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SURVIVAL AMONG SOME NORTH AMERICAN WOOD WARBLERS

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INTRODUCTION

Published data on the survival and life expectancy of adult passerine birds show considerable variation among species. Farner (1955) concludes that average annual survival ranges from approximately 30 to 60%. Estimates for Wood Warblers (Parulidae) are few.

While banding during successive spring migrations at Point Pelee, Ontario, the Point Pelee Bird Observatory recorded returns of Yellow Warblers (*Dendroica petechia*). The banding area was well populated with breeding Yellow Warblers and virtually all of those returning were probably from this local population. Numbers of Yellow Warblers newly banded each year, however, varied considerably and undoubtedly included transients. Similar return data are reported by Anderson and Maxfield (1967) for some other wood warblers in Massachusetts. Because of the presence of transients, established methods of analyzing these return data to derive average survival are not applicable. The method developed and applied in this paper is based on isolating a sub-sample of birds which returned at least once and analyzing the pattern of multiple returns within this sub-sample.

YELLOW WARBLER RETURNS TO POINT PELEE

The flora and fauna of Point Pelee, which extends southwards into the western end of Lake Erie, have been extensively described by Urquhart (1941) and others. Diagrams of the point showing the main banding areas may be found in Roberts (1966 and 1968). From 1957 through 1964, Yellow Warblers were mist-netted at the east beach along the sand dune that parallels the marsh, separating it from Lake Erie. Retrap dates for each of the 35 returns of the 25 returning individuals are shown in Table 1. In Table 2, numbers trapped and returning are summarized together with days of operation. While the number of days of netting as well as the number, type and precise location of the nets varied from year to year, there was no regular pattern and it is assumed in the analysis presented later that any variations in sampling of the local population were randomly distributed.

TABLE 1. DATES OF RETURNS OF YELLOW WARBLERS AT POINT PELEE, EAST BEACH (INITIAL DATE FOR EACH INDIVIDUAL IS DATE OF BANDING)

Band No.	Sex	1958	1959	1960	1961	1962	1963	1974
26-87825	M	5/17		5/7	5/14			
26-87826	M	5/17	5/10	5/14	5/22			
26-87830	F	5/17	5/17					
26-87849	M	5/20	5/17					
26-87856	F	5/20	5/19					
26-88035	M		5/6	5/2				
26-88088	M		5/10	5/15	5/14	5/12		
26-88824	F		5/22				5/14	
26-88833	M		5/22				5/12	
26-89791	F			5/5	5/21			
26-89810	M			5/6	5/14		5/16	
26-91028	M			5/7		5/12		
26-90075	M				5/7	5/12	5/8	
26-90387	F				5/21		5/9	
26-91290	U				5/13		5/14	
26-91434	F				5/14			5/17
26-91615	F					5/12	6/15	
26-91616	M					5/12	5/10	
26-91622	M					5/12	5/12	5/2
26-91624	M					5/12	5/6	
26-91629	M					5/19	5/12	5/11
26-91635	M					5/19	5/8	
26-91636	F					5/19	5/10	
26-91649	M					5/19	5/5	5/17
102-06971	M						5/17	5/30

The Yellow Warbler is a common nesting species on the narrow strip of dry land which borders the east beach. Although the banding totals undoubtedly include a variable and indeterminate proportion of transients, all the returns are probably of birds which breed there. During the later years when most birds were sexed, males outnumbered females almost two for one among birds banded. However, this was also true for returns and probably results from greater activity on the part of the males rather than from difference in mortality between the sexes. Anderson and Maxfield (1967) found a similar preponderance of males among returning warblers in Massachusetts.

TABLE 2. SUMMARY OF BANDING AND RETURNS AT POINT PELEE, EAST BEACH

Year	Days of Operation May/June	Number Banded in Year	Number of Returns in Year	Number Banded in Year, which Subsequently Returned
1958	10*	10*	—	5
1959	14*	38*	4	4
1960	12	43	4	3
1961	6	33	5	4
1962	6	22	3	8
1963	23	53	14	1
1964	10	9	5	—

*approximate.

CALCULATION OF ADULT SURVIVAL

Assumptions inherent in using banding data for calculating annual survival have been extensively discussed by Hickey (1952 and Farner (1955).

According to Farner, experience has shown that in many species there is a stabilization of annual mortality rate at a value apparently independent of age after an initial juvenile period of higher mortality.

In the analysis presented here, all the returning individuals were in at least their third calendar year of life. As this is well beyond any period of juvenile vulnerability, it is reasonable to assume that mortality is independent of age. It also seems reasonable to assume that there is no band loss and that netting and wearing of bands have no significant effect on survival. The most important assumptions, however, relate to the interpretation of results rather than to the validity of the data. The final estimate of survival is an average for the sampled population over the period of study. Its value as an indicator of average survival for the species depends on assuming that the sampled population was stable and representative of the general population over longer periods of time. Differences in adult survival may occur not only regionally but also between breeding and non-breeding individuals, between successful breeding populations and less successful marginal ones, as suggested by Nice (1937) for the Song Sparrow (*Melospiza melodia*) and between more densely and less densely populated habitats as suggested by Fretwell (1968) for the Field Sparrow (*Spizella pusilla*). Irregular catastrophic mortality may occur and be offset by subsequent increase in productivity or fledgling survival.

