

ESA Supplementary Publication Service

Document No. ESPS 8524

Model Program Listing and Parameter Estimation

Supplement to

"Habitat patch connectivity and population survival"

by

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ECOLOGY Vol. 66 (1985)

APPENDIX 1

Model Program Listing (Fahrig 1983)

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1 - C This program is a simulation of the population dynamics
2 - C of Peromyscus leucopus in 4 woodlots. The woodlots are
3 - C denoted by 'I' or 'J'. Mice can move from one woodlot
4 - C (eg:I) to another (eg:J) only if there is a connection
5 - C (eg:Fencerow) between them. The program calculates the
6 - C population sizes in the four woodlots each week from the
7 - C second week of March to the second week in October for
8 - C 100 consecutive years.
9 - C
10 - C 'Nrun' is a counter which denotes the year of the simulation
11 - C 'Min' is an array containing the minimum population sizes
12 - C in each woodlot in each year. 'Av' is an array containing
13 - C the averages, calculated over 100 years, of the final
14 - C population sizes for the year (in the second week of
15 - C October) in each woodlot. 'Varav' is an array containing
16 - C the variances of the 'av' values and the covariances
17 - C between pairs of them. 'Corr' is an array containing the
18 - C correlation coefficients of pairs of 'av' values.
19 - C 'N' is an array containing the population sizes of each of
20 - C the three age classes - juvenile, subadult, and adult - in
21 - C each woodlot in each week for each year. Age classes is
22 - C denoted by 'K' or 'L'.
23 - C 'O' is an array containing the probabilities of adult
24 - C females 'giving birth' to a juvenile during a particular
25 - C year. The females will have actually given birth three
26 - C weeks previously; it takes three weeks for a baby mouse
27 - C to become a juvenile. Juveniles are counted instead of
28 - C babies because population estimates of babies in the
29 - C field are very difficult to obtain; babies are not
30 - C 'trappable'.
31 - C 'W' is an array containing the probability that juvenile
32 - C mice survive and graduate into the subadult age class.
33 - C 'S' is an array containing the probability that subadult
34 - C mice survive and graduate into the adult age class.
35 - C 'E' is an array containing the proportion of each age class
36 - C which emigrates from a woodlot (I) to another woodlot (J) in
37 - C a week.
38 - C 'D' is an array containing the proportion of each age class
39 - C which dies each week.
40 - C 'Z' is an array containing values which determine the rate
41 - C of immigration into a woodlot (I). The values of Z are the
42 - C proportions of the three age classes in each of the woodlots
43 - C connected to I (eg:J) which immigrate to I in a week.
44 - C 'X' is an array containing the combined effects of death (D)
45 - C emigration (E) and immigration (Z). X is calculated later
46 - C in the program.
47 - C 'NT' is an array containing the total population sizes
48 - C (juveniles + subadults + adults) in four woodlots each
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49 - C      week for 100 years.
50 - C      'T' is a counter denoting the week.
51 - C      'I' and 'J' are counters denoting woodlots.
52 - C      'K' and 'L' are counters denoting age classes.
53 - C
54 -      Integer Nrun
55 -      Real min(4), av(4), varav(4,4), Corr(4,4)
56 -      Do 1 I = 1,4
57 -      Av(I) = 0.0
58 -      Do 1 J = 1,4
59 -      1 varav (J,I) = 0.0
60 -      Do 8010 Nrun = 1,100
61 -      Write(6,16)Nrun
62 - 16      Format (//3X, 'simulation for year', 13/)
63 -      Real N (3,4,33,100), O (3,4,5:32), W (3,4), S (3,4)
64 -      Real E (3,4,3,4), D (3,4,3,4), Z (3,4,3,4), X (3,4,3,4)
65 -      Real NT (4,29,100)
66 -      Integer T,I,J,K,L
67 - C
68 - C      In the following section the values of N for the first five
69 - C      weeks of year 1 are read from a file (7).
70 - C
71 -      Real Rnom
72 -      Do 100 T = 1,5
73 -      Do 100 I = 1,4
74 -      Do 100 K = 1,3
75 - 100      N (K,I,T,Nrun) = 0
76 -      IF (Nrun,Eq.1) then
77 - 200      Read (7,15)T,I,K,Valn
78 -      If (T,NE.0) then
79 -      N (K,I,T,1) = Valn
80 -      Go to 200
81 -      Endif
82 -      Endif
83 - C
84 - C      In the following section values of N for the first five
85 - C      weeks of all years but the first are calculated. These
86 - C      values depend on the final values of N (in the second week
87 - C      of October) in the previous year (Nrun-1).
88 - C
89 -      If (Nrun.Ne.1) then
90 -      Do 203 I = 1,4
91 -      N (3,I,1,Nrun) = NT (I,33,Nrun-1)/4.
92 - 203      continue
93 -      Do 204 T = 2,5
94 -      Do 204 I = 1,4
95 -      N (3,I,T,Nrun) = 0.9355*N (3,I,T-1,Nrun)
96 - 204      Continue
97 -      Do 205 T = 1,5
98 -      Do 205 I = 1,4
99 -      N (3,I,T,Nrun) = Int (N (3,I,T,Nrun) + 0.5)
100 -205      continue
101 -      Endif
102 -15      format (3I5,F10.6)
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103 - C
