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## Cost comparison of marking techniques in long-term population studies: PIT-tags versus pattern maps

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Conservation biology requires the assessment of demographic parameters and life-history data in wildlife populations. Such data can be gathered through capture-mark-recapture (CMR) of individuals. Marking techniques may vary for study organisms, research objectives and conditions, but all CMR studies have in common that the workload and expenditure is substantial, urging for cost-effective planning (Southwood, 1978; Hammer and Blankenship, 2001; Schmidt et al., 2002).

A common method for individual identification of wild animals is the recording of individual, unique spot patterns (by photographing, drawing, or photocopying: Hagström, 1973; Gill, 1978; Glandt, 1980; Hiby and Lovell, 1990; Heyer et al., 1994 — note that although pattern mapping is non-invasive we refer to it as ‘marking’). More recently, surgically implanted Passive Integrated Transponders (PIT-tags), small glass-encased electromagnetic coils bearing a unique alphanumeric code, were introduced to population studies of amphibians, reptiles and other small vertebrates (e.g., Sinsch, 1992; Zydlewski et

al., 2001). Various papers have already discussed the biological, legal and ethical issues of these methods (Henle et al., 1997; Braude and Cizek, 1998; Ott and Scott, 1999), but the cost-effectiveness of the use of pattern maps versus PIT tags has received no attention so far. We here develop an analytical model that identifies the marking technique that is best from an economic point of view. In particular, we investigate how costs per recapture data point relate to population parameters such as survival and population size, and parameters of study design such as duration and sample size. Note that capture histories such as '11' (two subsequent captures), '110' (two captures and a miss), '101', '1001' etc. all represent but a single recapture data point.

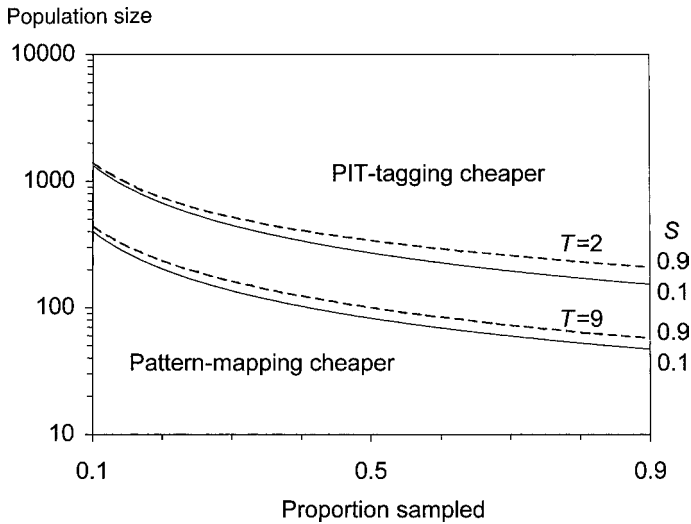
The model and its assumptions are developed with a focus on studies of single breeding populations of amphibians, but could be extended to other classes of deme-structured organisms. As opposed to toe clipping, for example, the methods considered here have in common that they do not pose an upper limit to the number of animals that can be individually recognized, and can thus be used in populations of any size.

There is now a vast body of literature discussing models for the analysis of data from CMR studies (e.g. Seber, 1982; Zar, 1996; Williams et al., 2002). To gain tractability, our model, in which we assume a population of constant size, is a somewhat simplified form of those commonly used. Our exposition uses the terminology for open populations, for which we therefore assume that immigration and emigration are both negligible and that births equal deaths. On each sampling occasion, a sample of predetermined size  $n$  is drawn with all animals in the population having equal probabilities of inclusion. The number of recaptures  $r$  depends on the sample size  $n$ , the population size  $N$ , the survival probability  $S$  and the study duration  $T$ , and, as such, is a function of human effort and the biology of the species.

The expected costs under our model are derived in appendix 1, and results for some illustrative parameter settings are presented below. Alternative parameter settings are easily explored with the help of a spreadsheet (in Microsoft Excel) available from the third author (JH) upon request.

