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Introduction

The impact of bird populations upon the properties or processes of ecosystems is mediated through patterns and magnitudes of energy flow. This impact may be either direct, by processing of large quantities of energy or nutrients, or indirect, through feedback control of other ecosystem rate processes or components. In either case, however, the impact is a result of the population dynamics and the pattern and magnitude of food consumption of the birds.

Recent research by several groups points to a relatively small direct impact on birds on most natural ecosystems (Wiens 1973). Impact through feedback control, a more difficult relationship to study, is just beginning to receive close attention in a total systems framework. In managed ecosystems, however, where our interest is in either the bird population or its prey as an aesthetic or economic resource, the direct impacts are of considerable importance. These direct impacts are a reflection of prey consumption, which in turn is a result of the interactions of prey selection and energy demand. There is little field information available on either of these components for most bird populations, however, and we have therefore employed simulation modelling, coupled with existing information on dietary composition, to generate estimates of prey consumption rates and thus of potential impact. Our modelling tactic has been to stress generality and biological realism at the expense of precision (Levins 1966), since we are interested in models which are both robust and broadly applicable. Also, we recognize that the data base of the model is frequently imprecise, and it seems intuitively illogical to build extremely precise models for imprecise data inputs, even though this if often done.

It is certainly a truism that before sensible management of a natural resource can be developed there must be sufficient insight into a problem. Management is not a simple task, although the approaches are far too often

simplistic in their assumptions of the overall situation. Frequently counter-intuitive features are elements of these management situations, and act to thwart simplistic management approaches. An example of such a counter-intuitive effect has been presented in another paper delivered at this conference (Dyer, Plant-Animal Interactions).

Thus sound management must be founded upon an overview of the entire resource-related system. Since the problems we encounter in the environment today are enormously complex, it is simply not possible to keep track of all the important actions, co-actions, and interactions without structuring flow diagrams of relationships. Once the flow diagrams are made, steps may be taken to quantify the relationships via computer analysis.

The economic relations of Red-winged Blackbirds (*Agelaius phoeniceus*) are typical of a system we feel may benefit from a modelling approach. Redwing populations are suggested to have severe economic impacts on grain crops in many parts of the country, and are the subject of intense control efforts in some areas. There are several steps to modelling Redwing-crop relations. The first involves developing the capability of providing deterministic output from modelling the bird parameters. Once this is done, then it is possible to construct additional routines that relate the population to its agricultural environment. We have done these two steps in this report, first by providing deterministic functions for Redwing populations via a Forrester (1961) flow-based model in which many important features of Redwing biology are considered, and second by suggesting means of relating Redwing populations to their environment, the agricultural ecosystem. The first step is carried out within the computer structure,while the second involves hand manipulations of computer output. It is only when this latter step is fully accomplished that there will be sufficient evidence available to make sensible management decisions. Our suggestions are intended to provide a start in this direction.

Model Structure

The population bioenergetics simulation model which we will employ here was originally developed by Wiens and Innis (in press) as part of the modelling exercises within the Grassland Biome Program of the U.S. IBP. The details of the structure and assumptions of the model are given in that paper and will only be briefly summarized here. The basic model procedure involves calculation of population density changes for each age class of the species over some specified time period, the estimation of individual body weights in each age class, and coupling of these values to data on ambient temperature regimes and various metabolic functions to estimate the bioenergetic demands placed upon the system by each age class of the species through time. Mathematically, the dynamics of the model are described as a set of non-linear difference equations.

There are two major submodels to the model (Fig. 1). In the population submodel, the adult breeding population changes through time as a result of immigration and emigration processes and through mortality rates. The reproductive output of this adult population is, of course, contributed by the breeding females, which comprise a specified portion of the total adult population. With a timing specified by phenological properties of the model (see below), the breeding females produce an egg population. The flow of individuals from this egg population is either to nestlings or to the mortality sink as dictated by the value of hatching success. The flow from the nestling

Fig. 1.   Generalized compartmental diagram of the population bioenergetics model structure. Rectangular boxes indicate state variables; five-sided boxes, computational controls; and circles, input variables (see Table 1). Solid arrows indicate flows of materials or energy or changes of state; dashed arrows indicate controls or computational transfers.

population to the fledgling population is likewise controlled by fledging success, and that from fledgling to juvenile is controlled by post-fledging survival. Mortality of both juveniles and adults is affected by specific mortality rates. Collectively, then, this submodel generates estimates of the density of each age class of the population at any given point in time.

The energy submodel is driven by ambient temperature, which is specified as input. Body weights of adults are specified as input while body weight of nestling and fledgling individuals is determined by a logistic growth function (Ricklefs 1968). Given these values the existence energy (metabolic) requirements of adult, juvenile, nestling, and fledgling age classes are calculated according to the equations given by Kendeigh (1970) for passerines:

$$M_0 = 4.337W^{0.53} \text{ at } 0^{\circ}C$$

$$M_{30} = 1.572W^{0.62} \text{ at } 30^{\circ}C$$

where W = body weight (in g). These equations thus generate an estimate of the energy demand of individuals at the ambient temperature at any given time. These existence energy demands, however, must be modified to account for various other energy demanding functions. The cost of producing eggs, for example, is given (on a per clutch basis, EC) by

$$EC = EW(CS) (1.23) (1.37) \text{ kcal}$$

where EW = egg weight (which is determined as a function of adult weight), CS = clutch size, 1.23 = the caloric value of a gram of egg, and 1.37 is an adjustment for the efficiency of egg production (73%).