The analysis is based on the distribution of returns grouped according to year of banding. Each return-year, a year in which at least one return is recorded, is considered as an independent event, regardless of whether the individual has returned before; the probability of a return-year occurring is assumed to depend only on survival and trapping effort. The mathematical approach is similar to Haldane's (1955) treatment of an incomplete series of recoveries using the method of maximum likelihood, but it also takes into account the effect of banding part of the local population each year on the number of individuals available for banding in the succeeding year. For a discussion of the maximum likelihood technique, reference may be made to Mather (1965).

To apply the technique here, we must first express the likelihood that the unknown survival rate S gives rise to the measured set of return-year frequencies $D_{J,K}$ as a result of the known sampling rate t, where $D_{J,K}$ is the number of return-years of birds banded in the Jth year of banding operations and retaken in the Kth year following banding. The best estimate of S is then the value at which the likelihood is a maximum. To simplify subsequent calculations it is customary to replace the likelihood expression by its logarithm which gives a maximum at the same value of S. The expected value of $D_{J,K}$ as a proportion of all returns is:

$$\frac{B_J S^K}{\sum_{j=1}^{I} \sum_{k=1}^{N} B_j S^k}$$

Where B_J is the number of unbanded summer resident individuals present in the Jth year of banding operations, S is the average fraction surviving from year to year and I is one less and N is j less than the number of years over which banding was conducted. j and k are dummy variables analogous to J and K respectively but distinguished from them for summation purposes. B_J, which comprises the unbanded survivors from the previous year's breeding population and new recruits, may be substituted by:

$$B_1 \{S^J (1-t)^{J-1} + \sum_{G=1}^{J} (1-S)(S(1-t))^{G-1}\}$$

Where t is the average fraction trapped each year and G is a dummy variable.

The logarithm of the likelihood may now be expressed as:

$$L = \sum_{K=1}^{I} D_K \ln S^K + \sum_{J=1}^{I} D_J \ln\{S^J (1-t)^{J-1} + \sum_{G=1}^{J} (1-S)(S(1-t))^{G-1}\}$$

$$- R \ln \sum_{J=1}^{I} \sum_{K=1}^{N} S^K\{(1-t)^{J-1} + \sum_{G=1}^{J} (1-S)(S(1-t))^{G-1}\}$$

TABLE 3. YELLOW WARBLER RETURNS ARRANGED FOR SURVIVAL CALCULATION

Year Banded	J	D_J	K					
			1	2	3	4	5	6
1958	1	8	4	2	2	0	0	0
1959	2	6	2	1	1	2	0	
1960	3	4	2	1	1	0		
1961	4	5	1	3	1			
1962	5	11	8	3				
1963	6	1	1					
D_K		R = 35	18	10	5	2	0	0

Where R is the total number of return-years recorded, D_J the total number recorded for birds banded in the Jth year of banding operations and D_K the total number recorded in the Kth year following banding. In the last term j has been replaced by J and k by K since the necessity for distinguishing between them has now disappeared. N of course is now J less than the number of years over which banding was conducted.

I originally calculated the values of S presented in this paper directly from the likelihood expression by using a trial and error procedure to find the expression's maximum. However, this method does not provide a basis for finding σ, the standard error of the estimate, which it has been shown (Mather, 1965) can be obtained from the second derivative where

$$\frac{d^2L}{dS^2} = -\frac{1}{\sigma^2} .$$

The standard errors were calculated for me by Dr. Salvadori. In view of the possibility that some readers may wish to apply the method to data of their own, he has kindly generalized the computer program which he wrote for inclusion as an appendix to this paper. This program calculates both the maximum likelihood value of S, using the more elegant method of putting the first derivative equal to zero, and its standard error.