We adopt the price of a PIT-tag as cost unit, in Europe currently at 4.30 Euros a piece when bought in quantity, such as with 'Trovan' electronic identification systems. The price of 100 pattern maps equals that of one PIT-tag and, in our hands, one PIT-tag matches the cost of one hour of work for 500 pattern map comparisons. Of course, parameter settings can be changed for more appropriate values, for example when PIT-tags become more affordable, or when photocopies are used instead of photographs. The price of a PIT-tag reader and a pattern map recorder (e.g. photocopier or camera) is not considered here. Similarly, the effort of injecting a PIT-tag equals that of recording a pattern map. Error in the identification of animals is assumed negligible for both methods.

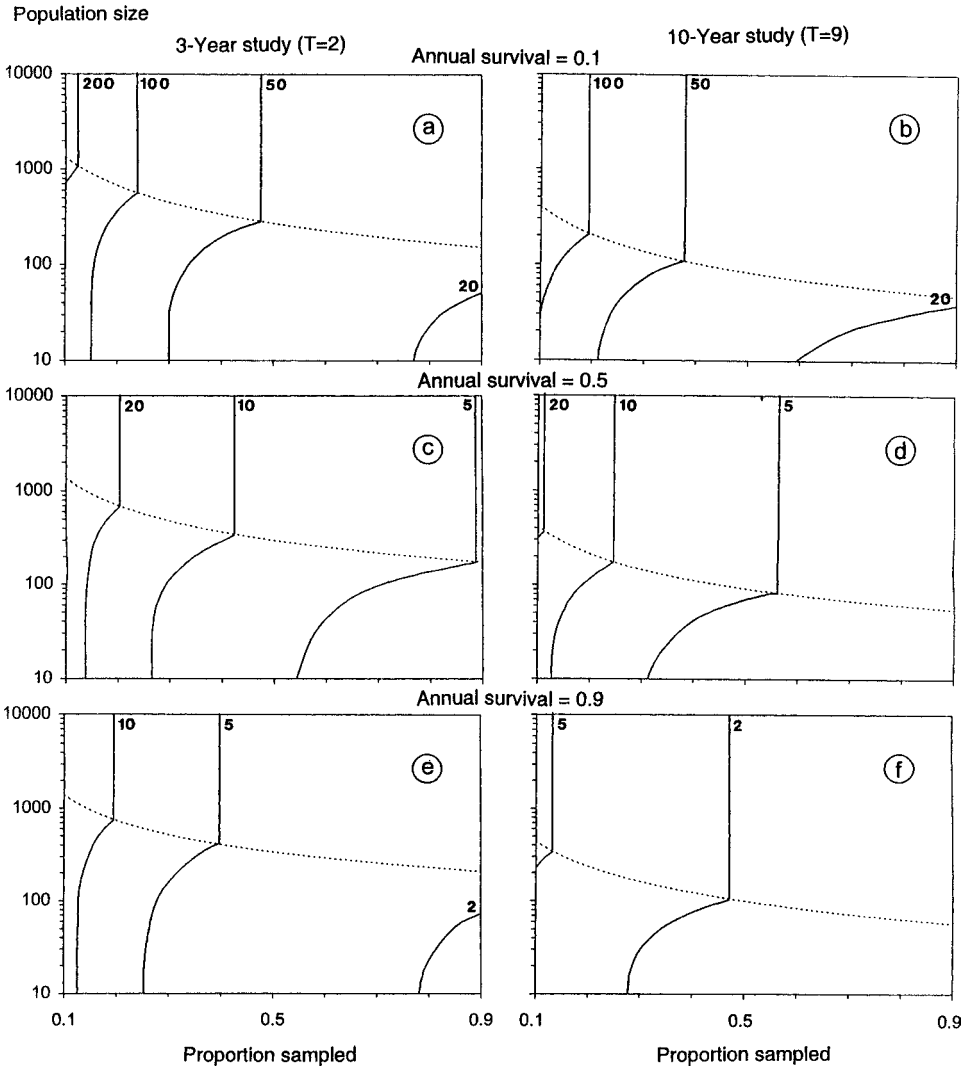
The choice for pattern-mapping or PIT-tagging as a marking method is largely determined by a trade-off between costs of labor and consumables. Pattern maps are recorded cheaply, but the time spent on matching newly recorded patterns to archived ones is substantial since comparisons must be carried out "by eye", and the expected number of comparisons rises with the square of sample size ( $n^2$ , see equation (22) in appendix 1). Conversely, PIT-tags are more expensive, but tagged individuals are recognized instantaneously, and the number of tags increases only linearly with the number of newly encountered individuals. In fig. 1 we show the conditions, in terms of population size  $N$  and sampling proportion  $p = n/N$ , for which the expected costs for pattern-mapping and PIT-tagging are equal (see also equations (14) and (19) in appendix 1). In a typical study of 3-year duration, with intensive sampling and medium annual survival ( $T = 2$ ,  $p = 0.9$ ,  $S = 0.5$ ), pattern-mapping is the cheaper method for  $N < 176$ . A lower sampling pro-