Molting also imposes an energy cost; in our analyses we have assumed that existence energy demands of adults and juveniles are elevated by 12% during the molting period. The additional cost above existence level incurred by normal daily activity during the breeding season requires an adjustment of 40% of existence energy demands. Nestlings during their growth period are not especially active and, therefore, are not charged this particular cost. Their growth, however, does increase energy demands, and to account for this we elevate existence demands during the nestling period by 20% to account for growth. Fledglings are moderately active, and we elevate existence energy demands by 10% to account for this activity. Growth of fledglings, however, is much less rapid than that of nestlings, and we therefore assume that existence metabolism is increased by only 5% to account for growth. The daily existence energy demand, as modified by these various factors for each age class of the population, must then be adjusted for digestive or assimilation efficiency in order to calculate the total energy demand placed upon the system which must support the birds. Assuming a digestive efficiency of 70%, the calculated existence energy demand (as modified by these additional costs) is multiplied by 1.43 to produce an estimate of daily individual energy demands (kcal/bird-day) for each age class. Integrating these estimates with those of population density and age structure produced for a particular date by the population submodel allows estimation of the energy demand of the entire population and of each class of the population on any given day.

Various processes or flows within the population submodel are phased in time according to a set of phenological parameters (Fig. 2). These relation-
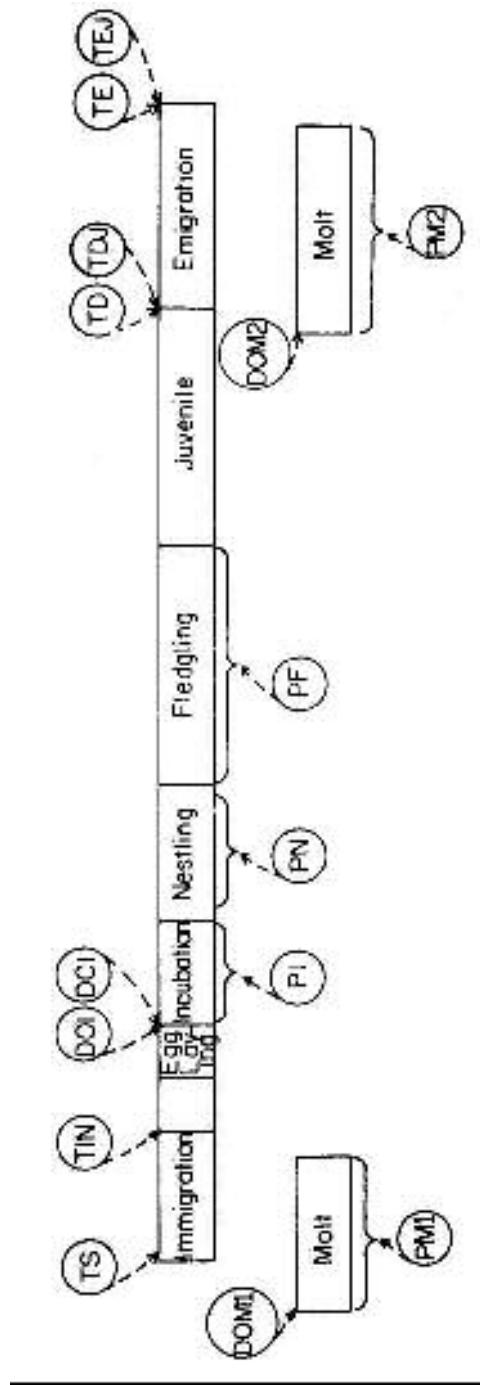
Fig. 2.   Diagram of the phenological stages considered in the model. Circled abbreviations indicate required data inputs (see Table 1).

ships are largely self-explanatory. Interested readers may consult the description in Wiens and Innis (in press) for details of these functions.

The model thus generates daily estimates of population density in each age class, total biomass in each age class, and the bioenergetic demands placed upon the food resources by each age class. It is the latter output especially which permits estimation of the potential empact of bird populations upon natural or managed systems.

CHARACTERISTICS OF THE RED-WINGED BLACKBIRD POPULATION

Wood County Breeding Population

To explore the utility of this simulation modelling approach in assessing the relationships between blackbird populations and agricultural crops, we will analyze the dynamics of the Wood County, Ohio, population which have been reported by Dyer and Webb (1970). In 1964 staff biologists of Patuxent Wildlife Research Center in Maryland initiated a 5-year study to follow the breeding density of male Redwings in Wood County. This study was coincidental with other studies started about the same time (Hewitt 1967). Since Ohio was one of the reported problem locations for Redwings in agricultural systems and since Wood County is reputed to be one of the most intensively cultivated counties in the U.S., the project was quite fitting. Two census techniques were used: (1) the Peterson-Lincoln roadside index method developed by Hewitt (1967), and (2) a 10 acre plot method reported by Meanley and Webb (1963). For the main part, one investigator (J.S. Webb) conducted the census for the 5-year period. This work is reported in a previous Bird Control Seminar report (Dyer and Webb 1970). In 1968 the census effort was expanded into adjoining regions of Ohio, Michigan and Ontario. A report of this work is given by Dyer *et al.* (1972). These studies provided the data base for our simulation analysis (Table 1).

Post-breeding Roost Dynamics

No definitive studies trace the phenological development of this population, but it is reasonable to expect that it is part of the larger concentration which gathers following the breeding season in the marsh roosts distributed along Lake Erie in northern Ohio. There are reports of trans-lake movements of the Northern Ohio population, (Richard 1968), but this phenomenon is only incidental to this report on ecosystem impact. We have assumed for convenience that the population raised in an upland agricultural region, such as Wood County, "collapses" in toward the marshes immediately after the breeding season (Fig. 3). At this time, the life history patterns change from wide distribution and territorial habits to highly gregarious and communal dwelling habits. During this latter period the Redwings roost in epicenters and range outward to forage, following the general model of Hamilton *et al.* (1967). It is during this period that the birds encounter the vast fields of growing field and sweetcorn. To a large degree, agricultural practices (monocultures) restrict foraging to these fields.