In table 3, the data for Yellow Warblers at Point Pelee are arranged for the maximum likelihood calculation. However, before proceeding with this calculation, an estimate of t is obtained by considering the histories of those birds known to have been alive two or more years after banding. Table 1 lists 14 such birds which were available for retrapping in a total of 23 intervening years; returns were recorded in only 10 of those years. Then t is equal to R′, the number of intervening years, divided by n, the number of

TABLE 4. RETURNS OF PREDOMINANT SPECIES FROM ANDERSON & MAXFIELD DATA ARRANGED FOR SURVIVAL CALCULATION

Species	Year Banded	J	D_J			K			
				1	2	3	4	5	6
Yellowthroat	1960	1	1	1	0	0	0	0	0
	1961	2	3	1	1	0	0	1	
	1962	3	9	3	1	3	2		
	1962	4	9	5	2	2			
	1964	5	4	2	2				
	1965	6	6	6					
	D_K		R = 32	18	6	5	2	1	0
Ovenbird	1960	1	17	8	2	2	1	2	2
	1961	2	5	1	2	1	1	0	
	1962	3	0	0	0	0	0		
	1963	4	2	1	0	1			
	1964	5	2	2	0				
	1965	6	1	1					
	D_K		R = 27	13	4	4	2	2	2
N. Waterthrush	1960	1	8	3	2	2	1	0	0
	1961	2	4	2	0	1	1	0	
	1962	3	3	1	0	1	1		
	1963	4	2	2	0	0			
	1964	5	1	1	0				
	1965	6	0	0					
	D_K		R = 18	9	2	4	3	0	0

those years in which returns were recorded, and here has a value of 0.435.

The best estimate of S is 0.526 with a standard error of 0.077. It should be noted that the standard error includes no contribution from possible error in the estimate of t. However, over a wide range of values of t a change of 0.1 results in a change of only about 0.01 in the value of S, opposite in sign. In view of the small sample size and short period of study, the inherent variability of survival, recruitment and experimental conditions from year to year may be a more important limitation to the precision of the estimate.

Anderson and Maxfield (1967) give data on warbler returns in southeastern Massachusetts. Table 4 shows their data for the three predominant species, Yellowthroat (*Geothlypis trichas*), Ovenbird

TABLE 5. RETURNS FOR GROUPED SPECIES ARRANGED FOR SURVIVAL CALCULATION

Species	Year Banded	J	D_J	K					
				1	2	3	4	5	6
I. Combined data from Anderson & Maxfield for three species Canada Warbler Black and white Warbler, American Redstart	1960	1	7	2	1	1	2	1	0
	1961	2	5	2	1	1	0	1	
	1962	3	4	3	1	0	0		
	1963	4	3	1	1	1			
	1964	5	1	1	0				
	1965	6	1	1					
	D_K		R = 21	10	4	3	2	2	0
II. Anderson & Maxfield data combined for all six warbler species	1960	1	33	14	5	5	4	3	2
	1961	2	17	6	4	3	2	2	
	1962	3	16	7	2	4	3		
	1963	4	16	9	3	4			
	1964	5	8	6	2				
	1965	6	8	8					
	D_K		R = 98	50	16	16	9	5	2
Anderson and Maxfield data for all six warbler species combined with Point Pelee Yellow warbler data	—	1	41	18	7	7	4	3	2
	—	2	23	8	5	4	4	2	
	—	3	20	9	3	5	3		
	—	4	21	10	6	5			
	—	5	19	14	5				
	—	6	9	9					
	D_K		R = 133	68	26	21	11	5	2

(*Seiurus aurocapillus*) and Northern Waterthrush (*Seiurus noveboracensis*) arranged for calculation. Table 5 shows their combined data (group 1) for the Canada Warbler (*Wilsonia canadensis*), Black-and-white Warbler (*Mniotilta varia*) and American Redstart (*Setophaga ruticilla*); combined data for all six of their warbler species (group II); and these data combined with the Point Pelee Yellow Warbler data (group III). In compiling these tables I considered birds banded as immatures *pari passu* with adults banded the following year. The assumptions involved appear to be the same as at Point Pelee except that trapping effort in Massachusetts was evidently more consistent from year to year.

TABLE 6. ESTIMATES OF AVERAGE ANNUAL SURVIVAL (S) FOR WARBLER SPECIES AND GROUPS

Species or group	Location	R′	n	t	s	σ
Yellow Warbler	Pt. Pelee	10	23	0.435	0.526	0.077
Yellowthroat	Mass	5	23	0.217	0.542	0.082
Ovenbird	Mass	11	20	0.550	0.845	0.071
N. Waterthrush	Mass	8	14	0.571	0.723	0.107
Group I	Mass	8	17	0.471	0.714	0.095
Group II	Mass	32	74	0.432	0.678	0.045
Group III	combined	42	97	0.433	0.640	0.039

Table 6 shows the calculated values of t and S for each species and group.

PRODUCTIVITY

Information on survival and productivity, taken together, imply population stability or change. It is therefore pertinent to review available productivity data. Estimates of fledgling production taken or deduced from published sources are shown in table 7 for seven species of wood warbler. In none of the studies involved was an obvious population change apparent between the beginning and the end of the study, nor were significantly unbalanced sex ratios or significant numbers of non-breeding individuals recorded. In compiling table 7 an effort was made to ensure that figures for warblers fledged per nest were reasonably consistent with corresponding figures for nests per pair, so as to arrive at a valid estimate of production of fledglings per pair. It should be noted that because of the difficulty in defining nesting attempts, figures shown for nest success, warblers fledged per nest and nests per pair from different studies are not necessarily comparable.

