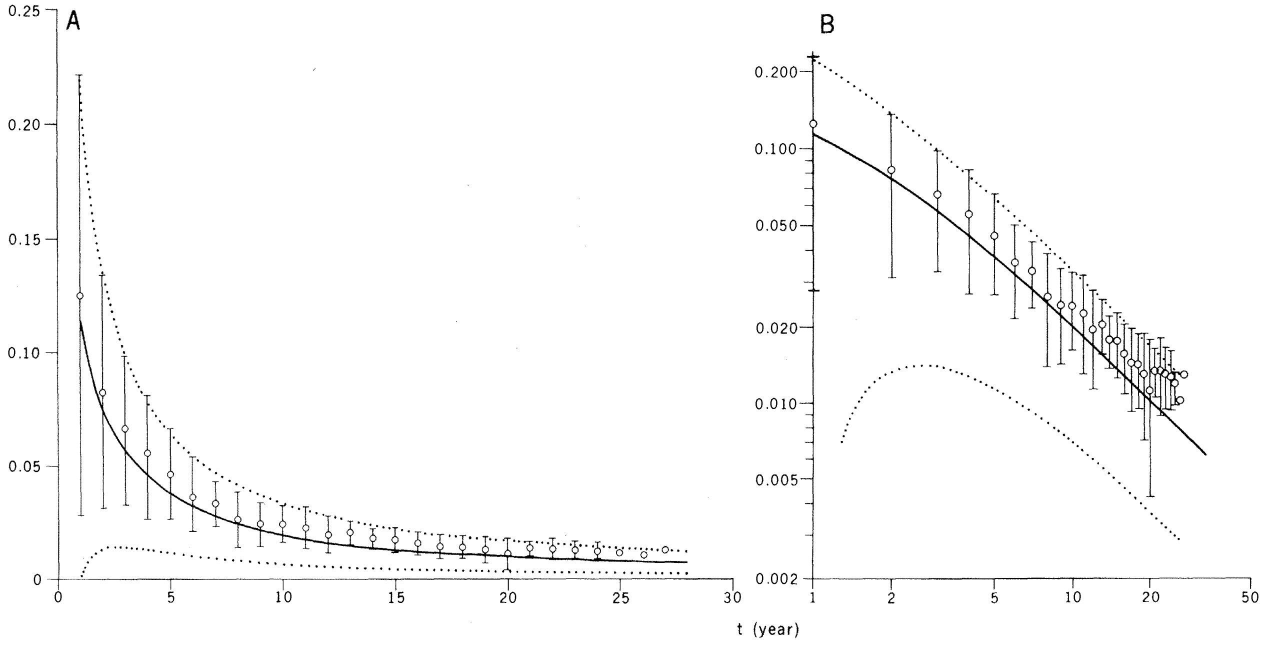

Fig. 1. Apparent turnover rate ($T$) of breeding land bird species on the Farne Islands, expressed as the fraction of breeding species immigrating or becoming extinct per year and calculated (Eq. 1) from differences in species list (Table 1) for pairs of census $t$ years apart. Circles, mean observed $T$; vertical bars, observed mean ± 1 standard deviation (S.D.). Solid curve, mean predicted $T$ (Eq. 7); dotted curves, predicted mean ± 1 S.D. (*10*). Axes are linear for (A) and logarithmic for (B).

winter of 1962–63 caused simultaneous extinctions of three species on the Farnes (Table 1), and the wet summer of 1927 permitted simultaneous immigrations of seven species to Helgoland.

2) A second consideration is of serial correlations within species. Our theory is in effect a two-state Markov model that describes species simply as present or absent and uses only two parameters, $\lambda$ and $\mu$, to characterize transition probabilities between these states. The simplest Markov model that took account of serial correlations within species would be a three-state model ("absent," "present for 1 year," "present for more than 1 year") with differing extinction probabilities from the last two states. The underlying biological mechanism is that when a species successfully colonizes an island from which it was previously absent, its population size tends to grow with time so that the probability of extinction decreases with time. Numerous examples from the data base show that recent colonist populations with small numbers contribute disproportionately to extinctions.