104 - C      In the following section the Q array is read from a file
          (8).
105 - C      a random number generator is used to obtain approximations
106 - C      of these values; in each year the Q values will be slightl
107 - C      different.
108 - C
109 -      Do 300 T = 5,32
110 -      Do 300 I = 1,4
111 -      Do 300 K = 1,3
112 - 300 Q (K,I,T) = 0.
113 - 400 read (8,25) T,I,K,Valq
114 -      If (T.NE.0) then
115 -      Q (K,I,T) = Valq
116 -      NN = 1
117 -      VQ = 0.0
118 -      Do 450 NN = 1,100
119 -      Call random (Rnom)
120 -      IF (Rnom.Le.Q(K,I,T)) then
121 -      Vq = Vq + 0.01
122 -      Endif
123 - 450 Continue
124 -      Q (K,I,T) = VQ
125 -      Go to 400
126 -      Endif
127 - C
128 - C      In the following section the W array is read from a file (
129 - C      Again, random approximations of these values are calculate
130 - C      each year.
131 - C
132 -      Do 500 I = 1,4
133 -      Do 500 K = 1,3
134 - 500 W (K,I) = 0.
135 - 600 Read (8,35) I,K,Valw
136 -      If (I.NE.0) then
137 -      W (K,I) = Valw
138 -      NN = 1
139 -      VW = 0.0
140 -      Do 650 NN = 1,100
141 -      Cal random (Rnom)
142 -      If (Rnom.Le.(K,I)) then
143 -      Vw = Vw + 0.01
144 -      Endif
145 - 650 continue
146 -      W (K,I) = Vw
147 -      Go to 600
148 -      Endif
149 - 25 format (315,F10.4)
150 - 35 format (215,F10.4)
151 - C
152 - C      In the following section the S array is read from a file (
153 - C      Random approximations are calculated each year.
154 - C
155 -      Do 700 I = 1,4
156 -      Do 700 K = 1,3
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157 - 700 S (K,I) = 0.
158 - 800 Read (8,35)I,K,Vals
159 -     If (I.Ne.0) then
160 -         S (K,I) = Vals
161 -         NN = 1
162 -         Vs = 0.0
163 -         Do 850 NN = 1,100
164 -             Call random (Rnom)
165 -             If (Rnom.Le.S(K,I)) then
166 -                 Vs = Vs + 0.01
167 -             Endif
168 - 850 continue
169 -         S(K,I) = Vs
170 -         Go to 800
171 -     Endif
172 - 55 format (4I5,F10.4)
173 - C
174 - C     In the following section the D array is read from a file (8)
175 - C     Random approximations are calculated for each year.
176 - C
177 -         Do 900 I = 1,4
178 -         Do 900 K = 1,3
179 -         Do 900 J = 1,4
180 -         Do 900 L = 1,3
181 - 900 D(L,J,K,I) = 0.
182 - 1000 read (8,55)I,K,J,L,Vald
183 -     If (I.Ne.0) then
184 -         D(L,J,K,I) = Vald
185 -         NN = 1
186 -         Vd = 0.0
187 -         Do 1050 NN = 1,100
188 -             Call random (Rnom)
189 -             If (Rnom.Le.D(L,J,K,I)) then
190 -                 Vd = Vd + 0.01
191 -             Endif
192 - 1050 continue
193 -         D(L,J,K,I) = Vd
194 -         Go to 1000
195 -     Endif
196 - C
197 - C     In the following section the E array is read from a file (8)
198 - C     Random approximations are taken each year.
199 - C
200 -         Do 1100 I = 1,4
201 -         Do 1100 K = 1,3
202 -         Do 1100 J = 1,4
203 -         Do 1100 L = 1,3
204 - 1100 E(L,J,K,I) = 0.
205 - 1200 Read (8,55)I,K,J,L, Vale
206 -     If (I.Ne.0) then
207 -         E(L,J,K,I) = Vale
208 -         NN = 1
209 -         Ve = 0.0
210 -         Do 1250 NN = 1,100
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211 -      Call random (Rnom)
212 -      If (Rnom.Le.E(L,J,K,I)) then
213 -      Ve = Ve + 0.01
214 -      Endif
215 - 1250 continue
216 -      E(L,J,K,I) = Ve
217 -      Go to 1200
218 -      Endif
219 - C
220 - C      In the following section the Z array is read from a file (5)
221 - C      Random approximations are taken each year.
222 - C
223 -      Do 1300 I = 1,4
224 -      Do 1300 K = 1,3
225 -      Do 1300 J = 1,4
226 -      Do 1300 L = 1,3
227 - 1300 Z(L,J,K,I) = 0.
228 - 1400 Read (5,55)I,K,J,L,Valz
229 -      If (I.Ne.0) then
230 -      Z(L,J,K,I) = Valz
231 -      NN = 1
232 -      Vz = 0.0
233 -      Do 1450 NN = 1,100
234 -      Call random (Rnom)
235 -      If (Rnom.Le.Z(L,J,K,I)) then
236 -      Vz = Vz + 0.01
237 -      Endif
238 - 1450 continue
239 -      Z(L,J,K,I) = Vz
240 -      Go to 1400
241 -      Endif
242 -      Rewind (5)
243 -      Rewind (8)
244 - C      Calculation of the X array.
245 -      Do 5000 I = 1,4
246 -      Do 5000 K = 1,3
247 -      Do 5000 J = 1,4
248 -      Do 5000 L = 1,3
249 -      X(L,J,K,I) = -D(L,J,K,I) -E(L,J,K,I) +Z(L,J,K,I)
250 - 5000 continue
251 -      Do 8000 T = 5,32
252 - C
253 - C      In the following section the X array is multiplied by the
254 - C      values of N in week T to give new values of N. These new
255 - C      values give the age class population sizes after the effects
256 - C      of death, immigration, and emigration for a week. Changes
257 - C      in N due to births and 'graduations' into the next age class
258 - C      will be accounted for later.
259 - C
260 -      Do 7000 I = 1,4
261 -      Do 7000 K = 1,3
262 -      N(K,I,T + Nrun) = 0.0
263 -      Do 6000 J = 1,4
264 -      Do 6000 L = 1,3

