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Modeling Avian Foraging: Implications for Assessing the Ecological Effects of Pesticides

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ABSTRACT

The impact of many pesticides on nontarget species occurs by chronic exposure through the food chain and reduction of their prey populations. This makes an understanding of diet choice by nontarget species critical to predicting potential effects. A conceptual method to assess these impacts and to adopt better pesticide application strategies is developed in a series of steps:

1. A model of foraging is developed based upon the ecological theory of optimal foraging. The model is tested using the cowbird (*Molothrus ater ater* [Boddaert]) and demonstrates that these birds maximize their daily energy intake during the summer by consuming a mixed diet of grasshoppers and seeds.
2. Assuming a pesticide is applied to control grasshoppers, the model can be used to determine the conditions under which the birds would experience chronic exposure to the pesticide and/or population reductions due to the pesticide's reduction of their prey.
3. The foraging model indicates that a level of pesticide application that is less than maximal for grasshopper control might lead to optimal pest control when combined with bird predation.

KEY WORDS

pest control, foraging, grasshoppers, birds

INTRODUCTION

The immediate poisoning (acute effects) of animals by environmental toxins may require careful experimental studies, but it is a straightforward problem. However, the assessment of chronic effects of exposure to environmental toxins in the food chain and/or reduction in prey populations is not as straightforward. To assess these potential effects on nontarget species requires a better understanding of diet choice by nontarget species.[1] While diet choice models from ecology occasionally have been employed in developing pest control strategies,[2] their application in assessing the impact on nontarget species of pesticides in the food chain has not been addressed. Therefore, risk assessment of pesticide applications and the development of integrated pest management strategies that combine pesticide use with biological control agents (e.g., predators and parasitoids) may benefit from the use of diet choice models.

Mathematical models of animal diet choice have been employed by ecologists for more than 20 years[3] (optimal foraging theory, or OFT). The majority of these models have employed principles of mathematical optimization that are widely used in economics to model consumer choices. These models are applied to animal diet choices based upon the assumption that individuals that select better diets than other individuals in the species population will be favored by natural selection (greater survival and reproductive success). This implies that foraging is related to individual survival and reproductive output, and individuals are "plastic" in their foraging behavior.

The mathematics of optimization often permits ecologists to make specific predictions about the ways that animals should select their diets under different environmental conditions. These predictions can be compared then with the observed foraging behavior of animals to assess how closely their behavior approaches the predicted optima. Birds have been most frequently employed to test these models.[3] Birds appear to be able to select diets very similar to the predicted optima; however, most of these tests have been conducted in the laboratory rather than in the field.

One set of OFT studies has employed the mathematical optimization technique of linear programming. Almost every deterministic diet choice model in OFT can be written as a linear programming model.[4] In addition, these studies have successfully predicted diet choices for a wide range of animals feeding on very different foods and in very different field environments.[4-10] Therefore, the linear programming method represents a very flexible and useful modeling format to address animal diet choices.

The linear programming studies have been cited as examples that may be applicable in developing better pest control strategies[2] and in assessing the risk of persistent pesticides on nontarget species.[1] This modeling approach also has been employed to address the effects on consumer diet choice of naturally occurring toxins in foods.[11] Therefore, it is a small step to adapt this modeling technique to an examination of how pesticides in the food chain affect consumers.

This chapter presents an example of how a linear programming model of diet choice can be used to examine the potential effects of a pesticide in the food chain on a nontarget species. If the nontarget species is a predator of the pest, the diet choice model can be used to help develop an optimal integrated pest management strategy. This example is developed by:

1. constructing the diet choice model;
2. examining the effects of the pesticide through the food chain by imposing its ingestion as a constraint in the model, and including its reduction of the nontarget species' prey populations; and
3. contrasting the reduction of the pest by the pesticide and predator at different levels of pest abundance, as a potential integrated pest management program.

The example is developed using cowbirds (*Molothrus ater ater* [Boddaert]) as the nontarget species and grasshoppers (Orthoptera: Acrididae) as the pest.

THE FORAGING MODEL

A linear programming diet choice model for the cowbird in a Montana prairie environment has been published.[12] The cowbird is an ideal example because its foraging behavior is determined solely by its individual nutritional requirements, as the cowbird is a nest parasite that does not feed its young. The cowbirds in this environment consume only two major food categories during the summer: seeds and insects, mostly grasshoppers. Also, the cowbird is second only to the western meadowlark (*Sturnella*

neglecta) as an avian predator of grasshoppers in the western United States[13] and is very abundant, making it a potential control agent of grasshoppers.

