Technical Report No. 3

A PRELIMINARY BIRD POPULATION DYNAMICS AND BIOMASS MODEL

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ABSTRACT

In this paper a preliminary model for the population and biomass change over time is given for bird populations. The interaction between biologist and modeller in the development of the model and its parameters is emphasized. The model consists of two constant coefficient differential equations. The output of the model, applied to the lark bunting, is compared with results of field experiments. Discussions of further extensions of the model as well as present difficulties are also included.

Purpose

This preliminary modelling effort was undertaken to promote interaction between the modeller and the biologist and to demonstrate that such an effort can lead to both the inclusion of biological "mechanism" in the model, based on information from the biologist, and to the defining of future research to be done by the biologist. The present effort can be viewed through the flow-chart in Figure 1.

The flow chart shows that the modelling effort may move through "feedback loops". Thus, the modeller may have to formulate or reformulate the model several times and the biologist may have to collect data for input to the model several times in order to arrive at a model which is based on reality and which also may be verified by comparison with output predictions from the model.

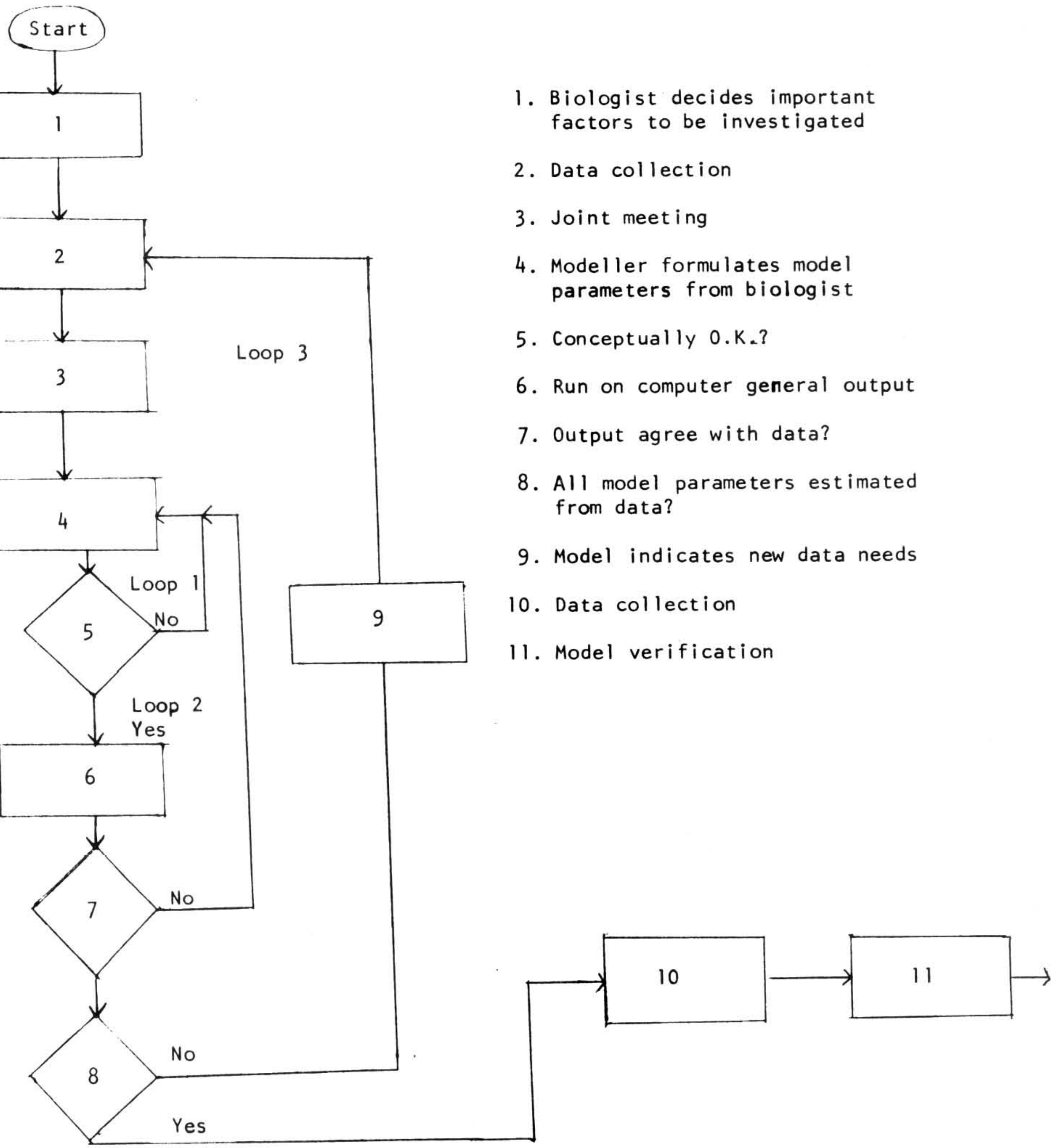
The model developed in this report was specifically based on bird data collected by Ryder and Baldwin. The model is a submodel of the consumer trophic level and is a component or community model (i.e., the bird community). The interaction shown in the flow chart in Figure 1 was conducted using lark bunting data. For this species we are presently at stage 8, having gone through loop 1 four times, loop 2 three times, and heading into our second time in loop 3.