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265 -      N(K,I,T+1,Nrun)=(N(K,I,T+1,Nrun))+(X(L,J,K,I)*N(L,J,T,Nrun))
266 - 6000 continue
267 - C
268 - C      Changes in N due to births and 'graduations' into next age
           class
269 - C
270 - C      In the following equation, additions to the juvenile age
271 - C      classes in the four woodlots from week T to week T + 1 are
272 - C      calculated. The change in the number of juveniles depends
273 - C      on the number of adult females present three weeks
274 - C      previously (it takes three weeks for a baby to become a
275 - C      juvenile), the value of Q for week T, and the number of
276 - C      juveniles that graduate to the subadult class during the
           week.
277 - C
278 -      If (K,Eq.1) then
279 -      N(K,I,T+1,Nrun)=N(K,I,T+1,Nrun)+((0.5)*Q(K,I,T)*
           N(3,I,T-3,Nrun))+N
280 -      1(K,I,T,Nrun)-(W(2,I)*N(1,I,T-3,Nrun))
281 -      Endif
282 - C
283 - C      In the following equation, additions to the subadult age
284 - C      classes in the four woodlots from week T to week T + 1 are
285 - C      calculated. The change in the number of subadults depends
286 - C      on the number of juveniles present three weeks previously
287 - C      (it takes three weeks for a juvenile to become a subadult),
288 - C      the value of W for week T, and the number of subadults that
289 - C      graduate to the adult class during the week.
290 - C
291 -      If (K,Eq.2) then
292 -      N(K,I,T+1,Nrun)=N(K,I,T+1,Nrun)+(W(K,I)*
           N(1,I,T-3,Nrun))+N(K,I,T,N
293 -      1run)-(S(3,I)*N(2,I,T-2,Nrun))
294 -      Endif
295 - C
296 - C      In the following equation, additions to the adult age
297 - C      classes in the four woodlots from week T to week T + 1 are
298 - C      calculated. The change in the number of adults depends
299 - C      on the number of subadults present two weeks previously
300 - C      (it takes two weeks for a subadult to become an adult) and
301 - C      the value of S for week T.
302 - C
303 -      If (K,Eq.3) then
304 -      N(K,I,T+1,Nrun)=N(K,I,T+1,Nrun)+(S(K,I)*
           N(2,I,T-2,Nrun))+N(K,I,T,N
305 -      1run)
306 -      Endif
307 - C
308 - C      Now the values calculated for N in week T+1 are converted to
309 - C      whole numbers.
310 - C
311 -      N(K,I,T+1,Nrun)=Int(N(K,I,T+1,Nrun)+0.5)
312 -      If (N(K,I,T+1,Nrun).Lt.0.)then
313 -      N(K,I,T+1,Nrun)=0