The linear programming model for cowbirds includes three constraints that might influence their decision on how much seed vs grasshoppers to include in their diet:[12] daily feeding time, daily digestive capacity, and daily energy requirements. Each constraint must be written as a linear inequality:

$$C \geq \text{ or } \leq aG + bS \qquad (1)$$

where C is the constraint value, a converts consumed grasshopper mass, G (grams dry mass per day), into the constraint units, and b converts consumed seed mass, S (grams dry mass per day), into the constraint units. Which inequality is applicable depends upon whether the constraint cannot be exceeded or must be exceeded by the forager. Average observed cowbird foraging constraints are presented in Table 1, and the observations used to determine them are summarized below from the original study[12].

Daily Feeding Time

The cowbird's foraging time during summer daylight hours was observed to be limited by the thermal environment with the mid-day being too hot for foraging. The daily time the birds have available to harvest seeds is greater than that to hunt grasshoppers, because grasshoppers can only be caught when they are active, and grasshoppers' activity is constrained more by the thermal environment than is the birds' activity. This means that the birds are active in the cooler hours of the day (morning and evening) when grasshoppers are inactive, and the grasshoppers are active during some of the warmer hours when the birds are inactive. Even when grasshoppers are active, the cowbirds cannot search for grasshoppers and seeds at the same instant, because each requires a different behavioral pattern of search.

Therefore, the daily feeding time constraint is composed of two equations:

1. temporal non-simultaneous search, when seeds are available but grasshoppers are not, and
2. spatial non-simultaneous search, when seeds and grasshoppers are both available but cannot be searched for using the same behavioral mode.

The first constraint sets an upper limit to grasshopper consumption that is less than the amount that could be consumed given total daily feeding time, because grasshoppers are not available for the entire feeding time. The second constraint converts the total daily feeding time into the consumption of seeds versus grasshoppers given a trade-off in the consumption of the two food types because they require different search modes.

The conversion of feeding time into consumption was measured using captive birds in an aviary, where either grasshoppers or seeds were available for consumption and their abundances could be controlled. The feeding observations on grasshoppers were further differentiated between grasshoppers of different sexes and body sizes. These measurements provided a measure of how much time on average a cowbird requires to encounter a food item at different food densities (functional response: Figure 1).[12] In addition, the time it takes for a bird to ingest a food item once captured was measured by feeding the captive birds different grasshoppers and seeds (handling time: Figure 2).[12]

Knowing abundances of different grasshoppers and seeds in the environment, the functional response and handling time data can be converted into the expected time

Table 1.   The Linear Programming Model's Constraints for Cowbird Foraging

Digestive Constraint

Physiological Measures	Observed
SEEDS: $\left(\dfrac{17 \text{ hours/day}}{4.4 \text{ hours/fill}} + 1 \text{ fill/day} \right) \times 0.94 \text{ g/fill} = 4.57 \text{ g/day}$	$4.57 + 0.07$ g/day ($N = 6$)
HOPPERS: $\left(\dfrac{17 \text{ hours/day}}{0.7 \text{ hours/fill}} + 1 \text{ fill/day} \right) \times 0.94 \text{ g/fill} = 23.77 \text{ g/day}$	$24.80 + 4.13$ g/day ($N = 6$)

Based on Activity Over a 12-H Period Each Day in the Field

$$\left(\frac{1.03 \text{ g-wet/g-dry}}{3.71 \text{ fills/day}} \times \text{SEEDS g-dry} \right) + \left(\frac{2.70 \text{ g-wet/g-dry}}{17.44 \text{ fills/day}} \times \text{HOPPERS g-dry} \right) < 0.94 \text{ g/fill}$$

Feeding Time Constraint

Determinants of daily feeding time in the field
Observed feeding from 0700–1900 hours
No feeding when air temperature >30°C
Actual feeding for only 7 hours/day
Grasshoppers only available (active) for 3.23 hours/7 hours

$$(41.90 \text{ min/g-dry} \times \text{SEEDS g-dry}) + (60.27 \text{ min/g-dry} \times \text{HOPPERS g-dry}) < 420 \text{ min/day}$$

$$60.27 \text{ min/g-dry} \times \text{HOPPERS g-dry} < 194 \text{ min/day}$$

Energy Constraint

$$(5 \text{ kcal/g-dry} \times 0.61 \text{ digestibility} \times \text{SEEDS g-dry}) +$$
$$(6.3 \text{ kcal/g-dry} \times 0.78 \text{ digestibility} \times \text{HOPPERS g-dry}) > 12.6 \text{ kcal/day}$$