3) A third proposed ingredient recognizes temporal variation in $\lambda$ and $\mu$. In reality, $\lambda_i$ and $\mu_i$ are not strict constants but undergo random or systematic changes caused by changes in the environment. We distinguish two cases, depending on whether or not the temporal fluctuations include components on a time scale comparable to the total census period.

If $\lambda_i$ and $\mu_i$ exhibit only short-term random fluctuations about steady average values, our simple model must be modified to treat $\lambda_i$ and $\mu_i$ as stochastic variables rather than deterministic ones. In such a stochastic treatment, $\overline{CVS}^*$ and the asymptotic $T(\infty)$ are both larger than for the corresponding case of constant $\lambda_i$ and $\mu_i$, but the asymptotic relation whereby a log-log plot of $T$ versus $t$ approaches a straight line of slope $-1$ is preserved.

A more interesting correlation arises in those cases in which there is evidence for systematic secular trends in $\lambda_i$ and $\mu_i$, on time scales comparable to the total time interval spanned by the census data. The reasons that a particular species would have different turnover characteristics on a given island at the start and the end of, say, a 25-year period are numerous. Some examples are low stonechat populations for many years after the harsh winter of 1962, low whitethroat populations resulting from the Sahel drought of the late 1960's, and growth of bracken favoring some species and hurting others. One cannot account for such secular trends by calculating mean $\lambda_i$ and $\mu_i$ for the whole survey period from all pairs of surveys at 1-year intervals. As an extreme example, consider an imaginary island that is ill-suited to a given species ($\lambda_i = 0$, $\mu_i = 1$) for 5 years and then favors the same species for the next 5 years ($\lambda_i = 1$, $\mu_i = 0$); breeding presence and absence surveys would show the pattern $-----+++++$. From this data, our simple treatment would estimate $\lambda_i = 1/5$ and $\mu_i = 0$. Hence the predicted contribution of that species to the $S^*$ of Eq. 4 is $p_i = 1$ (higher than the actual $p_i = 0.5$); as a result of the estimate $\mu_i = 0$, the species is predicted to make no contribution to $\overline{CVS}^*$, whereas it actually contributes conspicuously; and the species' predicted contribution to turnover $T(t)$ is also 0, whereas in fact it turns over in one of the nine 1-year-interval comparisons, in four of the seven 3-year-interval comparisons, and in all five 5-year-interval comparisons. Not only are these predicted $T$ values too low, but they become increasingly too low with increasing interval $t$. These systematic temporal trends yield a log $T$ versus log $t$ plot with asymptotic slope less negative than $-1$.

Thus, the discrepancies that secular trends in $\lambda_i$ and $\mu_i$ produce between $\overline{CVS}^*$, $T$, and $\overline{CVT}$ as observed and as predicted by our simplified model are in the direction of the actual discrepancies noted, especially for the five worst-fit islands. Of the three possible sources of discrepancy, secular trends are the only one that explain an asymptotic slope less than $-1$ in plots such as Fig. 1.

Thus, we have predicted and observed that pairs of censuses at intervals that are long compared to some values of $1/\lambda_i$ or $1/\mu_i$ greatly underestimate turnover rates. For available censuses of island bird communities at intervals of a decade or more, the underestimate (as com-

Table 1. Annual censuses of the number of breeding land birds on the Farnes Islands from 1946 to 1974 (*15*). The + symbol indicates that breeding occurred but that the number of pairs was not determined. Average $S^*$ = 5.9 species, $\overline{CVS}^*$ = 0.20.