The Model

As a "first pass" approach to the modelling of the change in bird populations and biomass let us consider a deterministic, dynamic differential equation for bird population change (Table 1). Let $P_i(t)$ be the total population of species i per hectare of birds at time t. The rate of change

Figure 1

Flow Chart of Interaction Between Biologist and Modeller for Model Building



1. Biologist decides important factors to be investigated
2. Data collection
3. Joint meeting
4. Modeller formulates model parameters from biologist
5. Conceptually O.K.?
6. Run on computer general output
7. Output agree with data?
8. All model parameters estimated from data?
9. Model indicates new data needs
10. Data collection
11. Model verification

of the population of species i is denoted by $\overset{\circ}{P}_i(t)$. We may express $\overset{\circ}{P}_i(t)$ as being equal to the immigration rate minus the emigration rate plus the birth rate minus the mortality rate; thus

$$\overset{\circ}{P}_i(t) = I_i(t) - E_i(t) + B_i(t) - M_i(t). \tag{1}$$

Here $I_i(t)$ is the immigration rate at time t (birds/unit time) for species i, $E_i(t)$ is the emigration rate, $B_i(t)$ is the birth rate and $M_i(t)$ the mortality rate.

In this preliminary model there is no distinction between adults, juveniles, nestlings, etc. This, of course, will result in large population increases during hatching periods. The birth rate, $B_i(t)$, was, in general, expressed as a function of clutch size, egg mortality, population size, and ratio of breeding females to the entire population. The relationship is that the birth rate at time t is equal to the egg-laying rate at time $t - h_i$, where h_i is the time eggs take to hatch, times the percentage that survive the incubation period times the percentage of breeding females in the population (because only these lay eggs) times the adult population of species i. This may be written by:

$$B_i(t) = L_i(t - h_i)\ S_i(t,h)\ R_i(t - h)\ P_i(t - h)$$

Here $L_i(t)$ is the average egg laying rate (eggs/unit time) for an individual of species i at time t, $S_i(t,h)$ is the percentage of the laid eggs which actually survive and hatch at time t (laid at $t - h_i$), h_i is the hatching period for species i, and $R_i(t)$ is the percentage of the population which are breeding females.

The weight of an individual of species i at time t is denoted by $w_i(t)$ and its rate of change by $\overset{\circ}{w}_i(t)$. $\overset{\circ}{w}_i(t)$ is equal to the rate of food intake times the assimilation efficiency minus the respiration rate. This is expressed by the following differential equation:

$$\mathring{w}_i(t) = e_i(t)\ F_i(t) - RE_i(t). \tag{2}$$

Here $F_i(t)$ is the food intake rate (grams/unit time) for an individual of species i, $e_i(t)$ is the assimilation efficiency for an individual and $RE_i(t)$ is the rate energy (weight) lost through respiration.

Differential equations (1) and (2) may be solved if the various rates on the right hand sides of the equation are known. The total biomass at time t for species i, $W_i(t)$, may be found by multiplying the population at time t by the average weight per individual. This is given by:

$$W_i(t) = P_i(t)\ w_i(t). \tag{3}$$

Parameters For The Model

Solutions for equations (1), (2), and (3) were attempted for the lark bunting, the predominate summer bird species on the Pawnee Site. Data were available for this species on population density estimates. From six 20-acre bi-weekly plot counts, for a total of 120 acres sampled (Ryder), weekly immigration and emigration rates were obtained. Food consumption estimates were available from stomach sample and herbage biomass data (Baldwin). Clutch size and pre-natal mortality data were available for lark buntings from nest observation (Baldwin). The other unknown rates and coefficients were either estimated from the literature, from observation, or from both.