The hole-nesting Prothonotary Warbler (*Protonotaria citria*) produced 1.6 and Kirtland's Warbler (*Dendroica kirtlandii*) 1.4 fledglings per pair. The figure of 1.1 fledglings per male for the Prairie Warbler (*Dendroica discolor*) may be low; in another paper, Nolan (1963b) reports a nesting success of 20%; if other factors remained the same this would increase the estimate of fledgling production to 1.5 per male. Productivity among the remaining species was higher. Ovenbirds produced 2.9 fledglings per female. Young's Yellow Warblers produced 2.0 fledglings per pair; Schrantz's evidently had a higher but unspecified rate of nest success and therefore probably a lower number of nests per pair resulting in production of perhaps 3 fledglings per pair. According to Cruickshank (1957) the American Redstart normally rears one brood, sometimes two; on this basis estimated productivity is in the range of 2 to 3 fledglings per pair.

TABLE 7. PRODUCTION OF FLEDGLINGS AMONG WOOD WARBLERS

Species	Location & Reference	Number	Nests Number per pair	% successful	Warblers Fledged	Fledged per nest	Fledglings per pair
Prothonotary Warbler	Michigan (Walkinshaw 1953)	178	1.5(1)	28	191	1.1	1.6
Kirtland's Warbler	Michigan (Mayfield 1960)	154	1.5(2)	45(2)	—	0.9(2)	1.4(2)
Prairie Warbler	Indiana (Nolan 1963a)	55	2.6(3)	15	24	0.4	1.1(3)
Ovenbird	Michigan (Hann 1937)	36	1.5(4)	—	70	1.9	2.9(4)
Yellow Warbler	Iowa (Schrantz 1943)	41	—	—	91	2.2(5)	—
Yellow Warbler	Wisconsin (Young 1949)	12(6)	1.7	42	14	1.2	2.0
American Redstart	Ohio (Sturm 1945)	18	—	52(5)	26	1.4(5)	—
Yellow-throat	Michigan (Stewart 1953)	19	3(7)	37	20	1.1	3.2
Yellow-throat	Michigan (Hofslund 1959)	38	—	55	64	1.7	—
Yellow-throat	Michigan (Hofslund 1959)	12	—	33	15	1.3	—

(1) based on 17 pairs for which 26 nests were recorded
(2) estimated by adjusting incomplete data for exposure to hazards during periods of no observation
(3) based on males of which there were 21
(4) based on females of which there were 24
(5) breeding season only partly covered
(6) does not include nests rebuilt over Cowbird eggs
(7) author's estimate

For Stewart's (1953) Yellowthroats, estimated production was approximately 3.2 fledglings per pair. Hofslund's (1959) figures for his Ann Arbor, Michigan, studies would probably correspond to a somewhat higher productivity but those for Duluth, Minnesota, where the Yellowthroat is normally single-brooded would correspond to a lower productivity.

DISCUSSION

In his critical review of available data on survival and life expectancy among birds, Farner (1955) indicates a range of 30 to 60% for average annual adult survival among passerines. The only estimate for a wood warbler included in this review was Hann's (1948) figure of 53.7% for the Ovenbird. This was based on returns over a ten year period of 38 adults on a 40-acre tract near Ann Arbor, Michigan; most were banded in two consecutive years and it was assumed that no individuals abandoned the breeding area and hence disappearance indicated death. The standard error of Hann's estimate is calculated to be 6.0%.

More recently, Mayfield (1960) estimated average annual survival for Kirtland's Warbler at 60%, based chiefly on the return in a single year of 39 out of 65 males.

Average annual survival estimated in the present paper ranges from 52.6% for Yellow Warblers at Point Pelee to 84.5% for Ovenbirds in Massachusetts. With the exception of the Yellowthroat the Massachusetts species all show remarkably high survival. Since bias in the sampling process would generally tend to lower the estimate it is likely that these high rates of survival are representative at least for the local populations and six-year period involved. The significant difference between my estimate for Ovenbirds of 84.5% and Hann's of 53.7% suggests wide variation between populations or time periods. As such differences may well be greater than those between the various wood warbler species, it is pertinent to examine the combined data. The estimated annual survival rate for all Massachusetts species is 67.8% with a standard error of 4.5%; including the Point Pelee data this becomes 64.0% with a standard error of 3.9%. These are remarkably high figures for a passerine group.

The annual production of about 3 fledglings per pair among the more successful wood warbler populations appears to be relatively low for a passerine. Meanley and Webb (1963) found a productivity of 4.2 for the Red-winged Blackbird (*Agelaius phoeniceus*) and Nice (1937) 4.3 for the Song Sparrow (*Melospiza melodia*). Lack (1966) gives a production per pair of 4.1 for a population of Blackbirds (*Turdus merula*) in England and much higher figures for the hole-nesting Pied Flycatcher (*Muscicapa hypoleuca*) and for the prolific Great and Blue Tits (*Parus major* and *Parus caeruleus*).