Roosting Redwings disperse from and return to the roost concentrations on a daily basis. Since their main economic impact, on corn, occurs at this time, we must determine how the birds distribute themselves from the roost site in order to realistically assess potential impact. Hamilton and Gilbert
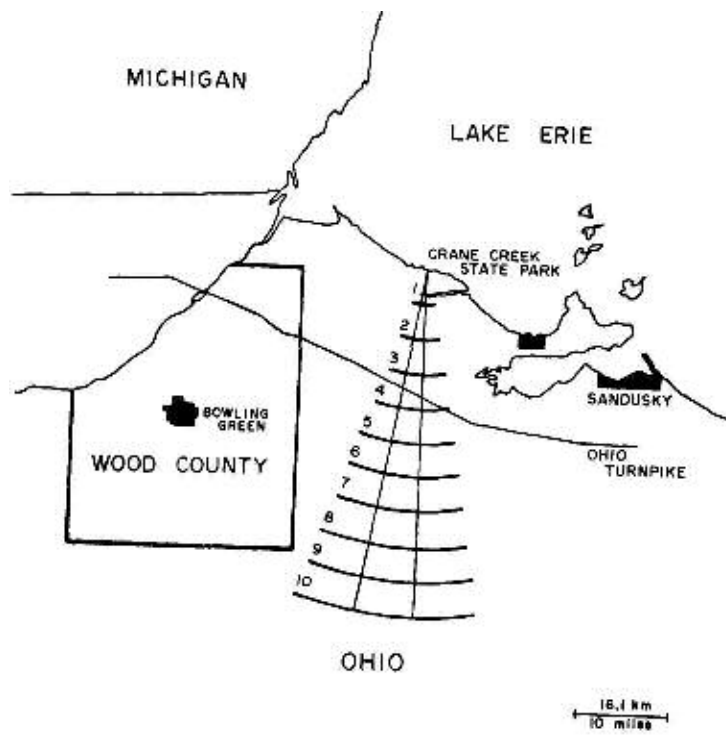
Fig. 3.   Northern Ohio, showing the locations of Wood County, the Crane Creek
           Marsh roost on Lake Erie, and the 10° x 60 km foraging dispersal
           sector from the roost. This sector is divided into 10 annull ar-
           ranged concentrically from the roost (see text).

Table 1. Values for input variables for the simulation analysis of Red-winged Blackbird population bioenergetics for Wood County, Ohio.[1]

Input Variable		Input Values [2]						Units	Sources
Description	Model Code	u_1[f]	u_2	M_3[g]	M_2	$I \times 10$[h]	$F \times 10$[i]		
Onset of immigration	TS	75	56	75	96	75	75	days since 1 Jan	Dyer, Miskimen, & Bason, unpublished
Completion of immigration	TIM	103	131	103	131	103	103	"	"
Onset of adult emigration	TD	253	253	253	253	253	253	"	"
End of adult emigration	TE	295	295	295	295	295	295	"	"
Onset of juvenile emigration	TOJ	229	229	329	229	229	229	"	"
End of juvenile emigration	TEJ	293	293	293	293	293	293	"	"
Population at start of immigration	PS	0	0	0	0	293	293	Index/km²	Assumptions of authors
Population at end of emigration	PE	0	0	0	0	0	0	"	Assumption of authors
Population breeding density	PBD	64.66	215.98	185.64	630.32	30.34	30.05	"	Dyer 1970, Laux 1970
Proportion of population breeding (yr): first brood	PPBF	0	1.0	0	1.0	0	0	Percent population	Assumption of authors
Proportion of population breeding (yr): second brood	PPBS	0	0.19	0	0.19	0	0	"	Jackson 1971
Onset of incubation activity: first brood	D11	--	134	--	134	--	--	days since 1 Jan	Francis, unpublished data
Incubation of last clutch of first brood started	SCI1	--	151	--	151	--	--	days since 1 Jan	Francis & Dyer, unpublished data
Onset of incubation activity: second brood	SCI2	--	151	--	151	--	--	"	Francis & Dyer, unpublished data
Incubation of last clutch of second brood started	SCI2	--	173	--	173	--	--	"	Francis & Dyer, unpublished data
Clutch size: first brood	CS1	--	3.59	--	3.52	--	--	number of eggs	Collins 1968
Clutch size: second brood	CS2	--	3.22	--	3.16	--	--	"	Collins 1968
Incubation period	PI	--	11.5	--	11.9	--	--	days length	Collins 1968

Table 1. Continued.

Input Variable		Input Values [2]								Sources
Description	Model Code	ug'	ug	Hg'	Hg	Ind'	Ind	Ptd	Units	
Nestling period	PN	--	10	--	10	--	--	--	days length	Francis & Dyers, unpublished data
Fledgling period	PF	--	30	--	30	--	--	--	"	Francis & Dyers, unpublished data
Hatching success	NS	--	0.71	--	0.41	--	--	--	percent eggs laid	Francis & Dyers, unpublished data
Fledgling success	FS	--	0.50	--	0.70	--	--	--	percent nestlings hatched	Francis & Dyers, unpublished data
Post-fledgling survival	PFS	--	0.67	--	0.67	--	--	--	percent indiv. fledged	Lack 1970
Adult mean body weight	ABW	63	63	63	93	63	63		grams	Williams 1940, Ricklefs 1968
Weight at hatching	HW	--	3.55	--	3.55	--	--	--	"	Francis & Dyers, unpublished data
Weight at fledgling	FW	--	37	--	37	--	--	--	"	Williams 1940, Ricklefs 1968
Growth rate	GR	--	0.516	--	0.516	--	--	--	---	Ricklefs 1968
Onset of postnuptial molt	OM2	212	212	232	212	212	212		days since 1 Jan	Assumption of authors
Duration of molt	PM2	61	61	61	61	61	61		days length	Manley and Bond 1970
Breeding season adult death rate	ADR	0.00043	0.00043	0.00043	0.00043	0.00013	0.00043		percent pop/day	Fankhauser 1967, Lack 1970
Breeding season juvenile death rate	JDR	0.005	0.005	0.005	0.005	0.005	0.005		"	Assumption of authors

1/ Temperature records, which are not shown here, were obtained from U.S. Weather Bureau records for the station.
2/ U = upland, M = marsh, In = literature, Fl = floating or non-breeding.