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314 -      Endif
315 - 7000 continue
316 - 8000 continue
317 - C
318 - C      Calculation of Nt for year Nrun
319 - C
320 -      Do 13 T = 5,33
321 -      Do 13 I = 1,4
322 -      Nt(I,T,Nrun) = 0.0
323 -      Do 12 K = 1,3
324 -      NT(I,T,Nrun)=Nt(I,T,Nrun)+N(K,I,T,Nrun)
325 - 12 continue
326 - 13 continue
327 -      If (nrun.Eq.1.or.Nrun.Eq.2.or.Nrun.Eq.5.or.Nrun.Eq.10. or.
      Nrun.Eq.20
328 -      1.or.Nrun.Eq.30.or.Nrun.Eq.40.orNrun.Eq.50.or.Nrun.Eq.70.
329 -      Nrun.E2Q.100.) then
330 -      Write (6,45)((Nt(I,T,Nrun),I = 1,4),T = 5,33)
331 - 45 format (3X,'number of mice in 4 woodlots during a summer'
332 -      ///7X,'wee 1K',8X,'woodlot 1',3X,'woodlot 2',3X,'woodlot 4'
333 -      //3X2,'Mar-week 2',4F12.0/3X,'Mar-Week 3',4F12.0/3X,
334 -      'Mar-Week 4',4F12.03/3X,'Apr-Week 1',4F12.0/3X,'Apr-Week 2',
335 -      4F12.0/3X,'Apr-Week 3',4F142.0/3X,'Apr-Week
336 -      4',4F12.0/3X,'May-Week 1',4F12.0/3X,'May-week 2',54F12.0/3X,
337 -      'May-week 3',4F12.0/3X,'May-Week 4',4F12.0/3X,'
338 -      June-week 61',4F12.0/3X,'Jun-week 2',4F12.0/3X,'Jun-wek 3',
339 -      4F12.0/3X,'Jun-Week 4',4F12.0/3X,'Jul-week 1',4F12.0/3X,
340 -      Jul-week 2',4F12.0/3X,'Jul8-week 3',4F12.0/3X,'Jul-week 4',
341 -      4F12.0/3X,'Aug-week 1',4F12.0/3X,'9Aug-week 2',4F12.0/3X,
342 -      'Aug-week 3',4F12.0/3X,'Aug-week 4',4F12.0/31X,'Sep-Week 1',
343 -      4F12.0/3X,'Sep-week 2',4F12.0/3X,'Sep-week 3',4f12,20/3X,
      'Sep-week 4'4F12.0/3X,'Oct-Week 1',4F12.0/3X,'Oct-week 2',
      4F312.0)
344 -      Endif
345 - C
346 - C      Calculation of min for year Nrun
347 - C
348 -      Do 102 I = 1,4
349 -      Min(I) = 1.E10
350 - 102 continue
351 -      Do 103 T = 5,33
352 -      Do 103 I = 1,4
353 -      If (Nt(I,T,Nrun).Lt.min(I)) then
354 -      Min(I) = NT (I,T,Nrun)
355 -      Endif
356 - 103 continue
357 -      Write (6,17)min
358 - 17 format(/1X,'minimum values for the year'//1X,
      'woodlot',9X,'1',9X,'
359 -      12',9X,'3',9X,'4'/F19.0,3F10.0)
360 - C
361 - C      Calculation of av and varav.
362 - C
363 -      Do 104 I = 1,4