**Figure 1.** Break-even lines for the cost of individual animal recognition by pattern-mapping and PIT-tagging (using equations (14) and (19) of appendix 1), under varying conditions of population size ( $N$ ), sampling proportion ( $p$ ), survival ( $S = 0.1$  shown by solid line,  $S = 0.9$  shown by interrupted line) and study duration ( $T = 2$ ,  $T = 9$ ). Pattern-mapping and PIT-tagging are cost-efficient for small and large populations, respectively. For populations of medium size the choice for either technique is dependent on study duration.

portion renders pattern-mapping economical at a wider range of conditions ( $p = 0.5$ ,  $N < 297$ ;  $p = 0.1$ ,  $N < 1360$ ). In a 10-year study, PIT-tagging is more economic than pattern-mapping under a wide range of conditions. At high sampling and medium survival conditions ( $T = 9$ ,  $p = 0.9$ ,  $S = 0.5$ ) the break-even point is at  $N = 55$ . Again, decreasing the sampling proportion increases the applicability of pattern-mapping ( $p = 0.5$ ,  $N = 92$ ;  $p = 0.1$ ,  $N = 412$ ). A large variation in survival ( $0.1 < S < 0.9$ ) has a small effect on the conditions at which recognition techniques are in cost equilibrium (fig. 1). The cost per recapture data point ( $C_r$ ) decreases with increasing study duration and survival (see equations (14), (19) and (20) in appendix 1), and varies by approximately one order of magnitude for  $0.1 < S < 0.9$  in a 3-year study (fig. 2a, c, e), and up to two orders of magnitude in a 10-year study (fig. 2b, d, f). When  $S$  is low, the reduction in costs with increasing study duration is marginal (fig. 2a, b); when  $S$  is high the reduction in costs is substantial (fig. 2e, f).

We examined the effectiveness of pattern-mapping versus PIT-tagging and calculated the cost per recapture data point. Factors considered were population size, study duration, sampling proportion, and survival. The issue of statistical inference (i.e. accuracy of estimation) is not considered in this paper, and the two methods compared are considered equivalent from an inferential point of view. In general, we have limited this study to the exploration of the relative economic merits of two popular methods under fairly simple conditions and a range of plausible parameter values.



**Figure 2.** Contour diagrams of cost per recapture data point under varying conditions of population size ( $N = 10-10,000$ ), sampling proportion ( $p = 0.1-0.9$ ), annual survival ( $S = 0.1$  top row,  $S = 0.5$  middle row and  $S = 0.9$  bottom row) and study duration ( $T = 2$  left hand column and  $T = 9$ , right hand column). One cost unit corresponds to the price of one PIT-tag (ca. 4.30 Euros). Note the correspondence with the choice for the pattern-mapping versus the PIT-tagging recognition method, indicated by the dotted line (from fig. 1).

Pattern-mapping is more appropriate for short studies on small populations, and PIT-tag marking pays off for long-term studies of large populations. At medium population size ( $100 < N < 500$ ), the choice for either technique depends largely on study duration and sampling proportion, but not on survival. However, typically, the conditions under

which pattern-mapping outperforms PIT-tagging are those for which precision is also poor. Accordingly, pattern-mapping tends to apply to preliminary and ad hoc, low budget studies and when rough estimates are better than no estimates at all (as is frequently the case in conservation practice). Even limited information, such as obtained from a pilot study, would help to design an optimally cost-effective CMR research strategy.