(1969) assumed a linear dispersion of Starlings (*sturnis vulgaris*) from the roost epicenter, with population density decreasing with increasing distance. Their data indicated a geometric decrease of density with distance from the roost (their Table 1). We have made similar assumptions, but have also considered the distributional patterns revealed by Redwing feeding records in Ontario corn fields (Dyer 1967). By re-analyzing these data we have chosen the Poisson distribution as a basic model to represent changes in bird density as distance from the roost increases (Table 2). The fact that densities do decrease is readily apparent from even casual field observations, but the exact mode is yet to be described. Actually when we fit the data presented by Dyer (1967) to the Poisson distribution, we reject the null hypothesis (X^2 = 25.49, 9d.f.); however, the fit is reasonable enough throughout the body of the curve (the extremes were in greatest contrast to the Poisson model), so we have chosen to use this model anyway, for want of better material. Given the monocultural (corn) agriculture of the study area, it seems unlikely that food distribution has a direct effect upon the form of this spatial distribution of individuals. Other mechanisms, perhaps largely density-related behavioral responses (Hamilton *et al.*1967) may be more important in determining the formation and distribution of flock foraging units.

Having established an hypothetical pattern of Redwing distribution from their roost during foraging activities, we must then provide a method of allocating the birds within a sector of the area surrounding the roost. For convenience, we have considered relations within a 10° sector radiating from the roost located in Ottawa County near the Crane Creek Marsh. This sector is then divided into 10 concentric zones or annuli ranging outward to 60 km from the roost site (Fig. 3). Characteristics of these annuli are given in Table 2. Our analysis thus assumes that on the average the total population will behave in a predictable fashion by distributing itself through this sector according to a Poisson distribution, irrespective of the food resource in the region. We also assume that once a feeding pattern is established by a flock it will be maintained while the flock is present in the general area (Dyer 1967).

The 10° sectoral representation is capable of being extrapolated to other locations. Further, when sufficient evidence is available, the 10° arc can be expanded or contracted in a linear fashion, depending upon the Redwing population size and distribution habits. Thus, by accounting for numbers of Redwings produced and maintained in a breeding area, such as Wood County, and then assuming they will roost and forage in areas suggested by the model in Figure 3, we can focus attention on the potential impacts of these birds on the agricultural ecosystem within the confines of the described sector(s). It is apparent that the northern Ohio population is far larger than we have structured, but we suggest that all that needs to be done is simply make similar apportionments of population size and area of bird distribution. The sum total of all these apportionments may then represent the overall dynamics of Redwings in agriculture in northern Ohio.

Table 2. Characteristics of 6 km-radius annul of a 10° dispersal sector radiating a distance of 60 km from the Crane Creek Marsh roost.

Annulus	Distance from Roost (km)	Area (km²)	Proportion of bird Population[1]	Percent of area In:		Corn Production (bu/acre)[3]
				Cropland[2]	Corn[2]	
1	0 – 6	3.14	4.58	82	12	66.20
2	6 – 12	9.43	9.23	78	16.7	66.20
3	12 – 18	15.70	14.95	73	21	67.50
4	18 – 24	22.00	18.08	67	17	69.95
5	24 – 30	28.27	17.54	68	23.5	74.95
6	30 – 36	34.56	14.21	69	23	78.63
7	36 – 42	40.84	9.80	64	25	78.69
8	42 – 48	47.12	5.98	64	25	78.69
9	48 – 54	53.41	3.23	(64)	(25)	78.69
10	54 – 60	59.69	2.28	(64)	(25)	78.69

1/ Expected values from Poisson distribution.

2/ From unpublished data, Bureau of the Census, U.S. Dept. of Commerce.

3/ U.S. Department of Commerce, 1969.

SIMULATION RESULTS

The results of our simulation modelling exercise with Redwing populations may be discussed with reference to seasonal population dynamics and energy demands, and also with respect to the particular relationships which hold during the post-breeding season when the population is aggregated at the central roost. Since this latter period coincides with the time of greatest corn availability and, therefore, greatest potential impact upon corn crops, it will receive the most detailed discussion.

Seasonal trends in the population dynamics of upland and marsh populations of Redwings in Wood County are shown in the graphical output of simulations given in Fig. 4. Since males and females were considered separately in simulation runs (because of their differences in phenology and body weight) simulation output graphs are given separately for each sex. Since only females are directly capable of reproduction, the reproductive output of upland and marsh populations is given on the graphs of female population dynamics. Note that the density scales in Fig. 4 are quite different for marsh and upland populations and that as expected the density (individuals/km^2) is much greater in marsh than in upland populations. Note also the proportionately greater production of nestlings in the upland population, a reflection of the greater clutch size and hatching success of birds in upland habitats (Table 1). Fledging success is greater in marsh populations, as is evidenced in Fig. 4. Graphical output such as this permits a detailed assessment of the effects of habitat (or other factors) upon population dynamics. In order to obtain a clear picture of the overall Redwing population dynamics in Wood County, however, it is necessary to adjust these per square kilometer estimates to reflect the total acreage of marsh and upland habitats in Wood County. There are 48.8 km^2 of marsh habitat in Wood County and 301 km^2 of suitable upland habitat (Dyer and Webb 1970). When population density output for marsh and upland populations is adjusted for these total areas (Fig. 5) the dominance of the upland segment of Redwing populations in Wood County becomes apparent. Peak density in both populations coincides with peak production of nestlings (around June 9) but the upland peak is more than three times the peak density of the marsh population.