For the lark bunting the immigration rate is taken to be 60 birds/100 hectares/week from May 1 to 15, while the emigration rate is 50 birds/100 hectares/week starting at August 15. Immigration and emigration were zero at other times. The average clutch size was 3.6 eggs/clutch. The breeding females were taken to compromise 45% of the total adult population, based on an estimate of the number of stray males (non-territorially based) observed during breeding season bird counts. On the average, 40% of the laid eggs actually hatched (S = .4). The birds were assumed to lay eggs over a 3-week period beginning June 1 and the lark bunting hatching period h (time as an egg) was taken as a constant 9 days. The egg-laying rate was therefore 1.2 eggs per breeding female per week. About one third of the birds (perhaps the early breeders) were observed to have a second breeding period with hatching beginning July 10 and ending by the first week in August.

It is difficult to estimate mortality of lark buntings accurately since dead birds are not easily observed. Mortality was estimated as 1.5% of the population per week before breeding and 2.5% of the population after breeding to include the increased mortality of the juveniles.

The assimilation efficiency, e(t), was assumed constant at 0.7, based on experiments in the literature conducted upon species[1] similar to the lark bunting. The birds were assumed to each eat 41 grams of food a week. This was based on literature values[2] and preliminary estimates from bird stomach sample data and from herbage samples collected on the Pawnee Site of items found in the bird's stomachs. The difficulty with such estimates is the unknown time duration between when the bird has last eaten and when it is collected. Another difficulty is that the food composition in these bird's (and many other species as well) stomachs consists of both plants and animals (i.e., they are omnivores). The food composition will quite obviously affect both the amount consumed as well as the assimilation efficiency e.

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1 West, G. C., Seasonal Variation in the Energy Balance of the Tree Sparrow in Relation to Migration, Auk, Vol. 77, No. 3, July 1960

2 Kenedeigh, Relation of Existence Energy Requirements to Size of Bird, American Zoologist, Vol. 3, No. 4, Nov., 1963

The accuracy of the weight-change equation (2) is further reduced by the fact that no estimates are available on respiration of these birds. Thus the respiration rates used in this preliminary equation are only rough estimates from the literature and observation. They were based on the fact that the bird's weights remain fairly constant until the breeding season, when they lose weight, probably because of increased respiration due to increased breeding activity. The pre-breeding respiration rate RE(t) was taken to be 28 grams/bird/week. During the first breeding period the respiration rate increased to 29.5 grams/bird/week and during the second breeding period it was 29 grams/bird/week. After the breeding period the respiration rate again returned to 28 grams/bird/week.

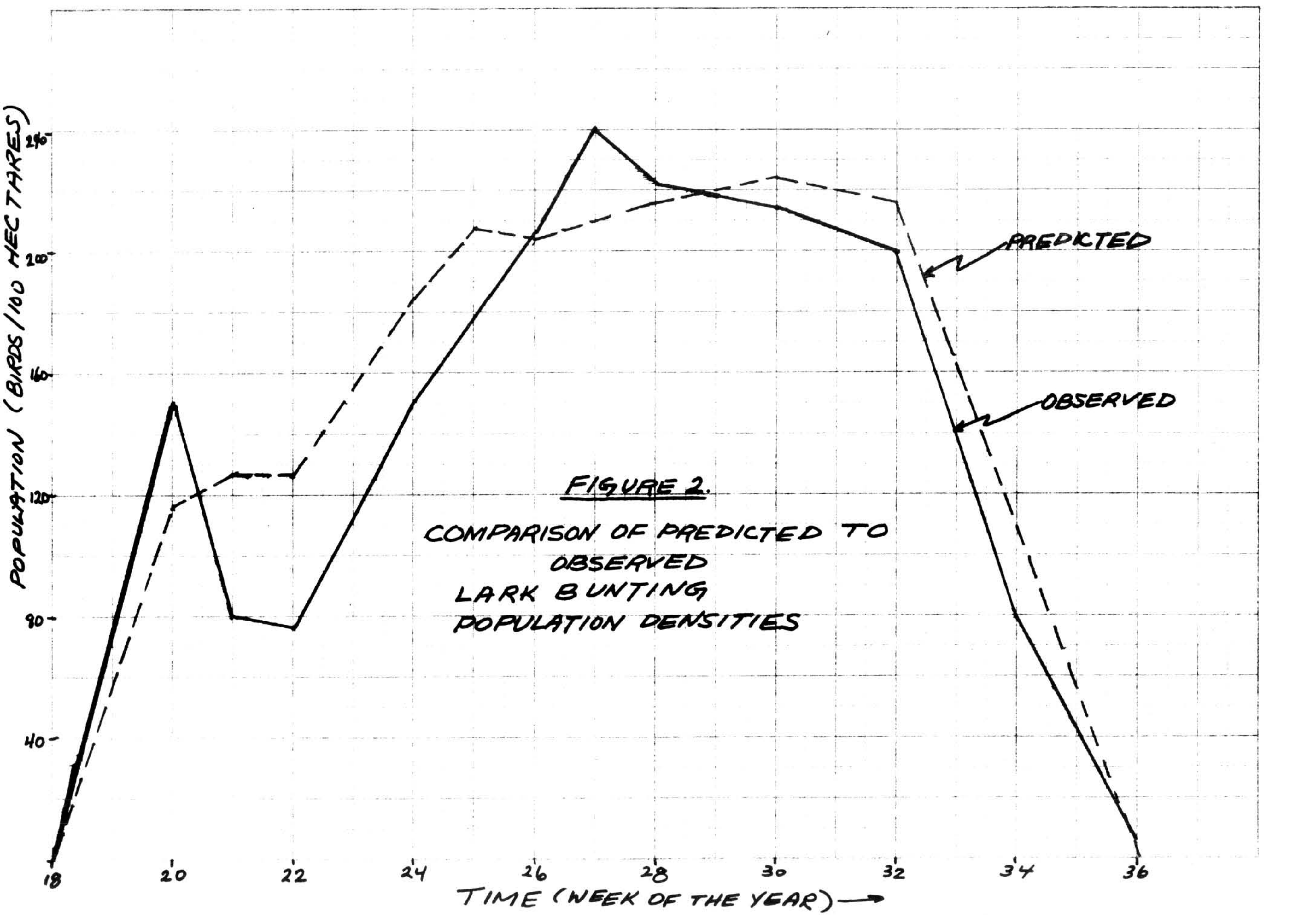
The equations were coded in FORTRAN and the Runge-Kutta method was used to integrate them. A complete listing is given in the Appendix.