Monetary cost for a population study may be substantial. At low sampling proportion the cost per recapture data point appears excessive. A high cost is also encountered when survival is low, especially in combination with short study duration. It is important to note, however, that scantiness of recapture data may represent important information, e.g. suggesting that survival is low or dispersal is high. Parameter values observed in a 3-year population study of the newt *Triturus cristatus* ( $n = 1000$ ,  $N = 1400$ ,  $S = 0.88$ ; Arntzen et al., 1999) corresponded to the use of approximately 1400 PIT-tags (equaling 6000 Euros), or 2.6 Euros per recapture data point. In a 10-year study on the newt *T. dobrogicus* ( $n = 90$ ,  $S = 0.34$  — Ellinger and Jehle, 1997;  $p = 0.76$ , Arntzen et al., 1995) the cost was approximately 600 PIT-tags, or 4.3 Euros per recapture data point (note that in fact several recognition methods were used in combination).

The workload for pattern-mapping is overestimated in our model because once-matched pattern maps can be merged. A temporal search window would also reduce the workload. For some species it may be possible to split the collection of images into subgroups, according to gender or some basic feature of the pattern, lowering the number of comparisons to be made. Attempts are being made to recognize pattern maps by computer-aided image analysis (e.g., Hiby and Lovell, 1990; Sweeney et al., 1995; Streich et al., 1997). This would render the pattern-mapping technique applicable to large populations at negligible cost. Toe clipping is not considered in this study because the number of individual marks that can be applied is limited, and because it is by some considered to be unethical. A practical, low-cost alternative to PIT-tagging would be to combine pattern-mapping with group marking, such as with a panjet tattoo or the removal of a single toe. Only marked, recaptured individuals would require an image search, therewith securing the quality of the results. A toe clip has the additional advantage that the tissue can be used for genetic analysis (Gonser and Collura, 1996).

The lack of population demographic data for many organisms is crippling implementation of pressing conservation measures. More insights into the dynamics of natural amphibian populations are urgently required for addressing issues surrounding their observed global decline (Alford and Richards, 1999; Houlahan et al., 2000; Carey et al., 2001), and more fundamental research is required to improve our understanding of population processes (Halley et al., 1996). Although amphibians are relatively well studied, life tables from data covering at least one generation are still sparse. A further cost reduction and miniaturization of individual tags would generate a breakthrough in amphibian field research, but for the time being our research potential is restricted to studying a limited number of mostly adult individuals. A caveat to this end is that the study of adults in large,

healthy and accessible populations may not result in the gathering of the most urgently required or representative data.

### Appendix 1. Derivation of expected costs for a population study employing PIT-tags and pattern maps

#### 1.1. The Number of Marks in the Population in a $T$ -year Study

We assume that, of the  $N$  animals in the population, exactly  $n$  are caught in years  $0, 1, 2, \dots, T$ . Marking takes place only in years  $0, 1, 2, \dots, T - 1$ , and analysis of marks only in years  $1, 2, 3, \dots, T$ . We denote by  $n_t$  the number of animals in the population which by the end of year  $t$  have been identified either by tagging or by the recording of their pattern maps. Since exactly  $n$  animals are identified in year zero, we set  $n_0 = n$ .

We assume that, independently of other animals, each animal survives from the end of the trapping season one year to the start of the season the following year with a constant probability  $S$ . Hence, conditional on the number  $n_{t-1}$  of animals identified at the end of year  $t - 1$  ( $t = 1, 2, 3, \dots, T$ ), the number  $s_t$  of identified animals surviving to the start of the season in year  $t$  has the binomial distribution given by

$$s_t | n_{t-1} \sim \text{Bin}(n_{t-1}, S), \quad t = 1, 2, 3, \dots, T. \quad (1)$$