Seasonal patterns of energy flow in the two habitats show generally similar relationships (Fig. 6,7). The peak in energy demand, however, does not coincide so dramatically with the production of nestlings, since nestlings (being small) have a relatively minor effect upon overall population energy demands. In the upland population energy demand is highest from around June 10 to June 30 while in the marsh population the peak of energy demand is less well defined. Again, the energy demand of upland birds in toto is much greater than that of the marsh-breeding population. The total seasonal energy demand of the upland birds is more than twice that of the marsh birds. In both populations, breeding females consume the greatest share of the energy flow through the various age classes (seasonal total in upland = 542 x 10^6 Kcal), while territorial males account for a relatively small fraction of the total energy flow through the populations (seasonal total in uplands = 190 x 10^6 Kcal; in marsh - 89 x 10^6 Kcal). Redwings from both upland and marsh habitats collapse into post-breeding roosts along the shores of Lake Erie in late July (here arbitrarily assumed to occur on July 28; see Fig. 5 and 7). The
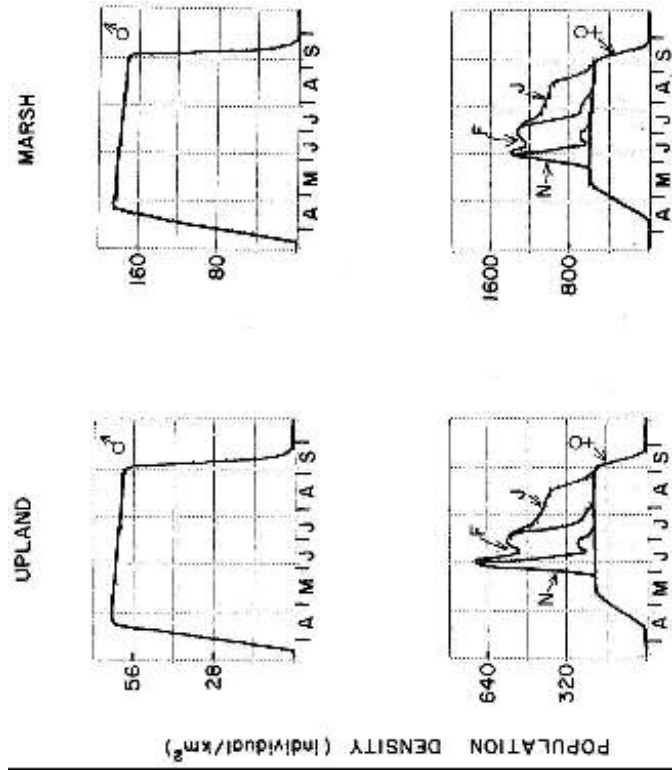
Fig. 4. Simulation output 22. Population densities of breeding males, females, and offspring age classes in upland and marsh populations of redwings. Note that density scales are different for the two populations. Immature and floating males are not depicted here.
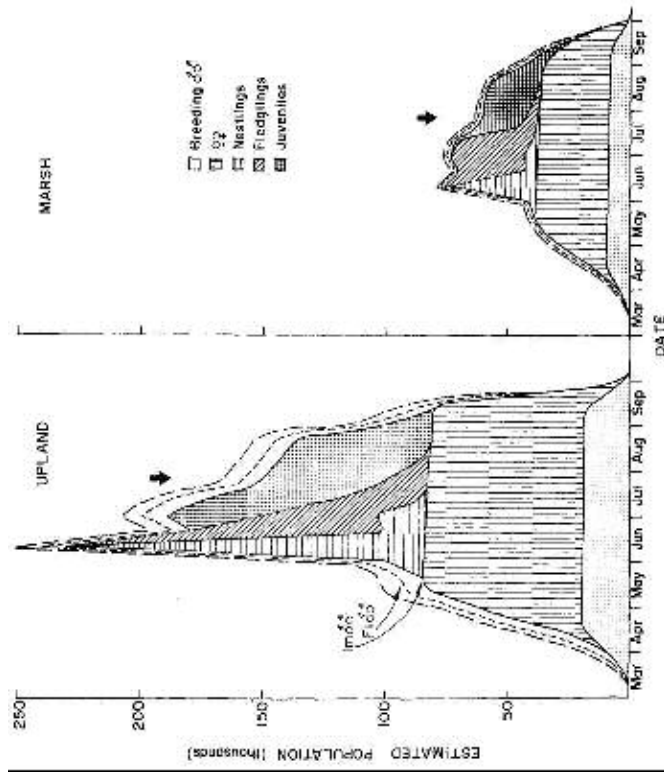
Fig. 5 Total populations of upland- and marsh-nesting redwings for Wood County, as estimated by the simulation model. The vertical arrow indicates the time at which both populations are assumed to leave Wood County and aggregate in the Crane Creek Marsh.
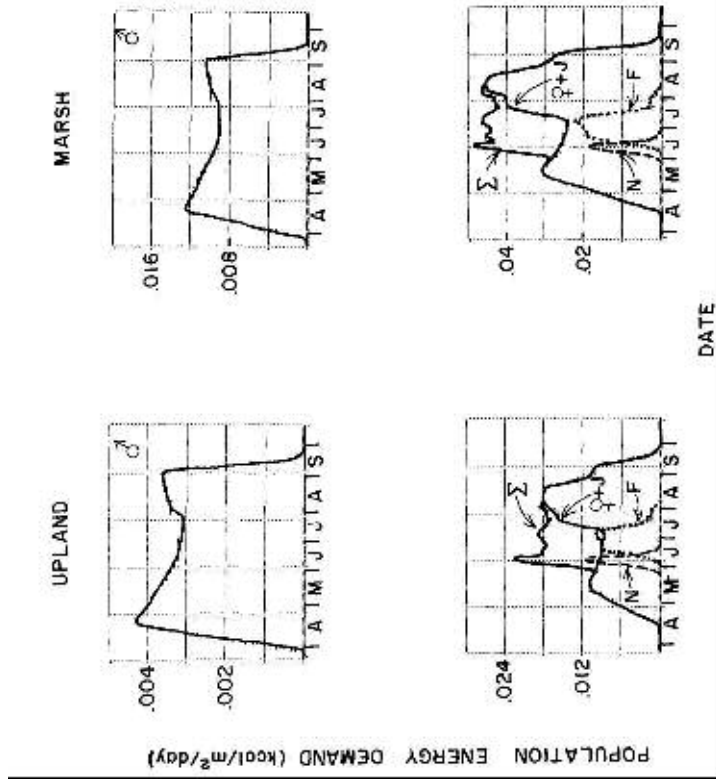
Fig. 6.   Simulation output of estimated daily energy demands (kcal/m^2) of sex and age classes of upland and marsh populations of redwings. Note that scales for the populations differ.