Predictions From The Model

The lark bunting population change generated by the above model is compared with the 1969 20-acre plot count data (Ryder) in Figure 2. The agreement is quite close. This is partially because the bird count was used used in part in estimating the immigration and emigration rates. The weight change per bird predicted by the model are compared with the average weights of birds collected in 1969 on the Pawnee Site in Figure 3 (Baldwin). Here again the agreement is good although the criticism that the model is really only an advanced excercise in curve fitting is partially valid since adequate respiration data were not available.

Discussion

This is only a preliminary model for bird population and weight change. The fact that it does have fairly good curve-fitting ability shows that


PREDICTED
OBSERVED
FIGURE 2.
COMPARISON OF PREDICTED TO
OBSERVED
LARK BUNTING
POPULATION DENSITIES
POPULATION (BIRDS/100 HECTARES)
240
200
160
120
80
40
18
20
22
24
26
28
30
32
34
36
TIME (WEEK OF THE YEAR)

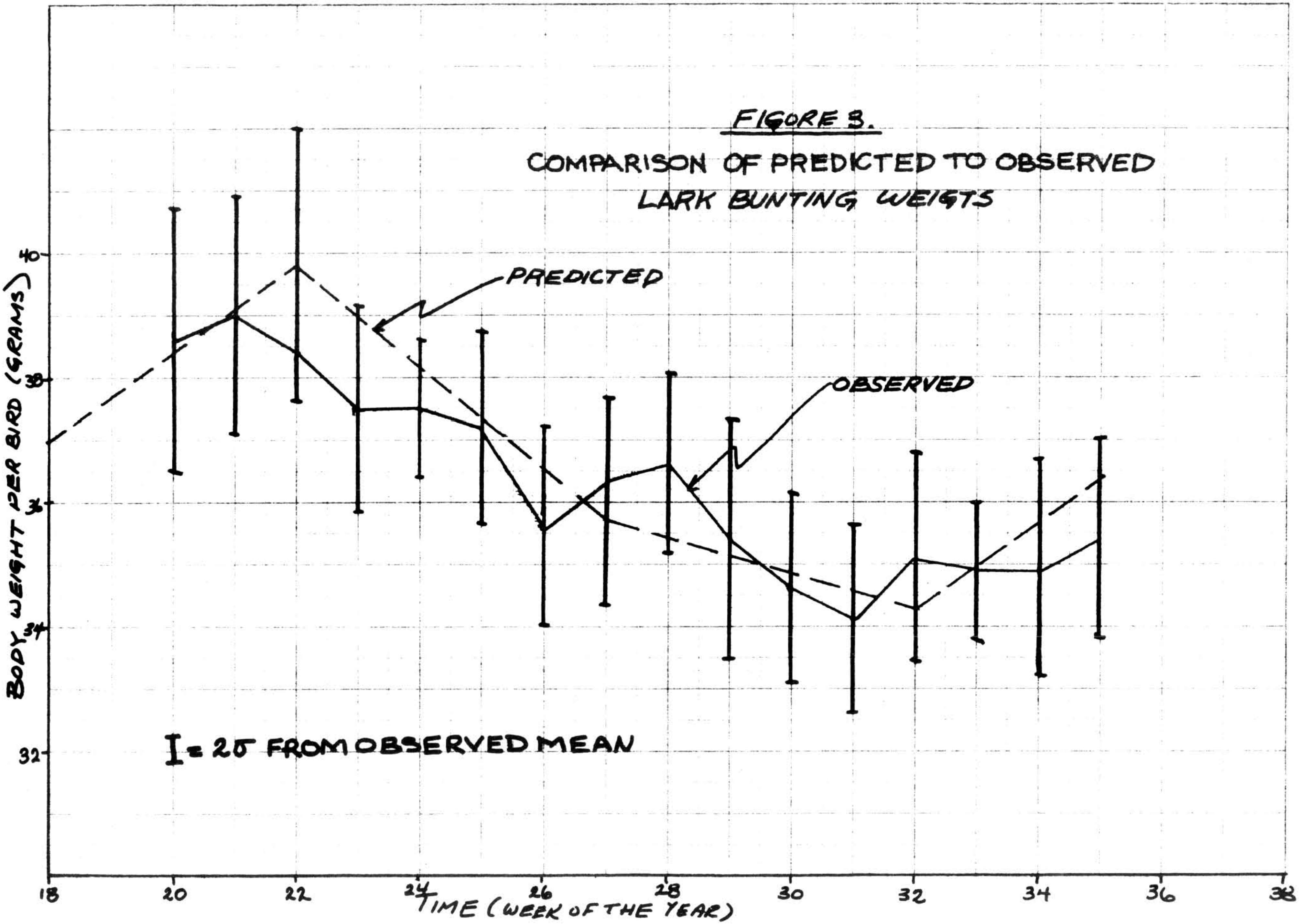


FIGURE 3.

COMPARISON OF PREDICTED TO OBSERVED LARK BUNTING WEIGTS a model, involving some biological reality, can be developed which will coincide with field results. It also illustrates the value of collaboration between the modellers and biologists. The need is evident for a coordinated effort between these two groups.

The present model is understandably based on averages and estimates. It could be refined in a great many ways, e.g., first by including juvenile age classes in the model (nestlings, parentally-fed non-nestlings, and the various molt stages) with corresponding differences in weight change and mortality rate, for the different juvenile periods. Extension of the model presented here has featured the inclusion of a single juvenile age class. The model then must be concerned about recruitment of the juveniles into the adult age class and the increased weight change of young juveniles. Inadequate data exists at present on juvenile weight change to consider this anything more than a "ball park" model.

The output of the model at present leaves us at stage 8 in Figure 1 -- waiting for another data collection for further refinement of the model. The formulation of the model indicates the need for further data in the following areas:

(i) data on bird respiration rates, probably done on caged birds

(ii) further data on assimilation efficiency, also probably on caged birds

(iii) bird population counts for verification of the present model for $P(t)$

(iv) some bird weights for verification of the model for $w(t)$

(v) data on juvenile weight change, perhaps through caged birds

(vi) juvenile population and mortality estimates through increased field observation during breeding season

It is recognized that the bird model should fit into the consumer portion of a whole grassland model and should interface with other consumer models (e.g., insects) and with other community models as well (e.g., herbage dynamics of families of plants, litter model, etc.). As food web information about birds becomes increasingly available, interfacing the various species, community, and trophic level models should reveal data collection needs other than those presented above.

The time resolution of the model at present is limited to 1 week due to the data being collected only weekly. Greater resolution in the model could not be verified by a new data set unless the data was taken more often than once a week.

No model is going to go far enough into biological mechanism to be able to predict the effects of changes not previously observed or foreseen. The chief value of the model lies, therefore, in its ability to grant insight into the processes which contribute to observed phenomena. This is more evident when the bird model is seen as a segment of the consumer portion of a whole grassland model. The major effort at present must mainly involve converting some of the cruder estimates into biologically and experimentally sound estimates to escape the syndrome of the "curve fitter".

Table 1. Summary of bird model with inputs estimated for the lark buntings.