Hence

$$E[s_t | n_{t-1}] = n_{t-1}S. \quad (2)$$

Let  $r_t$  denote the number of recaptured animals in year  $t$  ( $t = 0, 1, 2, \dots, T$ ). As there can be no recaptures in year zero, we have  $r_0 = 0$ . For  $t = 1, 2, 3, \dots, T$ , the conditional distribution of  $r_t$ , given  $s_t$ , is the hypergeometric distribution  $H(N, n, s_t)$  with probability function

$$P[r_t = r | s_t] = \frac{\binom{s_t}{r} \binom{N - s_t}{n - r}}{\binom{N}{n}}, \quad r = 0, 1, 2, \dots, n,$$

and conditional mean  $ns_t/N$ . By a standard property of conditional expectation (see, for example Grimmett & Stirzaker, 1992, p. 307), we have, for  $t = 1, 2, 3, \dots, T$ ,

$$E[r_t | n_{t-1}] = E\{E[r_t | n_{t-1}, s_t] | n_{t-1}\} = E\{ns_t/N | n_{t-1}\} = nn_{t-1}S/N, \quad (3)$$

where the final equality follows from equation (2). At some points below it will be more convenient to consider the number of surviving marked animals that are not recaptured in year  $t$ , which is given by the random variable

$$v_t = s_t - r_t = n_t - n, \quad t = 1, 2, 3, \dots, T. \quad (4)$$

The conditional distribution of  $v_t$ , given  $s_t$ , is given by

$$v_t | s_t \sim H(N, N - n, s_t), \quad (5)$$

and its conditional mean is

$$E[v_t | s_t] = \beta s_t/S, \quad t = 1, 2, 3, \dots, T, \quad (6)$$

where  $\beta = S(1 - n/N)$ , the probability that an animal survives from one year to the next without being captured in the latter year. From (4), (2) and (3) we have

$$E[v_t | n_{t-1}] = E[s_t - r_t | n_{t-1}] = \beta n_{t-1}, \quad t = 1, 2, 3, \dots, T. \quad (7)$$

Thus, for  $t = 1, 2, 3, \dots, T - 1$ , we obtain, using equations (4) and (7)

$$E[n_t | n_{t-1}] = E[n + v_t | n_{t-1}] = n + \beta n_{t-1}.$$

If, for  $i < t$ , we let  $\theta_{t,i} = E[n_t | n_i]$ , it follows that

$$\theta_{t,i} = E\{E\{n_t | n_{t-1}, n_i\} | n_i\} = E\{E\{n_t | n_{t-1}\} | n_i\} = n + \beta\theta_{t-1,i}.$$

This recurrence relation implies that

$$\theta_{t,i} = \beta^{t-i}n_i + n(1 - \beta^{t-i})/(1 - \beta).$$

Now let  $\theta_t = E(n_t)$  denote the expected number of identified animals at the end of year  $t$  ( $t = 0, 1, 2, \dots, T - 1$ ). Since  $\theta_t = \theta_{t,0}$ , and  $n_0 = n$ , we get that

$$\theta_t = n(1 - \beta^{t+1})/(1 - \beta), \quad t = 0, 1, 2, \dots, T - 1.$$

Observe that  $\theta_t = E(n_t)$  can be written as the sum, over  $i = 0, 1, 2, \dots, t$ , of  $n\beta^{t-i}$ , which is the expected number of animals captured at time  $i$  which survive without being captured up to time  $t$ . The conditional expectation  $\theta_{t,i} = E[n_t | n_i]$  can be similarly interpreted, with  $\beta^{t-i}n_i$  being the expected number of animals marked at time  $i$  which survive without being captured up to time  $t$ . We note also that

$$\theta_{t,i} = \beta^{t-i}n_i + \theta_{t-i-1}. \tag{8}$$

We can also use these results to find, for  $t = 1, 2, 3, \dots, T$ , both the expected number of identified animals surviving to the start of the season in year  $t$  and the expected number of recaptured animals in year  $t$ . If we let  $\mu_t = E(s_t)$  and  $\psi_t = E(r_t)$ , it follows from (2) that

$$\mu_t = E\{E\{s_t | n_{t-1}\}\} = E(n_{t-1}S) = S\theta_{t-1}, \quad t = 1, 2, 3, \dots, T, \tag{9}$$

and from (3) that

$$\psi_t = E\{E\{r_t | n_{t-1}\}\} = (nS/N)E(n_{t-1}) = (nS/N)\theta_{t-1}, \quad t = 1, 2, 3, \dots, T. \tag{10}$$