Although parasitization by the Brown-headed Cowbird (*Molothrus ater*) was significant in the studies of all species in table 7 except the American Redstart, it appears to have substantially reduced productivity in only two. Among Kirtland's Warblers

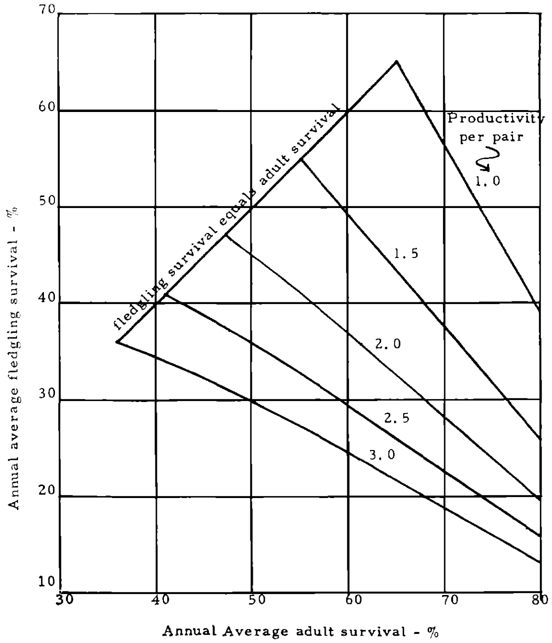
Mayfield (1960) found 55% of the nests parasitized and survival to fledging greatly reduced; he estimates that without Cowbird interference fledgling production would average about 2.2 per pair. Both Stewart (1953) and Hofslund (1957) found about 45% of Yellowthroat nests parasitized with very low production of Yellowthroat fledglings in these nests. On the other hand among Ovenbirds, Prothonotary Warblers and Prairie Warblers the young hatched and survived well in parasitized nests. Although his Ovenbirds were heavily parasitized, Hann (1937) estimated the effective loss of production potential, after allowing for renesting, at only 13.5%. Among Yellow Warblers the effect of parasitization was small because of the species' frequent habit of burying a parasitized clutch and relaying. Therefore, even without the Cowbird, only the Yellowthroat might have achieved a level of fledgling production much above 3.

All the studies of Wood Warbler productivity were made in the vicinity of the Great Lakes. It is significant that for the three species with the lowest fledgling production the populations studied were either relict or close to the northern limit of regular breeding. The four more successful species, on the other hand, are generally common in the region, wherever the habitat is suitable. As the populations of the less successful species were apparently stable it appears that an annual productivity of 1.5 fledglings for every two adults living at the start of the breeding season is sufficient to maintain them. The more successful species appear to be producing a surplus of young. This surplus may well be a key factor in their broader distribution, providing a mechanism for rapid replacement of the population after a disaster as well as for expansion into peripheral or other unoccupied areas that may become favourable for breeding. The conclusion that a surplus of young exists among these more successful species is supported by Hann's (1937) observation that his Ovenbirds' production of 2.9 fledglings per female was reduced to 1.6 before independence. Furthermore, Mayfield's (1960) conclusion from many years of observation that Kirtland's Warbler, once fledged, survived remarkably well on the breeding grounds implies that high mortality among juveniles is not inevitable, but is indeed related to a surplus.

In figure 1 the implied relationship between average annual survival of adults and of fledglings during their first twelve months is shown for fledgling production per pair ranging from 1 to 3. The calculations were made on the assumption that breeding begins on June 1, fledgling mortality becomes equal to adult mortality from January 1 and production figures relate to the number of adults living June 1, as follows:

Let S_A and S_a be the annual and monthly average survival rates for adults, S_I the average annual survival rate for immatures during their first twelve months after fledging, S_i the average monthly survival rate for fledglings from August 1 to December 31 and n the number of fledglings produced per adult. Then for a stable population

FIGURE 1



$$S_A + nS_i^5 S_a^5 = 1$$

and $$S_I = S_i^5 S_a^7 = S_a^2 (1-S_A)/n$$

The minimum annual average adult survival for productivity of 1.5 fledglings per pair is 55%; this figure requires that fledglings survive as well as adults. My estimate of 64% adult survival implies first year survival among fledglings of the less successful species of 45%. For the more successful species having a productivity between 2 and 3 the implied first year survival is from 12 to 24%. These figures seem reasonable and support the conclusion that average annual survival of 60% or more is common among North American Wood Warblers.

SUMMARY

A method of estimating average annual adult survival from return data obtained in consecutive years of banding of an unknown mix of summer residents and transients is developed and applied. The method is based on isolating a sub-sample of birds which returned

at least once and analyzing the pattern of multiple returns within this sub-sample.