| Species | Year | | | | | | | | | | | | | | | | | | | | | | | | | | | | | $\lambda_i$ | $\mu_i$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | | |
| Moorhen | | 1 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.038 | 0.500 |
| Oystercatcher | ~24 | 26 | 25 | ~32 | ~29 | 26 | 29 | 28 | 30 | + | 12 | 25 | 18 | 9 | 5 | ~25 | ~28 | 30 | 27 | 17 | 21 | 12 | 16 | 9 | 23 | ~18 | 23 | 20 | 23 | ~1 | 0 |
| Lapwing | 2 | | | | | | | | | | | | 2 | 2 | 2 | 3 | 1 | | | | | | | | | | | | | 0.045 | 0.333 |
| Ringed plover | ~12 | 12 | 12 | 11 | 10 | 17 | 22 | 19 | 15 | 15 | 12 | 16 | 11 | 11 | 13 | 21 | 12 | 12 | 12 | 13 | 13 | 15 | 11 | 11 | 9 | ~10 | 9 | 10 | 13 | ~1 | 0 |
| Redshank | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 | 1 |
| Stock dove | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | 0.038 | 1 |
| House martin | | | | | 6 | | | | | | | | | | | | | | | | | | | | | | | | | 0.037 | 1 |
| Jackdaw | | | | 1 | | | | | | | | | | | | | | | 2 | 2 | 2 | | | | | | | | | 0.083 | 0.500 |
| Blackbird | | | | | | | | | | | | | | | | | 1 | | 3 | 1 | 1 | 2 | 3 | 3 | 2 | 1 | 1 | 1 | 1 | 0.118 | 0.091 |
| Wheatear | | | | | 1 | | | | | | | | 1 | 1 | | | | | | | | | | | | | | | | 0.080 | 0.667 |
| Stonechat | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 | 1 |
| Robin | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | 0.037 | 1 |
| Meadow pipit | 2 | 1 | | | | | | 1 | | | | | | 1 | | 1 | 1 | | | | | 1 | | 1 | 2 | 1 | 2 | 3 | | 0.313 | 0.500 |
| Rock pipit | 37 | 50 | + | 60 | 55 | 50 | 35 | 31 | 30 | 33 | 30 | 34 | 24 | 12 | 15 | 30 | 34 | + | + | + | + | + | + | + | + | ~18 | 26 | 24 | 22 | ~1 | 0 |
| Pied wagtail | | | | | | | | 1 | 1 | 1 | | | | | | 1 | 1 | 1 | | | | | | | | | 1 | 1 | 1 | 0.150 | 0.250 |
| Starling | 8 | 10 | 7 | 6 | 5 | 2 | 3 | 5 | 12 | 12 | 8 | 8 | 3 | 4 | 4 | 6 | 8 | 7 | 6 | 7 | 6 | 8 | + | 2 | + | + | 2 | 3 | 2 | ~1 | 0 |
| $S^*$ | 9 | 6 | 5 | 5 | 6 | 5 | 4 | 6 | 5 | 5 | 4 | 4 | 6 | 7 | 5 | 7 | 8 | 5 | 6 | 6 | 6 | 6 | 5 | 6 | 6 | 6 | 8 | 7 | 6 | | |

pared to the $T$ value obtained from 1-year intervals) is by about an order of magnitude. The few studies of island bird turnover published to date (*2, 3*) (those for the California Channel Islands, Karkar Island, and Mona Island) primarily used survey intervals of several decades and yielded turnover estimates of 0.1 to 1.7 percent per year. These values can now be appreciated to be underestimates by considerable factors (*13*). The ongoing turnover studies of the California Channel Islands and other islands at 1-year intervals (*5, 6*) are yielding the considerably higher rates of 0.2 to 20 percent per year, mostly 1 to 10 percent per year, depending on area and other island properties. Thus, turnover studies of bird communities should be based on repeated censuses at 1-year intervals (*14*).