### 1.2. The Cost of a PIT Tagging Study

The number of new marks  $m_t$  recorded in year  $t$  is

$$m_t = n - r_t, \quad t = 0, 1, 2, \dots, T - 1. \tag{11}$$

As there are no recaptures in year 0, we have  $m_0 = n = n_0$ . Recalling that no marking takes place in year  $T$ , the number of identified animals in the population at the end of the season in year  $t$  is given by

$$n_t = \begin{cases} s_t + m_t, & t = 1, 2, 3, \dots, T - 1; \\ s_t, & t = T. \end{cases} \tag{12}$$

If we are using PIT tags, the total number of tags used is

$$M_T = m_0 + m_1 + \dots + m_{T-1}, \quad T = 1, 2, 3, \dots. \tag{13}$$

Thus, using (13), (12) and (9),

$$E[M_T] = n + \sum_{t=1}^{T-1} E(n_t - s_t) = \theta_0 + \sum_{t=1}^{T-1} (\theta_t - S\theta_{t-1}) = \theta_{T-1} + (1 - S) \sum_{t=0}^{T-2} \theta_t.$$

This intuitive result simply says that  $E[M_T]$  is the sum of the mean number tagged at the end of the season in year  $T - 1$  and the mean numbers failing to survive between each pair of adjacent years up until that time.

The total expected cost of using PIT tags is thus

$$C_1 = (T + 1)nC_e + C_t E[M_T], \tag{14}$$

where  $C_e$  is the cost of catching an animal in the field and  $C_t$  is the cost of a single tag. Note that we are assuming that the latter cost is the same for all members of the population and does not change over time.

1.3. Probabilistic Results

In §4 we will consider the cost of a pattern mapping study, which depends, in particular, on the expected number  $\phi_t$  of comparisons made in year  $t$  between the images of animals caught in that year and those images previously obtained. The expression for  $\phi_t$  that we will derive in §4 includes expectations of the form  $E(r_t r_i)$ , where  $i < t$ , and so the goal of the present section is to evaluate such expectations. The derivation requires us to obtain the second factorial moment of  $s_i$ , and the expectation of the product  $r_t n_i$  ( $i = 1, 2, 3, \dots, T$ ).

It follows from distributions (1) and (5) that the conditional second factorial moments of  $s_t$  given  $n_{t-1}$  and of  $v_t$  given  $s_t$  are given by

$$E\{s_t(s_t - 1) \mid n_{t-1}\} = n_{t-1}(n_{t-1} - 1)S^2, \quad t = 1, 2, 3, \dots, T, \tag{15}$$

and

$$E\{v_t(v_t - 1) \mid s_t\} = \gamma s_t(s_t - 1)/S^2, \quad t = 1, 2, 3, \dots, T, \tag{16}$$

where  $\gamma = (N - n)(N - n - 1)S^2/[N(N - 1)]$ .

Now set  $\omega_i = E\{s_i(s_i - 1)\}$ , the unconditional second factorial moment of  $s_i$  ( $i = 1, 2, 3, \dots, T$ ). Using equation (15), we have

$$\omega_i = E[E\{s_i(s_i - 1) \mid n_{i-1}\}] = S^2 E[n_{i-1}(n_{i-1} - 1)] = S^2 E[E\{n_{i-1}(n_{i-1} - 1) \mid s_{i-1}\}],$$

$$(i = 2, 3, 4, \dots, T).$$

Hence, by (4), (16), (6) and (9),

$$\begin{aligned} \omega_i &= S^2 E[E\{(n + v_{i-1})(n + v_{i-1} - 1) \mid s_{i-1}\}] \\ &= S^2 E[E\{v_{i-1}(v_{i-1} - 1) \mid s_{i-1}\} + 2nE\{v_{i-1} \mid s_{i-1}\} + n(n - 1)] \\ &= \gamma E\{s_{i-1}(s_{i-1} - 1)\} + 2n\beta S E\{s_{i-1}\} + n(n - 1)S^2 \\ &= \gamma\omega_{i-1} + 2n^2 S^2 \beta(1 - \beta^{i-1})/(1 - \beta) + n(n - 1)S^2 \end{aligned}$$