Average annual adult survival based on new return data for Yellow Warblers at Point Pelee and for published return data for six species of Wood Warbler in Massachusetts is estimated to be 64.0%. with a standard error of 3.9%. Based on the small samples available, estimates for individual species range from 52.6% to 84.5%.

Analysis of published data on reproductive success in stable populations of various Wood Warblers suggests that average annual fledgling production ranges from about 1.5 per pair for marginal populations to about 3.0 for more broadly established populations. The lower figure infers minimum adult survival of 55% and this requires that fledglings survive as well as adults. It is concluded that average annual survival of 60% or more is normal among North American Wood Warblers. This is a remarkably high figure for a passerine group.

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APPENDIX

The Evaluation of the Maximum Likelihood of S by a Newton-Raphson Method

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The logarithm of the likelihood expression has been shown to be

$$L = \sum_{K=1}^{N} D_K \ln S^K + \sum_{J=1}^{N} D_J \ln\{S^J (1-t)^{J-1} + \sum_{G=1}^{J} (1-S)(S(1-t))^{G-1}\}$$

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$$- R \ln \sum_{J=1}^{N} \sum_{K=1}^{N+1-J} S^{K}\{S^{J}(1-t)^{J-1} + \sum_{G=1}^{J} (1-S)(S(1-t))^{G-1}\} \tag{1}$$

$$\text{where } D_J = \sum_{K=1}^{N+1-J} D_{J,K}$$

$$D_K = \sum_{J=1}^{N+1-K} D_{J,K}$$

$$R = \sum_{J=1}^{N} \sum_{K=1}^{N+1-J} D_{J,K}$$

and N = number of years. Differentiating term by term, the first derivative of L is given by

$$\frac{dL}{dS} = \sum_{K=1}^{N} \frac{KD_K}{S} + \sum_{J=1}^{N} \frac{D_J}{\alpha_J} \gamma_J - \frac{R\delta}{\beta} \tag{2}$$

$$\text{where } A_r \equiv (1-t)^{r-1}$$

$$\alpha_J \equiv S^J A_J + \sum_{G=1}^{J} (1-S) S^{G-1} A_G$$

$$\beta \equiv \sum_{J=1}^{N} \sum_{K=1}^{N+1-J} S^K \alpha_J$$

$$\gamma_J \equiv J S^{J-1} A_J + \sum_{G=1}^{J} \{(G-1) S^{G-2} - G\, S^{G-1}\} A_G$$

$$\delta \equiv \sum_{J=1}^{N} \sum_{K=1}^{N+1-J} \{K S^{K-1} \alpha_J + S^K \gamma_J\}$$

The maximum likelihood estimate of S is given by the solution of

$$\frac{dL}{dS} = 0 \tag{3}$$

In order to solve (3) the Newton-Raphson iterative method is used i.e.

$$S_{\text{final}} = S_{\text{initial}} - \left(\frac{dL}{dS}\right) / \left(\frac{d^2L}{dS^2}\right) \tag{4}$$

where S_{initial} is some starting value for S and S_{final} is calculated from (4). If $|S_{\text{final}} - S_{\text{initial}}| < \epsilon$, a sufficiently small number, then S_{final} is the solution required, otherwise we repeat the process setting $S_{\text{initial}} = S_{\text{final}}$.

Differentiating (2) term by term the second derivative is given by

$$\frac{d^2L}{dS^2} = - \sum_{K=1}^{N} \frac{KD_K}{S^2} + \sum_{J=1}^{N} D_J \left(\frac{\alpha_J \varepsilon_J - \gamma_J^2}{\alpha_J^2}\right) - R\left(\frac{\beta\phi - \delta^2}{\beta^2}\right) \tag{5}$$

$$\text{where } \varepsilon_J = J(J-1)S^{J-2}A_J + \sum_{G=1}^{J} \{(G-1)(G-2)S^{G-3} - G(G-1)S^{G-2}\}A_G$$

$$\text{and } \phi = \sum_{J=1}^{N} \sum_{K=1}^{N+1-J} \{K(K-1)S^{K-2}\alpha_J + 2KS^{K-1}\gamma_J + S^K\varepsilon_J\}$$

This expression is not only required for the evaluation of (4) but it also gives $-1/\sigma^2$ so that

$$\sigma = \sqrt{-\frac{1}{\frac{d^2L}{dS^2}}} \tag{6}$$

The computer program to evaluate (4) and (6) is written in FORTRAN and was run on an IBM/360 model 50. In order to make the program as machine independent as possible, the input/output statements were simplified and no string manipulations were used. The program is straightforward and follows the procedure outlined above. The input cards are arranged as follows:—

Card 1: Cols. 1-2: contain the number of sets of data to be analysed (NS).

Card 2: Cols. 1-2: contain the number of years in a set of data (N).