Note: The methods used to measure the parameters and construct the constraint equations are described in Belovsky.[12]
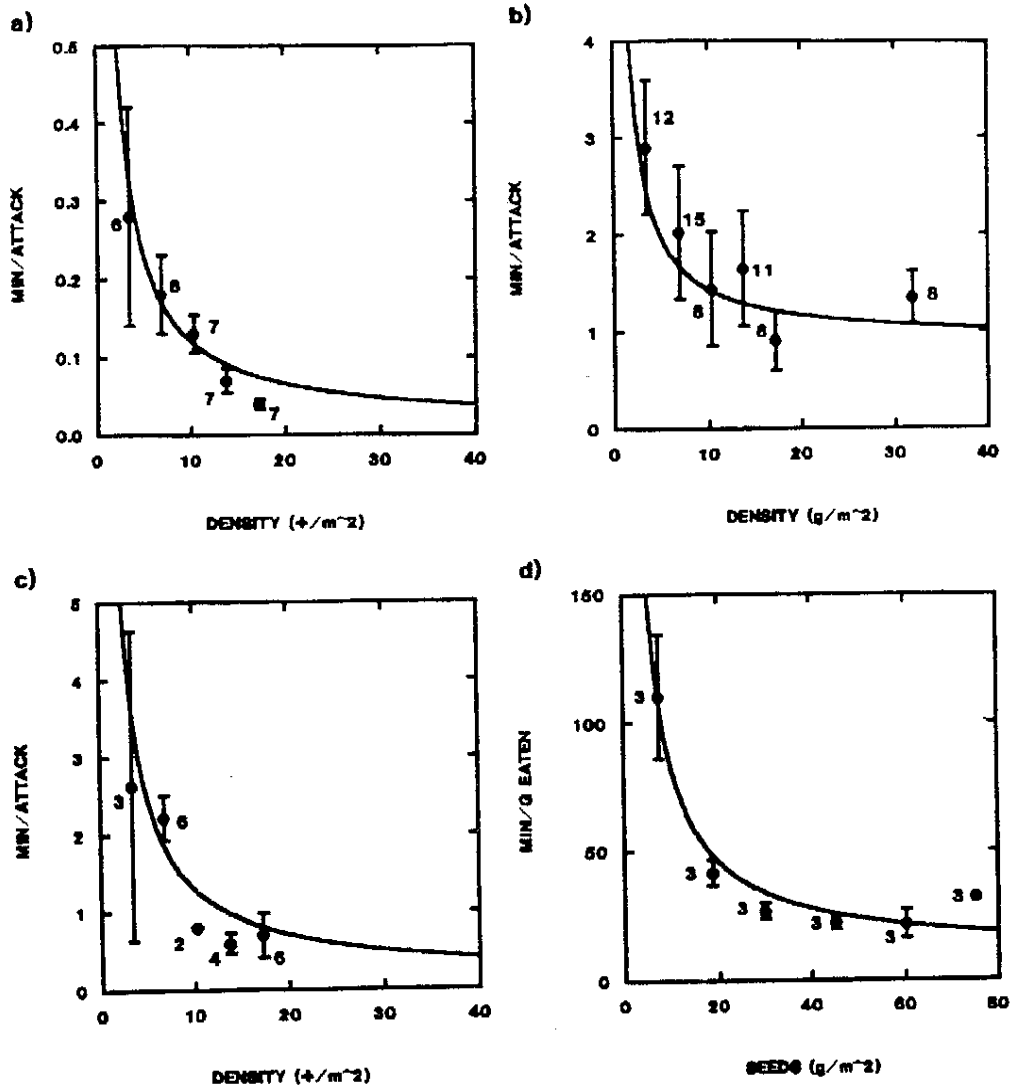
FIGURE 1. The functional response curves for cowbirds, as reported in Belovsky[12] for (a) small grasshoppers (<100 mg), (b) intermediate-sized grasshoppers (100–400 mg), (c) large grasshoppers (>400 mg), and (d) seeds. These curves represent the time between encounters with potential food items.

required to ingest a food item by a free-roaming bird. These values were computed for an average grasshopper and seed in the environment, and were used to convert the daily feeding time into potential consumption. Therefore, the feeding time constraint reflects the maximum intake of different combinations of the two foods (diets), given the cowbird's daily feeding time.

Daily Digestive Capacity

A bird's daily digestive capacity depends upon the amount of food that can be processed through its alimentary tract in a day. This quantity will be limited by the capacity of the crop, the organ in which food is stored while awaiting digestion. Crop capacity was measured as the maximum mass of grasshoppers or seeds that a captive
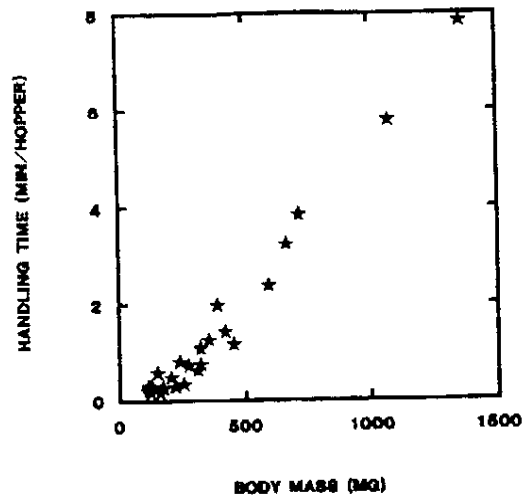
FIGURE 2. The cowbird's handling times for grasshoppers of different body sizes, as reported by Belovsky.[12] This is the time necessary to subdue and ingest a grasshopper.

bird could ingest before it becomes satiated (stopped feeding), after it has been starved for 3 hours to ensure that its crop is empty.