Thus  $\omega_i$  satisfies the recurrence relation

$$\omega_i = \gamma\omega_{i-1} - \lambda\beta^i + \alpha, \quad i = 2, 3, 4, \dots, T,$$

where  $\lambda = 2n^2 S^2/(1 - \beta)$  and  $\alpha = \beta\lambda + n(n - 1)S^2$ , subject to the initial condition that  $\omega_1 = n(n - 1)S^2$ . Hence we obtain

$$\omega_i = \{\alpha(\gamma^i - 1)/(\gamma - 1)\} + \{\lambda\beta(\gamma^i - \beta^i)/(\beta - \gamma)\}, \quad i = 1, 2, 3, \dots, T.$$

Now let  $\xi_i = E(r_i n_i)$ . Using (4), we have

$$\begin{aligned} \xi_i &= E[E\{(s_i - v_i)(n + v_i) \mid s_i\}] \\ &= nE\{s_i\} + E\{(s_i - n - 1)E\{v_i \mid s_i\}\} - E[E\{v_i(v_i - 1) \mid s_i\}]. \end{aligned}$$

Applying equations (6) and (16) gives

$$\xi_i = n\mu_i + (\beta/S)E\{(s_i - n - 1)s_i\} - (\gamma/S^2)\omega_i = n\{1 - (\beta/S)\}\mu_i + \{(\beta S - \gamma)/S^2\}\omega_i.$$

If we set  $\zeta = n(N - n)/\{N(N - 1)\}$ , this simplifies to give

$$\xi_i = (n^2/N)\mu_i + \zeta\omega_i.$$

We can now obtain an expression for  $E(r_t r_i)$  where  $i < t$ . Using equation (3), we obtain

$$E(r_t r_i) = E\{E(r_t r_i \mid n_{t-1}, r_i)\} = E\{r_i E(r_t \mid n_{t-1})\} = (nS/N)E(r_i n_{t-1}).$$

Now

$$E(r_i n_{t-1}) = E\{E(r_i n_{t-1} \mid r_i, n_i)\} = E\{r_i E(n_{t-1} \mid n_i)\}.$$

Hence, by (8),

$$E(r_t r_i) = (nS/N)E\{r_i(\beta^{t-i-1}n_i + \theta_{t-i-2})\} = (nS/N)(\beta^{t-i-1}\xi_i + \theta_{t-i-2}\psi_i). \tag{17}$$

1.4. *The Cost of a Pattern Mapping Study and Cost per Recapture*

In order to carry out pattern mapping on the population, the researcher must build up a “gallery” of images of animals. From the start the captured animals are compared with the images in the gallery. This can take a long time. The expected cost can be worked out as follows. For  $t = 1, 2, 3, \dots, T$ , the number of pictures in the gallery at the end of season  $t - 1$  is the total number of animals newly encountered during that season or any previous one, namely  $m_0 + m_1 + \dots + m_{t-1} = M_t$ .

In year  $t$ , there are  $m_t$  animals caught for the first time, and, for each of these, the number of comparisons will be  $M_t$ , giving a total of  $m_t M_t$  comparisons associated with newly encountered animals. For any recaptured animal, a match may be seen with the first image or may not happen until the last. More precisely, let  $u_i$  denote the number of comparisons required for the  $i^{\text{th}}$  recaptured animal ( $i = 1, 2, 3, \dots, r_t$ ). The total number of comparisons in year  $t$  can then be written as

$$Y_t = m_t M_t + \sum_{i=1}^{r_t} u_i = (n - r_t) M_t + \sum_{i=1}^{r_t} u_i. \tag{18}$$

The total expected cost of using pattern comparison is thus

$$C_2 = (T + 1)nC_e + TnC_p + C_c \sum_{t=1}^T E[Y_t], \tag{19}$$

where  $C_p$  is the cost of photographing an animal,  $C_c$  is the cost of a single pattern comparison, and, as earlier,  $C_e$  is the cost of catching an animal in the field.