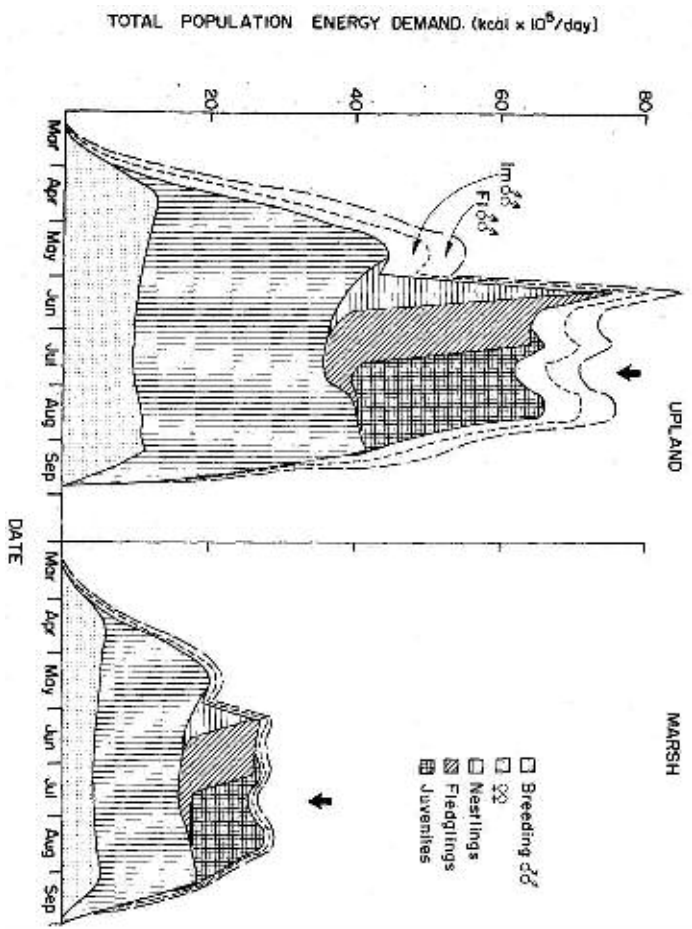TOTAL POPULATION ENERGY DEMAND. (kcal x 10^6/day)

Fig. 7. Energy demand of the total populations of upland- and marsh-nesting redwings for Wood County, from model output. Symbols as in Figure 5.

peak density of this combined total Wood County population, 231,700 birds, occurs at this time. Using the Poisson distribution of individuals in this roosting population among the annuli of the foraging sector, we may partition the daily total energy demand estimates generated by the model into an energy demand for each annulus of the foraging area. Knowing the diet of birds during this time period (Hintz and Dyer 1970) (Table 3) and the caloric values of each of the food types (insects = 5.45 Kcal/g dry wt, corn = 4.74 Kcal dry wt, wheat-oats = 4.16 Kcal dry wt, and weeds = 4.74 Kcal dry wt; from Cummins and Wuycheck 1971), it is a straightforward procedure to convert these model estimates of caloric energy demand into estimates of consumption of each of these four major prey types. These consumption values may then be partitioned among the annuli according to the distribution of energy demand, so that we may obtain an overall picture of the spatial (among annuli) and temporal (between dates) patterns of food consumption of this population.

To demonstrate these temporal and spatial patterns we have rather arbitrarily selected four dates during this roosting phase for detailed analysis. The patterns are shown in Fig. 8. In all cases the peak of consumption for any particular date or pray type occurs in annuli 4 and 5 (18-30 km from the roost). This of course simply reflects the application of a Poisson distribution to the dispersal of the birds from the roost. Temporarily, the consumption of insects shows a steady decrease from late July through mid-September. This decreasing pattern is a consequence of the adoption of more omnivorous diets by young birds as they mature and of the decreasing availability of insects with the colder nights of late summer and early fall. Weed seeds do not really become important dietary components until fall, while wheat and oat "detritus" is an important dietary component of Redwings at all times except when corn is plentiful. At this time (peaking around August 28) consumption of corn dominates the Redwing's diet, and it is thus at this time that their potential impact upon corn crops may be most severe. Further, the spatial pattern of corn consumption indicates that the magnitude of this impact may be greatest in the general area 12 to 36 km from the roost. Beyong 45 km or so the consumption is relatively low.

The consumption patterns plotted in Fig. 8 are of course daily consumption rates, and some insight into the overall patterns of food consumption and potential impact may be obtained by calculating seasonal total consumption of each food type (from July 24 to October 1). These values (given in Table 4) indicate the magnitude of corn consumption by the birds. Corn comprises 30% of the total consumption by the flocks.