Differential Equations

1. $\mathring{P}(t) = I(t) - E(t) + B(t) - M(t)$

where $B(t) = L(t - h)\, S(t,h)\, P(t - h)\, R(t - h)$

2. $\mathring{w}(t) = e(t)\, F(t) - RE(t)$

Output Variables

Notation	Name	Units	Source
$P(t)$	population density at time t	birds/100 hectares	solve equation 1
$\mathring{P}(t)$	rate of change of population at time t	birds/100 hectares-week	equation 1
$w(t)$	average weight per bird at time t	grams/bird	solve equation 2
$\mathring{w}(t)$	rate of change of bird weight at time t	grams/bird-week	equation 2
$W(t)$	total bird biomass density	grams/100 hectares	$W(t) = w(t)\, P(t)$

Input Variables

Variable Notation	Variable Name	Value (for Lark Bunting)	Units	Source of Value
$I(t)$	immigration rate at time t	$\begin{cases} 60 & \text{May 1-15} \\ 0 & \text{otherwise} \end{cases}$	birds/100 hectares/week	observation (Ryder)
$E(t)$	emigration rate at time t	$\begin{cases} 50 & \text{after Aug. 15} \\ 0 & \text{otherwise} \end{cases}$	birds/100 hectares/week	observation (Ryder)
$B(t)$	birth rate at time t	obtained from other variables	birds/100 hectares/week	

$M(t)$	mortality rate at time t	.015 $P(t)$ before June 10 .025 + $P(t)$ after June 10	birds/100 hectares/week	observation estimates (Ryder, Baldwin)
$e(t)$	assimilation efficiency at time t	.7 for all time		literature
$F(t)$	food intake rate at time t	41 for all time	grams/bird/week	literature + data (Baldwin)
$RE(t)$	respiration rate at time t	28 before June 1 29.5 June 2-July 10 29 July 11-30 28 after July 30	grams/bird/week	literature + observation (Baldwin)
h	hatching period	9 days		observation (Baldwin)
$L(t - h)$	egg laying rate at time t - h	1.2 June 1-21 .4 July 10-21 0 otherwise	eggs/breeding female/week	data (Ryder, Baldwin)
$S(t,h)$	percentage egg survival	.4		observation (Baldwin)
$R(t - h)$	percentage breeding females	.45		observation (Ryder, Baldwin)