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364 -      Av(I) = Av (I) + Nt (I,33,Nrun)
365 -      Do 104 J = 1,4
366 -      Varav(J,I)=varav(J,I)+NT(I,33,Nrun)*NT(J,33,Nrun)
367 - 104 continue
368 - 8010 continue
369 -      Do 8011 I=1,4
370 -      Do 8011 J=1,4
371 -      Varav(J,I)=(varav(J,I)-(Av(j))/100.)/99.
372 - 8011 continue
373 -      Do 8012 I = 1,4
374 -      Av(I) = Av(I)/50
375 - 8012 continue
376 -      Write (6,18)av,varav
377 - 18 Format(////1X, Averages of Yearly Finals
      (AYF)'/1X,'Woodlot',10X,
378 -      1'1',10X,'2',10X,'3',10X,'4'//F24,5,3F11.5////1X,'Variances
      and Cov
379 -      2Ariances of AYF'/1X,'Woodlot',10X,'1',10X,'2',10X,'3',
      10X,'4'//4X
380 -      3,'1',2X,E17,4,2X,E9,4,2C,E9,4,2X,E9.4//4X,'2',2X,E17,4,2X,
381 -      4E,4,2X,E9.4,2X,E9.4//4X,'3',2X,E9,4,2X,E9,4,2X,E
382 -      59.4//4X,'4',2X,E17.4,2X,E9.4,2X,E9.4)
383 - C
384 - C      Calculation of corr.
385 - C
386 -      Do 8014 I=2,4
387 -      11=I-1
388 -      Do 8013 J=1, 11
389 -      Corr(J,I)=varav(J,I)/sort(varav(I,I)*varav(J,J))
390 -      Corr(I,J)=corr(J,I)
391 - 8013 Continue
392 -      Corr(I,I)=1.0
393 - 8014 Continue
394 -      Corr(1,1)=1.0
395 -      Write(6,19)Corr
396 - 19 Format(////1X,'Correlations Between Pairs of
      AYF'/1X,'Woodlot',10
397 -      1X,'1'10X,'2',10X,'3',10X,'3','4'//4X,'1',2X,F17,5,2X,F9,5,2
      X,F9,5,2X,
398 -      2F(.5//4X,'2',2X,F17.5,2X,F9.5,2X,F9.5//4X,'3',2X,F17.5,2X,
399 -      3F(.5,2X,F9.5,2X,F9.5//4X,'4'2X,F17.5,2X,F9.5,2X,F9.5,2X.F9.
      5)
400 -      Stop
401 -      End

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APPENDIX 2

Parameter Estimation

P. leucopus populations consist of three 'trappable' stage classes, namely, juveniles, subadults and adults. Infant mice are not counted until they become juveniles, because they cannot be trapped. It is, therefore, necessary to include in the model the 'modified Leslie matrices' referred to in the model description.