JARED M. DIAMOND

*Physiology Department,*
*University of California Medical Center,*
*Los Angeles 90024*

ROBERT M. MAY

*Biology Department, Princeton*
*University, Princeton, New Jersey 08540*

### References and Notes

1. R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, N.J., 1967).
2. J. M. Diamond, *Proc. Natl. Acad. Sci. U.S.A.* **64**, 57 (1969).
3. _→_, *ibid.* **68**, 2742 (19→ J. W. Terborgh and J. Faaborg, *Auk* **90**, 759 (1973); G. Hunt and M. Hunt, *Condor* **76**, 363 (1974).
4. I. Abbott and P. R. Grant [*Am. Nat.* **110**, 507 (1976)] calculated avifaunal turnover rates from censuses performed at very long intervals (as long as 184 years) on Australian and New Zealand satellite islands. However, these avifaunas were grossly perturbed during the survey period; most of the observed immigrations (63 of 85 on all islands, and 37 of 40 on the New Zealand satellites) were of European species introduced to Australia and New Zealand after or only shortly before the initial survey.
5. H. L. Jones and J. M. Diamond, *Condor* **78**, 526 (1976).
6. H. L. Jones, thesis, University of California, Los Angeles (1974); J. M. Diamond and H. L. Jones, in preparation.
7. For other organisms it may be more appropriate to treat time as a continuous variable, and to work with differential equations. Eq. 2a then becomes

$$I_i(t) = [\lambda_i/(\mu_i + \lambda_i)]\,[1 - e^{-t(\mu_i + \lambda_i)}]$$

and Eqs. 2b and 7 and the second equation of (*11*) are correspondingly modified.

8. J. M. Diamond, in *Ecology and Evolution of Communities*, M. L. Cody and J. M. Diamond, Eds. (Harvard Univ. Press, Cambridge, Mass., 1975), pp. 342–444.
9. M. E. Gilpin and J. M. Diamond, in preparation.
10. $$\overline{\mathrm{CV}I}_i(t) = [I_i(1 - I_i)]^{1/2}/I_i$$
$$\overline{\mathrm{CV}E}_i(t) = [E_i(1 - E_i)]^{1/2}/E_i$$

with $I_i(t)$ and $E_i(t)$ given by Eq. 2.

11. The relation is

$$\overline{\mathrm{CV}T}(t) = A^{1/2}/(\sqrt{2}tS^*T(t)$$

with $T(t)$ given by Eq. 7, and $A$ defined by

$$A = \sum_i \mu_i\lambda_i[\mu_i + \lambda_i]^{-2}[1 - (1 - \mu_i - \lambda_i)^{2t}]$$

With the help of Eq. 9, it may be seen that for $t \rightarrow \infty$ this reduces to

$$\overline{\mathrm{CV}T}(t \rightarrow \infty) = [2 \sum_i \mu_i\lambda_i/(\mu_i + \lambda_i)^2]^{-1/2}$$

Together with Eqs. 3 and 5, this gives the limiting result, Eq. 11.

12. For the four species that bred in all 29 census years, $\lambda_i$ cannot be calculated. However, this uncertainty does not affect turnover calculations, since $\mu_i$ for these species is 0.
13. Lynch and Johnson have repeatedly claimed that the estimates of turnover rates for island bird communities (in *2, 3*) based on survey intervals of several decades are seriously in error by being overestimates [N. K. Johnson, *Condor* **74**, 295 (1972); J. F. Lynch and N. K. Johnson, *Abstr. Cooper Ornithol. Soc.* (1973), Abstr. 44; *Condor* **76**, 370 (1974)]. Our analysis suggests that the opposite is true; for more detailed refutation of Lynch and Johnson's claim, see (*4*).
14. Accurate censuses of insular faunas at annual intervals are rarely available for groups other than birds. How should one correct for the in-and-out effect and estimate the true turnover rate if an island has been censused only a few times? We suggest calculating $T$ from all pairwise combinations of censuses and fitting a straight line through a graph of $\log T$ versus $\log t$. The ordinate intercept then approximates $T(1)$ within wide confidence limits.
15. Data were extracted from records of the Farne Island Committee of the National Trust by T. Reed and G. Hickling. Carrion crow was omitted because its nesting is usually prevented by the resident warden as a matter of policy.
16. We thank T. Reed, G. Hickling, and many others, for information on island bird censuses, and G. F. Oster, for helpful discussion. Supported by NSF grant BMS 7510464 and the Lievre Memorial Fund.