APPENDIX

Program for Bird Model

```
C       PRØGRAM ØDE
C PRØGRAM FØR BIRD PØPULATIØN DYNAMICS AND WEIGHT CHANGE
        DIMENSIØN V(10),VP(10)
        CØMMØN P(100)
      1 ACCEPT NCØM,NP,NT,T1,TDEL,ACC,DEL,ITER
C NCØM = NUMBER ØF EQUATIØNS
C NP = NUMBER ØF PARAMETERS (NØT USED IN THIS RUN)
C NT = NUMBER ØF TIMES ØUTPUT IS PRINTED ØUT
C TDEL = TIME INTERVAL FØR PRINTING
C DEL = 1/(NUMBER ØF STEPS TAKE  BETWEEN PRINTØUTS) (FØR KUTTA)
C ACC = ACCURACY ØF SØLUTIØN (.01 IN TIS RUN) (FØR KUTTA)
C ITER = MAX. NØ. ØF STEP SIZE CHANGES (FØR KUTTA)
C T1 = STARTING TIME FØR RUN
        IF (NCØM.LE.0) GØ TØ 11
        WRITE(1,200)T1,TDEL,NT
        WRITE (1,210)NCØM,NP,ACC,DEL,ITER
        ACCEPT(V(I),I=1,NCØM)
C V(1) = TØTAL ADULT PØPULATIØN
C V(2) = AVERAGE BØDY WEIGHT PER ADULT
C V(3) = TØTAL ADULT BIØMASS
C V(4) = TØTAL JUVENILE PØPULATIØN
C V(5) = AVERAGE BØDY WEIGHT PER JUVENILE
C V(6) = TØTAL JUVENILE BIØMASS
        DISPLAY "DEBUG?",#
        ACCEPT DEBUG
        CALL INPUT
        WRITE (1,600)
        T=T1-TDEL
        CALL INIT
        DØ 20 I=1,NT
        T=T+TDEL
        T2=T+TDEL
        DØ 17 J=1,NCØM
17      V(J)=AMAX1(0,V(J))
        WRITE (1,800)T,(V(J),J=1,NCØM)
        CALL KUTTA1(T,T2,V,NCØM,DEL,ACC,ITER,EQUA)
        CALL ALGY(T2,V)
        IF (DB.NE.1.) GØ TØ 20
        CALL DELT(T,V,VP)
        WRITE (1,900)(VP(J),J=1,NCØM)
C     VP(I) IS EQUAL TØ THE RATE ØF CHANGE ØF V(I)
     20 WRITE (1,1100)
        GØ TØ 1
     11 STØP
    200 FØRMAT("DE SØLUTIØN"//"TIME STARTS AT "F10.3
 ,", INCREMENTS BY "F10.5,"FØR"I5," STEPS"/)
    210 FØRMAT(I5," EQUATIØNS, "I5," CØNSTANTS"/
 'KUTTA PARAMETERS ARE "2F12.5,I5)
    600 FØRMAT(//"TIME, VARIABLE VALUES")
    800 FØRMAT(F10.2,7F10.4)
    900 FØRMAT("DER"7X,7F10.4/(10X,7F10.4))
   1100 FØRMAT(/)
        END
*
```

```
C SUBRØUTINE SØLVES DIFFERENTIAL EQUATIØNS USING THE RUNGE-KUTTA
C                            TECHNIQUE
      SUBRØUTINE KUTTA1(XL,XU,V,N,DEL,D1,IT,EQUA)
      DIMENSIØN V(10),VP(10)
      DT=(XU-XL)*DEL
      T=XL-DT
      ND=1./DEL+.0001
      DØ 20 K=1,ND
      T=T+DT
      CALL DELT(T,V,VP)
      DØ 20 I=1,N
   20 V(I)=V(I)+DT*VP(I)
      RETURN
      END

      SUBRØUTINE ALGY(T,V)
      DIMENSIØNV(10)
      V(3)=V(1)*V(2)
      V(6)=V(4)*V(5)
      RETURN
      END

      SUBRØUTINE INIT
      CØMMØN P(100)
      RETURN
      END

      SUBRØUTINE INPUT
      CØMMØN P(100)