We approximate the cost per recapture by the expected cost of the study divided by the expected total number of recaptures:

$$C_r = C_X / \sum_{t=1}^T \psi_t. \tag{20}$$

$C_X$  is  $C_1$  given by equation (14) for PIT tags and is  $C_2$  given by equation (19) for pattern-mapping. In general, this will not be the same as the expectation of the ratio of the total cost to the number recaptured, which is more difficult to derive.

The remainder of this appendix is devoted to finding an expression for  $\phi_t = E[Y_t]$ , the expected total number of comparisons in year  $t$ . Suppose now that we ignore entirely any changes to the gallery that could be made during the matching process in a given year. For example, if an individual  $\mathbf{Z}$  is recognized initially, time could obviously be saved by noting that other animals captured that year need not be compared with the image of  $\mathbf{Z}$ . Time could also be saved by making sure that images are arranged in last-in-first-out order, so that the first comparisons made are not with the images of the animals which are most likely to be dead. This will make an enormous difference if the study duration  $T$  is much longer than the expected lifetime of an animal. We suppose that no special time-saving devices are employed and that the duration  $T$  is not significantly longer than the animal’s lifetime.

In these circumstances it is reasonable to assume that the vector  $(u_1, u_2, \dots, u_{r_t})$  constitutes a sample, drawn without replacement, from the set  $\{1, 2, 3, \dots, M_t\}$ . Thus, given  $M_t$  and  $r_t$ , the expected total number of comparisons associated with recaptured animals is

$$\sum_{i=1}^{r_t} E(u_i | M_t, r_t) = \sum_{i=1}^{M_t} \{i P(\text{match occurs with image } i)\} = \left(\frac{r_t}{M_t}\right) \sum_{i=1}^{M_t} i = r_t(M_t + 1)/2. \tag{21}$$

Thus, setting  $\phi_t = E(Y_t)$ , we have from (18) and (21) that

$$\phi_t = E\{E(Y_t | M_t, r_t)\} = E[(n - r_t)M_t + \{r_t(M_t + 1)/2\}].$$

Hence by (13) and (11)

$$\begin{aligned}\phi_t &= E\{(2n - r_t)M_t/2\} + E(r_t/2) \\ &= E\left[\left\{n - \frac{r_t}{2}\right\}\left\{nt - \sum_1^{t-1} r_i\right\}\right] + \frac{1}{2}E(r_t) \\ &= \frac{1}{2}\sum_{i=1}^{t-1} E(r_t r_i) - n\sum_1^{t-1} \psi_i - \frac{(nt-1)}{2}\psi_t + n^2 t.\end{aligned}$$

This expression may now be evaluated, by recalling that  $\psi_i$  and  $E(r_t - r_i)$  are given by equations (10) and (17) respectively. An approximation to  $\phi_t$  can be obtained by noting that

$$\phi_t = \tilde{\phi}_t + \frac{1}{2}\sum_{i=1}^{t-1} \text{cov}(r_t, r_i),$$

where

$$\begin{aligned}\tilde{\phi}_t &= \frac{1}{2}E(r_t)\sum_{i=1}^{t-1} E(r_i) - n\sum_1^{t-1} \psi_i - \frac{(nt-1)}{2}\psi_t + n^2 t \\ &= \left(\frac{1}{2}\psi_t - n\right)\sum_1^{t-1} \psi_i - \frac{(nt-1)}{2}\psi_t + n^2 t.\end{aligned}\tag{22}$$

The approximation  $\tilde{\phi}_t$  given by equation (22) to the expected total number  $\phi_t$  of comparisons thus disregards the correlation between  $r_t$  and each of the random variables  $r_i$  ( $i = 1, 2, 3, \dots, t-1$ ). Since  $\tilde{\phi}_t$  depends only on the values of  $\psi_i$  for  $i = 1, 2, 3, \dots, t$ , it is easier to evaluate than  $\phi_t$ .

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