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# Antiserums to Neurons and to Oligodendroglia from Mammalian Brain

Abstract. *Two specific antiserums were produced, one to rat neurons and one to lamb oligodendroglia isolated in bulk from brain. On the basis of immunofluorescence and absorption studies with bulk isolated cells, the antiserums were produced to specific surface components. The antiserums are useful as markers for cell identification and for studying proteins in plasma membranes.*

Two antiserums, one specific to rat neurons and the other to lamb oligodendroglia, isolated in bulk from normal brain, have been produced (*1*). The specificities of the antiserums were determined by both immunofluorescence of the respective target cells and absorption of the antiserums by isolated cell populations from different tissues. Recent methods for the bulk isolation of the three major cell types from brain (*2*) and the subsequent maintenance of neurons and oligodendroglia (*3*) have made the production and characterization of these antiserums possible. Our studies differ from previous attempts to study cell markers in which whole regions of brain such as corpus callosum or cerebellum (*4*) have been used to produce antiserums, as well as subcellular fractions [myelin synaptosomes, or synaptic membranes (*5*)], cell lines derived from neuronal or glial tumors (*6*), or soluble brain proteins (*7*). Of the soluble proteins, the glial fibrillary acidic protein does seem specific for astroglial cytoplasm (*8*).

At present, it is not possible to obtain all three cell types from one brain sample. Neurons and an astrocyte fraction were isolated from 12-day-old rat brain (*1*); oligodendroglia were isolated from the subcortical white matter of lamb, calf, or human autopsy tissue (*1*). The procedure involves incubation of minced brain tissue in a trypsin solution, dissociation of the tissue through several screens of 100 and 200 mesh, and separation of the cells on discontinuous sucrose gradients. With rat brain, a mixed cell layer was also obtained which contained all three cell types. The cells were identified by both phase and electron microscopy and have been biochemically characterized (*9*). The neurons are more than 90 percent pure; the cells are large, 15 to 40 μm in diameter, with a large nucleus, a frequently visible nucleolus, and abundant cytoplasm. The astrocytic layer is only 60 percent pure, being contaminated with cell fragments trapped by the elaborate processes. Astrocyte cell bodies are smaller, 10 to 30 μm in diameter, with nuclei of irregular shape, and with scant cytoplasm. The oligodendroglia are round cells, 7 to 10 μm, with a small round nucleus surrounded by a rim of cytoplasm; the fraction is more than 90 percent pure by particle count.

Neurons obtained from the gradients were washed three times in 50 percent fetal calf serum, pH 6.0, to remove residual trypsin activity. Oligodendroglia were washed three times in 5 percent fetal calf serum, with a gradual shift in pH from 6 to 7.0. Both cell types were maintained in glass flasks at 37°C in a moist incubator (90 percent air and 10 percent $CO_2$), in Dulbecco's high glucose tissue culture medium (*10*) with requirements specific for each cell type. The cells remained morphologically intact during these manipulations.

For the production of antiserums, two rabbits were each injected intravenously with 70 × $10^6$ to 120 × $10^6$ freshly isolated and serum-washed rat neurons that were then washed in Dulbecco's phosphate-buffered saline (PBS) (*10*) and suspended in 1 ml of PBS. Oligodendroglia could not be injected intravenously owing to their clumping in serum, which caused death of the rabbits before the injections were finished. Thus oligoden-