      RETURN
      END

C SUBRØUTINE UPDATES PØPULATIØN AND WEIGHT DIFF. EQUATIØNS
      SUBRØUTINE DELT(T,V,VP)
      DIMENSIØN V(10),VP(10)
      VP(1)=IMM(T)+REC(V(4),T)-EM(V(1),T)-MØRT(V(1),T)
      VP(2)=EPSI(T)* FDHAR(T)              -RESP1(V(2),T)
      VP(3)=0.
      VP(4)=REP(V(1),T)-MØRTJ(V(4),T)-REC(V(4),T)
      VP(5)=EPSI(T)*FDHARJ(T)-RESP2(V(5),T)
      RETURN
      END

C          BIRD IMMIGRATIØN RATE FUNCTIØN
      FUNCTIØN IMM(T)
      IMM=0.
      IF ((T.GE.18.).AND.(T.LE.20.))IMM=30.
      RETURN
      END

      FUNCTIØN EM(BN,T)
      EM=0.
      TST=AMØD(T,52.)
      IF ((TST.GE.32.).AND.(BN.GE.0.)) EM=25.
      RETURN
      END
```

```
C SUBRØUTINE SØLVES DIFFERENTIAL EQUATIØNS USING THE RUNGE-KUTTA
C                          TECHNIQUE
      SUBRØUTINE KUTTA1(XL,XU,V,N,DEL,D1,IT,EQUA)
      DIMENSIØN V(10),VP(10)
      DT=(XU-XL)*DEL
      T=XL-DT
      ND=1./DEL+.0001
      DØ 20 K=1,ND
      T=T+DT
      CALL DELT(T,V,VP)
      DØ 20 I=1,N
   20 V(I)=V(I)+DT*VP(I)
      RETURN
      END

      SUBRØUTINE ALGY(T,V)
      DIMENSIØNV(10)
      V(3)=V(1)*V(2)
      V(6)=V(4)*V(5)
      RETURN
      END

      SUBRØUTINE INIT
      CØMMØN P(100)
      RETURN
      END

      SUBRØUTINE INPUT
      CØMMØN P(100)
      RETURN
      END

C SUBRØUTINE UPDATES PØPULATIØN AND WEIGHT DIFF. EQUATIØNS
      SUBRØUTINE DELT(T,V,VP)
      DIMENSIØN V(10),VP(10)
      VP(1)=IMM(T)+REC(V(4),T)-EM(V(1),T)-MØRT(V(1),T)
      VP(2)=EPSI(T)* FDHAR(T)            -RESP1(V(2),T)
      VP(3)=0.
      VP(4)=REP(V(1),T)-MØRTJ(V(4),T)-REC(V(4),T)
      VP(5)=EPSI(T)*FDHARJ(T)-RESP2(V(5),T)
      RETURN
      END

C        BIRD IMMIGRATIØN RATE FUNCTIØN
      FUNCTIØN IMM(T)
      IMM=0.
      IF ((T.GE.18.).AND.(T.LE.20.))IMM=30.
      RETURN
      END

      FUNCTIØN EM(BN,T)
      EM=0.
      TST=AMØD(T,52.)
      IF ((TST.GE.32.).AND.(BN.GE.0.)) EM=25.
      RETURN
      END
```

```
C SUBRØUTINE SØLVES DIFFERENTIAL EQUATIØNS USING THE RUNGE-KUTTA
C                              TECHNIQUE
      SUBRØUTINE KUTTA1(XL,XU,V,N,DEL,D1,IT,EQUA)
      DIMENSIØN V(10),VP(10)
      DT=(XU-XL)*DEL
      T=XL-DT
      ND=1./DEL+.0001
      DØ 20 K=1,ND
      T=T+DT
      CALL DELT(T,V,VP)
      DØ 20 I=1,N
   20 V(I)=V(I)+DT*VP(I)
      RETURN
      END

      SUBRØUTINE ALGY(T,V)
      DIMENSIØNV(10)
      V(3)=V(1)*V(2)
      V(6)=V(4)*V(5)