Card 3: Cols. 1-2, 3-4, 5-6, etc.: contain the D_K's $K = 1,N$.

Card 4: Cols. 1-2, 3-4, 5-6, etc.: contain the D_J's $J = 1,N$.

Card 5: Cols. 1-4: contain t
Cols. 5-7: contain R

Cards 2-5 are repeated for each set of data. All numbers are right aligned. At the end of the program which follows an example set is given. The output from the program is fully documented and needs no explanation. However, if the program is run at an installation where the parameters for the input and output devices are not 5 and 6 as shown, the pertinent numbers in the read and write statements must be changed accordingly.

```
C  MAXIMUM LIKELIHOOD OF S BY A NEWTON-RAPHSON METHOD
C
      DIMENSION ((10), DA(10)
C     INPUT FORMAT STATEMENTS
      1  FORMAT (6F2.0)
      2  FORMAT (I2)
      3  FORMAT (F4.3, F3.0)
C     OUTPUT FORMAT STATEMENTS
      5  FORMAT (//20X, 16 HVALUES OF DK ARE, 6F4.0)
      6  FORMAT (//20X, 16HVALUES OF DJ ARE, 6F5.1)
      7  FORMAT (//20X,5H  S =,F6.3,7H   T =,F6.3,7H  R =, F5.1)
     13  FORMAT (///20X,18H FIRST DERIVATIVE =,F15.5)
     12  FORMAT (///20X,9H   SUM4 =,F15.5)
     14  FORMAT (//20X,9H    SUM3 =,F15.5)
     15  FORMAT (//20X,9H    SUM2 =,F15.5)
     16  FORMAT (///20X,9H   SUM1 =,F15.5)
     18  FORMAT (//20X,9H    SUM5 =,F15.5)
     19  FORMAT (//20X,9H    SUM6 =,F15.5)
     20  FORMAT (/20X,19HSECOND DERIVATIVE =,F15.5)
     54  FORMAT (3X,4H S =,F10.4,22H    FIRST DERIVATIVE =,
            F4.1, 17H STANDARD ERROR =,F10.4)
C
C        ERROR = CONVERGENCE TOLERANCE
         ERROR = 0.00001
C        S     = INITIAL TRIAL VALUE
         S=.5
C      INPUT STATEMENTS
C        NS = # OF SETS OF DATA TO BE ANALYSED
C        NJ = # OF YEARS ( N OF TEXT )
C        D  = DK OF TEXT
C        DA = DJ OF TEXT
C        T & R DEFINED IN TEXT
         READ(5,2) NS
         DO 100 II = 1,NS
         READ(5,2) NJ
         READ(5,1)  (D(K),K = 1,NJ)
         READ(5,1)  (DA(J),J = 1,NJ)
         READ(5,3)  T,R
C      END OF READ STATEMENTS.  CHECK ON CORRECT INPUT
         WRITE(6,5)  (D(K),K = 1,NJ)
         WRITE(6,6)  (DA(J),J =1,NJ)
         WRITE(6,7)  S,T,R
C
C        END OF INPUT CHECK . START OF FIRST DERIVATIVE
             CALCULATION
C
         I COUNT=0
C      I COUNT KEEPS TRACK OF ITERATION . MAX ALLOWED = 20
       53 IF (I COUNT-20) 55,56, 56
```

```
C          FIRST SUM
     55    SUM 1=0.
           DO 8 K=1,NJ
      8    SUM 1=SUM 1+FLOAT (K)*D(K)/S
           WRITE (6,16) SUM1
C        SECOND SUM
           SUM 2=0.
           DO 9 J=1,NJ
           CALL ALPHA (S,T,J,X)
           CALL GAMMA (S,T,J,XA)
      9    SUM 2=SUM2+DA(J)*XA/X
           WRITE (6,15) SUM2
C        THIRD PART
           CALL BETA(NJ,S,T,B)
           CALL DELTA(NJ,S,T,C)
           SUM 3=-R*C/B
           WRITE (6,14) SUM3
C        FIRST DERIVATIVE
           DERIV I=SUM 1+ SUM2+SUM3
           WRITE(6,13) DERIV 1
C
C          START OF SECOND DERIVATIVE CALCULATION
C
C        FIRST SUM
           SUM 4=0.
           DO 11 K=1,NJ
     11    SUM4=SUM4-FLOAT(K)*D(K)/(S*S)
           WRITE (6,12) SUM4
C        SECOND SUM
           SUM5=0.
           DO 17 J=1,NJ
           CALL ALPHA (S,T,J,X)
           CALL EPSIL (S,T,J,P)
           CALL GAMMA (S,T,J,XA)
     17    SUM5=SUM5+DA(J)*(X*P-XA*XA)/((X*X)
           WRITE (6,18) SUM5
C        THIRD TERM
           CALL PHI (NJ,S,T,E)
           SUM6=-R*(B*E-C*C)/(B*B)
           WRITE (6,19) SUM6
C        SECOND DERIVATIVE
           DERV2=SUM4+SUM5+SUM6
           WRITE (6,20) DERV2
C
C          NEWTON-RAPHSON ITERATION
C
           S1=S-DERIV1/DERV2
           ICOUNT=ICOUNT+1
C        CONVERGENCE TEST
           IF(ABS(S-SI)-ERROR)51,51,52
     52    S=S1
           GO TO 53
C        EVALUATION OF STANDARD ERROR
     51    DERV2=1./SQRT(-DERV2)
           WRITE (6,54) S,DERIV1,DERV2
     56    CONTINUE
    100    CONTINUE
           STOP
           END
           SUBROUTINE ALPHA(S,T,J,X)
           Y=0.
           DO 1 M=1,J
           N=M-1
```

```
1   Y=Y + (1.-S)*(S*(1.-T) )**N
    K=J-1
    AM=S**J*(1.-T)**K
    X=Y+AM
    RETURN
    END
    SUBROUTINE GAMMA (S,T,J,XA)
    Y=0.
    DO 1 M=1,J
    N=M-1
    NA=M-2
1   Y=Y+(FLOAT(N)*S**NA-FLOAT(M)*S**N)*(1.-T)**N
    K=J-1
    AM=FLOAT(J)*(S*(1.-T) )**K
    XA=Y+AM
    RETURN
    END
    SUBROUTINE BETA (NJ,S,T,B)
    B=0.
    NJ1=NJ+1
    DO 1 M=1,NJ
    NA=NJ1-M
    DO 1 N=1,NA
    CALL ALPHA (S,T,M,X)
1   B=B+S**N*X
    RETURN
    END
    SUBROUTINE DELTA (NJ,S,T,C)
    C=0.
    NJ1=NJ+1
    DO 1 M=1,NJ
    NA=NJ1-M
    DO 1 N=1,NA
    NB=N-1
    CALL ALPHA (S,T,M,X)
    CALL GAMMA (S,T,M,XA)
1   C=C+FLOAT(N)*S**NB*X+S**N*XA
    RETURN
    END
    SUBROUTINE EPSIL (S,T,J,P)
    JA=J-1
    JB=J-2
    BAD=FLOAT(J)*FLOAT(JA)*S**JB*(1.-T)**JA
    CAD=0.
    DO 1 M = 1,J
    MA=M-1
    MB=M-2
    MC=M-3
1   CAD=CAD+(FLOAT(MA)*FLOAT(MB)*S**MC-FLOAT  (MA)*
           FLOAT(MA)*S**MB)*(1.-T)**MA
    P=BAD+CAD
    RETURN
    END
    SUBROUTINE  PHI(NJ,S,T,E)
    E=0.
    NJ1=NJ+1
    DO 1 M=1,NJ
    NA=NJ1-M
    DO 1 N=1,NA
    NB=N-1
    NC=N-2
    CALL ALPHA (S,T,M,X)
    CALL GAMMA (S,T,M,XA)
```

```
      CALL EPSIL (S,T,M,P)
    1 E=E+FLOAT(N)*FLOAT(NB)*S**NC*X+FLOAT(N)*S**NB*
     XA*2.+S**N*P
      RETURN
      END
C     SAMPLE DATA
 1
 6
1810 5 2 0 0
 8 6 4 511 1
.435 35
```