1) Birth Rates (b-values)

The b-values (Table A1) determine the number of mice which are born and which graduate from one stage class to the next during one time interval. In this model application we have chosen one week as the time interval. An individual element, $b_{i,k}$, is actually the proportion of individuals in a stage class, k, in woodlot i which become part of the stage class k+1 in one week. There are three such stage class changes to consider; adults give 'birth' to juveniles, juveniles become subadults, and subadults become adults.

Since it takes about three weeks for a newborn P. leucopus to become a juvenile (Sheppe 1965, Millar et al. 1979, Vestal et al. 1980), the number of juveniles added to a woodlot is approximately equal to the number born three weeks previously, minus the infant mortality over those three weeks. By combining the results of Harland et al. (1979) and Hansen and Batzli (1978), the following rates for survival from nestling to juvenile have been obtained:

mid-March	- mid-June	70%
mid-June	- mid-August	40%
mid-August	- mid-October	20%

To determine the probability of a female giving birth during a particular week, the data of Hansen and Batzli (1978) and of Sheppe (1965) have been used. Hansen and Batzli give proportions of females pregnant at different times in the breeding period, but since these values were obtained in Illinois, where the breeding period is longer than in southeastern Ontario, and since northern populations exhibit a more distinct bimodal breeding cycle than southern populations (Sheppe 1965), their data have been modified to conform with Sheppes' (1965) data of the proportions of juveniles in the population at different times during the summer. Millar et al. (1979) found that the average P. leucopus litter size was 4.9.

The weekly $b_{j,t}$ (t = week) values for juveniles over the summer are then calculated using the equation

$$b_{j,t} = \frac{\text{proportion of females pregnant at time } t-3}{3} \times 4.9 \times \text{nestling survival.}$$

The resulting $b_{j,t}$ values are given in Table A1.

Since it takes about three weeks for a juvenile to become a subadult (Snyder 1956, Madison 1977), the addition of subadults through ageing of juveniles depends on the number of juveniles present three weeks previously and the probability of survival from the juvenile to the subadult age classes, as calculated from the d -values. The subadult b_j value is 0.717.

It takes about two weeks for a subadult to become an adult (Harland et al. 1979. Millar et al. 1979). The addition of adults through ageing of subadults, therefore, depends on the number present two weeks previously and the probability of survival from the subadult

Table A1. Probability that a female present three weeks earlier gives birth to a juvenile in week "t" between the third week in March to the second week in October.

<u>t</u>	<u>probability</u>
1	0.03
2	0.03
3	0.03
4	0.03
5	0.03
6	0.05
7	0.15
8	0.25
9	0.35
10	0.45
11	0.45
12	0.45
13	0.45
14	0.45
15	0.45
16	0.45
17	0.35
18	0.35
19	0.20
20	0.20
21	0.10
22	0.10
23	0.10
24	0.25
25	0.25
26	0.35
27	0.45
28	0.25

to the adult age classes, as calculated from the d-values. The adult b_i value is 0.801.

2) Death Rates (d-values)

The probability of P. leucopus dying during a particular week appears to be independent of the age class of the mouse and also of the population density (Miller and Getz 1977b). Miller and Getz found that the average death rate was 55.3%/60 days, which is equivalent to a weekly death rate of 8.9%. Since this "death" rate probably includes some emigration, it is likely an overestimate. Snyder (1956) found a weekly death rate during the winter in Michigan of 3-8% per week. Therefore, we have estimated the mortality rate at 6% per week. This mortality rate was also used to calculate the probability of survival of juveniles to subadulthood and subadults to adulthood for the calculations of b-values for subadults and adults.

3) Dispersal Rates (p-values)

The dispersal rates are the most difficult parameters to estimate from the literature, primarily because most workers include immigration and additions due to reproduction in one value, 'recruitment'; losses due to death and emigration are also lumped. Therefore, it is difficult to distinguish between births and immigration and between deaths and emigration, creating a lack of information about P. leucopus dispersal. This is complicated by contradictions in the available data. Several questions concerning dispersal by P. leucopus had to be answered by weighing the evidence as reasonably as possible. They are as follows:

i) Is dispersal age-specific?