      RETURN
      END

      SUBRØUTINE INIT
      CØMMØN P(100)
      RETURN
      END

      SUBRØUTINE INPUT
      CØMMØN P(100)
      RETURN
      END

C SUBRØUTINE UPDATES PØPULATIØN AND WEIGHT DIFF. EQUATIØNS
      SUBRØUTINE DELT(T,V,VP)
      DIMENSIØN V(10),VP(10)
      VP(1)=IMM(T)+REC(V(4),T)-EM(V(1),T)-MØRT(V(1),T)
      VP(2)=EPSI(T)* FDHAR(T)              -RESP1(V(2),T)
      VP(3)=0.
      VP(4)=REP(V(1),T)-MØRTJ(V(4),T)-REC(V(4),T)
      VP(5)=EPSI(T)*FDHARJ(T)-RESP2(V(5),T)
      RETURN
      END

C         BIRD IMMIGRATIØN RATE FUNCTIØN
      FUNCTIØN IMM(T)
      IMM=0.
      IF ((T.GE.18.).AND.(T.LE.20.))IMM=30.
      RETURN
      END

      FUNCTIØN EM(BN,T)
      EM=0.
      TST=AMØD(T,52.)
      IF ((TST.GE.32.).AND.(BN.GE.0.)) EM=25.
      RETURN
      END
```

```
C        FUNCTIØN CØMPUTING REPRØDUCTIØN RATES
      FUNCTIØN REP(X,T)
      REP=0.
      IF (T.GE.22) REP=.228*X
      IF (T.GE.25) REP=0.
      IF (T.GE.26.) REP=.076*X
      IF (T.GE.30.) REP=0.
      RETURN
      END

      FUNCTIØN MØRT(BN,T)
C    BIRD MØRTALITY RATE FUNCTIØN
      MØRT=.015*BN
      IF (T.GE.24.) MØRT=.02*BN
      RETURN
      END

C  FUNCTIØN CØMPUTING RATE ØF FØØD INGESTIØN BY ADULTS
      FUNCTIØN FDHAR(T)
      FDHAR=41.
      RETURN
      END

C  ADULT RESPIRATIØN RATE FUNCTIØN
      FUNCTIØN RESP1(BW,T)
      RESP1=28.
      IF (T.GE.21.) RESP1=29.5
      IF (T.GE.26.) RESP1=29.
      IF (T.GE.31.)RESP1=28.
      RETURN
      END

      FUNCTIØN EPSI(T)
C    BIRD FØØD ASSIMILATIØN EFFICIENCY FUNCTIØN
      EPSI=.70
      RETURN
      END

C  RECRUITMENT RATE FRØM JUVENILE TØ ADULT FUNCTIØN
      FUNCTIØN REC(X,T)
      REC=0.
      I=T*1.00001
      IF (I.EQ.31)  REC=X
      RETURN
      END

C   JUVENILE MØRTALITY RATE FUNCTIØN
      FUNCTIØN MØRTJ(X,T)
      MØRTJ=.03*X
      RETURN
      END

C    JUVENILE RESPIRATIØN RATE FUNCTIØN
      FUNCTIØN RESP2(X,T)
      RESP2=0
      IF (T.GE.22.) RESP2=34.
      IF (T.GE.29.) RESP2=28.
      RETURN
      END
```

```
C     FUNCTIØN CØMPUTING RATE ØF FØØD INGESTIØN BY JUVENILES
      FUNCTIØN FDHARJ(T)
      FDHARJ=0.
      IF(T.GE.22.) FDHARJ=83.
      IF(T.GE.23.) FDHARJ=68.6
      IF(T.GE.24.) FDHARJ=59.1
      IF(T.GE.25.) FDHARJ=45.8
      IF(T.GE.26.) FDHARJ=44.75
      IF(T.GE.27.) FDHARJ=46.3
      IF(T.GE.29.) FDHARJ=41.5
      IF(T.GE.30.) FDHARJ=40.
      RETURN
      END
```