In order to assess the potential impact of these feeding patterns, consumption must be related to supply. We lack realistic measures of food supply for insects, wheat-oat detritus, and weed seeds, but we can use information on crop acreages and yield (Table 2) to estimate the amount of corn available to the birds in each annulus. Given that there are 56 lbs. (25.402 kg) of corn per bushel, and a water content of 15%, we can convert our estimates of kg dry wt consumption (Table 4, Fig. 8) to bushels consumption. These values are given in Table 5, together with the calculated yield of corn (acreage x bushels per acre production, from Table 2) in each annulus. The simplest measure of potential impact of the blackbirds upon the crop is obviously consumption as a percentage of yield. Total agricultural yield of corn increases steadily from the roost outward, largely because of the increasing area per annulus. The percent of the annulus area planted in corn

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Table 3. Composition of Red-winged Blackbird diets on four dates during the post-breeding roosting phase, as determined from the data of Hintz and Dyer (1970). These dates correspond with those depicted in Figure 8.

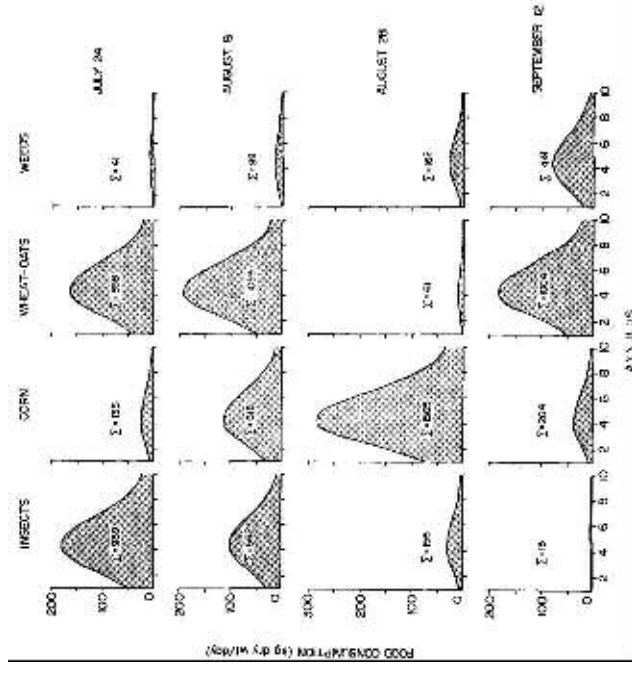| Date	Percent of Diet (volume) in			
	Insects	Corn	Wheat-Oats	Weeds (seeds)
July 24	53	6	39	2
August 8	29	25	42	4
August 28	10	78	3	9
September 12	1	12	58	29

Fig. 8. Temporal and spatial variations in the consumption of four food types by the roost population of Redwinged Blackbirds, as calculated from model output and dietary composition (Table 3). The curves depict changes in the magnitude of consumption with increasing distance from the roost (i.e., annuli 1-10). Summed values state the area under the curves, which equal the total consumption of a prey type on the given date over the entire sector.

Table 4. Estimated total seasonal consumption (kg dry wt.) of major food types by roosting Red-winged Blackbirds, July 24 - October 1.

Prey Type	Consumption by Annulus of Dispersal Sector										Total Consumption
	1	2	3	4	5	6	7	8	9	10	
Insects	11,258	22,583	36,578	44,247	42,915	34,767	23,977	14,631	7,903	5,578	244,437
Corn	21,564	43,145	70,368	85,101	82,559	66,891	46,126	28,147	15,204	10,732	470,139
Wheat-Oats	30,695	61,492	59,605	120,457	116,862	94,673	65,293	39,841	18,292	15,190	662,396
Weeds	7,734	15,666	25,378	30,698	29,774	24,108	16,636	10,151	5,483	3,870	169,560

Table 5. Model-derived estimates of corn consumption (bushels) by the 'Wood County Red-winged Blackbird population in relation to agricultural yield, by annuli of the roost dispersal sector. See text for the assumptions underlying these calculations.

	Annulus									
	1	2	3	4	5	6	7	8	9	10
CONSUMPTION:										
August 28 (bu/day)	3.32	6.30	11.85	13.33	12.73	10.31	7.11	4.36	7.34	3.65
Roost Season Total (July - September)	598.01	2,072.10	3,959.10	3,941.60	3,823.25	3,098.80	3,036.40	1,303.40	704.80	497.00
AGRICULTURAL YIELD (bushels tons)	6,157.60	25,738.20	54,998.00	64,171.50	164,171.00	154,565.00	158,535.00	225,667.00	339,635.60	290,185.00
BLACKBIRD IMPACT (seasonal consumption / yield) x 10²	16.20	7.80	5.90	6.10	2.30	2.03	1.10	0.60	0.30	0.20

increases over the first four annuli (i.e., out to 24 km from the roost), and then stabilizes (Table 2). Consumption, as noted above, peaks in annuli 4 and 5. The overall impact resulting from these distributional patterns steadily decreases from the roost outward with a "plateau" of sorts in annuli 2-4 (6-24 km from the roost) (Table 5).

Concluding Comments

We undertook this analysis of Redwing-crop relations with the view that simulation modelling could contribute to our overall understanding of the resource system, and thereby strengthen management decisions. Has this approach in fact contributed anything to our understanding of the situation which may be useful in management? Obviously, we believe it has. By employing this population bioenergetics simulation model, we have been able to estimate patterns of population dynamics and energy flow that are ordinarily unavailable from rather basic life history information. This in turn has allowed us to generate quantitative projections of temporal and spatial patterns of food consumption, especially in relation to corn crops. Our route to assessing the impact of Redwings on corn production is thus from information on Redwing life history, metabolism and environmental responses rather than from *post facto* samplings of field damage or from intuitive judgments. We do, of course, make some simplifying assumptions, as any modelling effort must, but the assumptions are biologically realistic, and are derived from our field experience with Redwings and other birds. Following such descriptions as we have made here it is necessary to provide for some series of field-oriented investigations to check on the validity of our statements. Such work often provides new insight for simulation modelling and thus the much sought iteration of information-modelling-experiment procedure is developed.