Madison (1977) found that the subadult dispersal rate measured as the proportion of "transient" (i.e. caught only once) individuals, was much higher than either the juvenile or adult rates. It is possible, however, that a large number of resident individuals will be caught only once, either through trap shyness, or because they entered the trappable population near the end of the trapping period. Since these would be included in the 'transient' estimate, Madison's transience numbers can be assumed to overestimate the actual dispersal rates.

ii) Is dispersal sex-specific?

Harland et al. (1979) found that male P. leucopus migrate more than females, but Taylor (1978) and Nadeau et al. (1981) found no significant differences between male and female dispersal tendencies. Coupled with the fact that Harland et al. (1979) found that the sex ratios in the populations they studied were consistently 1:1, this suggests that sexual differences in dispersal rates are not important enough to be included as a factor in the model.

iii) Does dispersal depend on the time of year?

We found no clear evidence that dispersal rates change during the breeding season. This may be partly due to the fact that most studies do not contain a sufficient sample size of population estimates to distinguish this from the other factors affecting dispersal. Therefore, we have not included time as a factor influencing dispersal rates, realizing that this may be an erroneous decision.

iv) Is dispersal density-dependent, density-independent, or both? Hansen and Batzli (1978) and Nadeau et al. (1981) found no significant correlation between the rate of dispersal and population density. Middleton and Merriam (1981) suggested that in northern areas (i.e. near Ottawa), because the winter death rate is very high and the breeding season is short, P. leucopus populations may not actually "fill" the available habitat. This could mean that the populations do not reach densities that are high enough to affect the rate of dispersal. We have assumed, therefore, that in our study area, the population density does not affect dispersal rate. Density-dependent dispersal will not be included in this application of the model.

v) Do mice disperse from a woodlot regardless of how unfavourable the surrounding environment is?

This question has implications for the relative population sizes and growth rates in isolated and nonisolated woodlots. If mice disperse from isolated woodlots and are not replaced by immigrants, the population sizes and growth rates in isolated woodlots may be lower than those in nonisolated ones.

There is some evidence that mice will disperse into inhospitable habitats such as fields (Stickel and Warbach 1960, Tardiff and Gray 1978). Gyug (1978) found that the autumn survival of P. leucopus populations in small isolated woodlots was very low because emigration was not balanced by immigration.

Although emigration occurs from isolated woodlots, P. leucopus is almost never trapped in the surrounding nonforested areas (M'Closky and Lajoie 1975, Hansen and Warnock 1978, Wegner and

Merriam 1979). This implies that the rate of dispersal from isolated woodlots is not as high as that from nonisolated ones.

- vi) Does the type of fencerow (i.e. length, width, type of vegetation) affect either the tendency for mice to use it, or the survival rate of mice that do?

Ogilvie and Furman (1959) are the only workers who have studied the effect of fencerow type on mice. They assessed the relative preferences of P. maniculatus, a species closely related to P. leucopus, for three types of fencerow: weedy, shrubby, and bare. They found that the bare fencerow was slightly less well used than the other two types. The effects of length and width of fencerow on mouse movement are still unknown.

It is clear from this discussion of P. leucopus dispersal that there will be a large amount of uncertainty associated with any estimates of dispersal rates. Madison (1977) gave the following proportions of transient individuals in his populations: juveniles - 0.154, sub-adults - 0.571, adults - 0.111. As already stated, these are probably overestimates of actual dispersal rates, even though the relative proportions in each age group may be accurate. Therefore, we have halved the values, producing dispersal rates of

juveniles	0.077
subadults	0.286
adults	0.0555

from the nonisolated woodlots. Although mice disperse from isolated woodlots as discussed above, they may do so with a lower frequency than those in nonisolated woodlots. This is supported by the extremely low capture rate of mice in open areas mentioned earlier.

Therefore, we have again halved the above values, producing dispersal rates of: juveniles 0.0385, subadults 0.143, and adults 0.0278 from the isolated woodlots.

Simulations of the populations in one of the two isolated woodlots and the group of four interconnected woodlots were made. The simulation assumed that the population dynamics over the summer is a deterministic process; the parameter values had no variances associated with them. Although the parameters are actually random variables, by eliminating variance in the simulation, we obtained results which, presumably, are equal to the average of many simulations using random variables instead of constants (Chapman and Schaufele 1970).