THE OCCURRENCE OF GREENLAND AND EUROPEAN BIRDS IN NEWFOUNDLAND

By Leslie M. Tuck*

Newfoundland is a large island of 42,734 square miles situated in the North Atlantic Ocean between 46° and 52° north latitude. The Avalon Peninsula, its most southeasterly portion, is in the same latitude as the Bay of Biscay, France. Newfoundland is some 1,650 miles from the coast of Ireland, the nearest land in Europe. It is 850 miles from Cape Farewell, the most southerly point in Greenland.

The physiography of Newfoundland is quite similar to that of the adjacent Maritime Provinces. The coast is indented with bays and inlets and the island itself is a plateau which, sloping in a northwesterly direction, reaches elevations up to 1,500 feet in the almost mountainous highlands along the west coast. A large part of the island's terrain is bleak and the soil is relatively shallow. In general, commercial forests are confined to the river valleys.

Because it is on the eastern side of the North American continent, Newfoundland is influenced by continental air masses and experiences a wide range of summer and winter temperatures. Moreover, as the island is virtually encircled by the cold waters of the Labrador Current, the sea moderates summer and winter temperatures.

Sea-ice from the arctic regions reaches Newfoundland in January (Figure 1) and in a normal year may surround the entire island except the south coast. However, on the east coast, from Cape Freels southward, the ice is generally loosely packed containing extensive leads. Those areas of open water are frequented in winter by seabirds, especially alcids, kittiwakes, and fulmars. The greatest

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