The utility of a modelling approach is not confined to generating estimates or describing relationships. We believe that additional insight into these relationships may follow from using the model as a gaming or simulation tool, to explore "what if" questions which are generally not amenable to direct field testing. For example, it is clear that the interrelationship between bird distribution from the roost site and corn acreage in each annulus is a major determinant of impact. We have assumed that the birds disperse in a Poisson distribution without regard to food availability, which is a justifiable assumption given the agricultural practices about the Crand Creek Marsh. It is also apparent (Fig. 8) that the birds exhibit a preference for corn over other food categories available in late August, altering their diets to consume primarily corn as it becomes available. One management ploy under such conditions might be to shift agricultural practices and reduce the corn acreage in annuli 3-6, where consumption is greatest, and increase corn acreage in the outer annuli. Given the birds' preference for corn, however, one might predict that they would respond to this agricultural shift by simply extending their dispersal, so that peak densities (and consumption) again coincided with areas of moderate to high corn acreage. There are definable limits, however, to how long the birds can continue to play this game. As prime food sources become located increasingly farther from the roost site, it must take longer flights to reach them. Not only does this increase the energy expenditure which the birds must balance by consumption,

but it reduces the time available for foraging and meeting these increased demands. There comes a point, obviously, at which the birds can no longer maintain an energy balance by flying great distnaces to prime food sources. When this occurs, the birds may be expected either to confine their attention to less preferred (and economically less valuable) food resources closer to the roost site, or to abandon the roost site and establish themselves elsewhere These circumstances are directly amenable to simulation analysis with the model we have described. Given basic information on flight speeds and rates of feeding during foraging, it should be possible to offer some preliminary predictions regarding the distance from a roost at which this "threshold of security" for the corn is achieved. Much of this speculation is supported by the work reported for Starlings by Hamilton *et al.* (1967).

While grains of various sorts make up the bulk of the diet of Redwings during the roosting phase, insects are the major food during the breeding season. The decrease in consumption of insects following breeding may be related to their availability. If insects are in fact a highly preferred prey, then increasing their availability during the period of greatest corn availability (late August and early September) might have the effect of reducing consumption of corn significantly. Overzealous use of insecticides and environmental simplification (tendencies toward monoculturing) obviously decrease insect diversity and availability, perhaps especially in late summer, and thus may contribute to the potential impact of the birds on corn crops. Again the basic relationships may be explored by simulating various situations within the model structure.

Finally, one more feeding relationship should be noted. Our analysis rather strongly suggests that the Redwings rely chiefly upon detritus in wheat and oat fields during the roosting phase when corn is not available (Fig. 8). If the supply of wheat-oat detritus is at all limiting to the birds during this time period, two management ploys might be feasible. First, increasing the amount of wheat-oats in areas close to the roost (in annuli 1-4) might have the effect of reducing the tendency of the birds to fly farther for a preferred food (corn) in the face of a less preferred but very abundant resource closer at hand. Conversely severe reductions in the availability of wheat-oatsdetritus over all annuli during the times when corn is not available might place a sufficient food stress upon the population to precipitate roost break-up.

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Question: How are the distance patterns determined?

Answer: One of the reasons is that corn is not very close to the marsh.
Another has to do with density-dependent factors and the way birds
sort themselves out away from the marsh. Now there is information
to support this. There is other information from Starlings to
show that this should be a geometric decay curve the other way.
But again you can see we have gaming devices here in which we can
interject the field position. I would suggest that we had better
estimate per unit area of corn damage than what we can actually
measure in the fields. You can argue with that if you want, but
it's testable.

Question: What is utilization of energy based on?

Answer: The energy utilization is based on distance energy, which is
known for something like 150 species of birds. The way that
this has been set up, the studies divide existence energy be-
tween 30°C and 0°C, and we feel that expressions of existence
energy needs are very good.

Question: Your model is simplistic in late summer in assuming the Wood
County population comes to one roost, and no account is taken
of the turnover rate of birds coming in from Canada or where-
ever else. I think this would be a major drawback in trying
to say that these estimates are good in determining how much
corn is being removed.

Answer: If you knew the perimeter of this breeding range, then you
would know the total impact for the Lake Erie region. You'd
go one step beyond the simplistic approach, and you would
take a cruder estimate. I think you're going to be pretty

close to the old ball park on these estimates.

In that area adjacent to the lake we would estimate that 16% of the corn raised can be mutilated by birds. By the time we're about twenty miles out, we're down to about 0.6%. That's the amount of corn from that particular area which is available to the birds expanding into that part of the ecosystem.

I can show you the number of kilocalories, for instance, that are removed. You know the number of bushels raised in the area, the number of bushels the birds removed, and the density of the birds in that particular area. The total average loss is going to be very close to between 2 and 3%. For a population raised in Wood County that is feeding in Ottawa County or Sandusky County you just keep adding population to your right sectors, and you add population levels.

You can take this model to simulate those population density parameters. You can assume one bird per square foot or ten. You might want to know if there are population density limiting factors. Up to a certain level you could define energy require-ments, or population density, or whatever you wanted, for a given set of gaming parameters. This is quite adaptable, and the biologist can select the parameters.

Question: Assuming that your actual damage figures, which of course are based on assumptions, are correct to an order of magnitude, doesn't this sort of negate the assumption you've been working on, because corn damage is due to the peak immigration of vast flocks from Ontario and Michigan? Actually the damage that we get is capable of being explained by the locally breeding birds. Is that right?

Answer: I think you could set up that sort of thing. You could test the hypothesis with the present output.