Different foods pass through the alimentary tract at different rates, determining how fast the crop is emptied. This passage rate was measured by feeding birds that had been starved for 3 hours, either grasshoppers or seeds that had been colored with an indigestible dye, and determining how much time was required before the dye was excreted. Dividing this passage rate into daylight hours (the time period over which feeding is distributed) and adding 1 for the bird's ability to empty the crop overnight provides an estimate of the number of times the crop can be emptied in a day for each food type.

The digestive constraint reflects the cowbird's crop capacity, and its conversion into daily ingestion of different amounts of grasshoppers and seeds (grams of dry mass per day) based upon each food's turnover and bulk (wet mass/dry mass). Therefore, this constraint, like the feeding time constraint, reflects a maximum ingestion of the two foods.

Energy Requirements

As mentioned above, a cowbird's daily energy requirements do not depend upon the provisioning of offspring because cowbirds are nest parasites. Cowbird metabolic requirements (kilocalories per day) are available in the literature,[14] as are the gross energetic values for seeds and grasshoppers (kilocalories per grams of dry mass).[15] However, gross energetic value is not as important as net value, which depends upon the bird's ability to assimilate the energy; this was measured by feeding captive birds known amounts of each food and measuring cloacal output.

The bird's energy requirements must be satisfied by the ingestion of grasshoppers and seeds, which differ in their net energy value. Therefore, this constraint defines the minimum ingestion of the two foods.

Predicting the Bird's Diet

Using the constraint equations in Table 1, the linear programming model of cowbird diet choice can be depicted graphically (Figure 3). Each constraint eliminates the con-
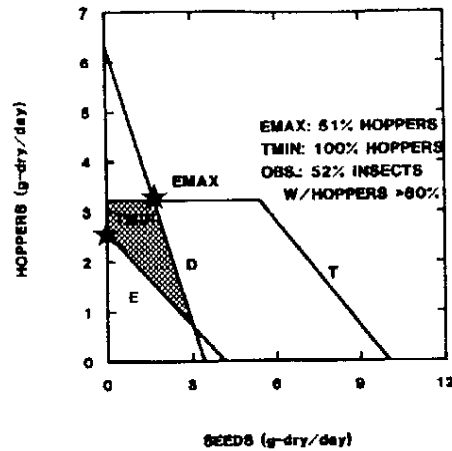
FIGURE 3. The graphic solution to the linear programming model of cowbird diet choice. Each constraint equation is labeled (see Table 1): D = digestive capacity, T = feeding time, and E = energy requirement. The cross-hatched region (feasible region) contains all diet combinations of seeds and grasshoppers that satisfy the constraints. The stars represent solutions to the energy-maximizing (EMAX) and time-minimizing (TMIN) goals. Also, the observed diet is presented, indicating that cowbirds appear to forage as energy maximizers.[12]

sumption of certain combinations of grasshoppers and seeds, and in total, the constraints define a region of diets that is feasible for the bird to consume. Using the Simplex algorithm of linear programming,[16] we know that if an optimal solution to the problem exists, it must occur at a corner of the feasible region. The corners are defined by the intersection of two constraint equations or a constraint equation and an axis. Finally, the optimal solution depends upon the goal being sought by the forager.

OFT has traditionally assumed that foragers have two dichotomous goals: feeding time minimization and nutrient maximization.[9] Feeding time minimization should occur if the forager's evolutionary fitness (survival and reproduction) increases when the forager spends less time feeding after minimum nutritional requirements are attained. This goal may be sought if the forager's fitness increases when it has more time to look for mates, care for young, or hide from predators. Nutrient maximization should occur if the forager's evolutionary fitness increases as its intake of some nutrient increases. This goal may be sought if the forager's survival and reproductive output continually increase with its nutritional status.

The solutions for the two foraging goals are presented in Figure 3, along with the cowbird's observed diet. Given observed cowbird diets, it appears that they select a nutrient-maximizing diet and, in particular, a diet that maximizes their daily energy intake in summer. Finally, the diet solutions are very robust (i.e., insensitive to parameter changes within the standard errors of the parameter estimates).

THE TOXIC IMPACTS OF A PERSISTENT PESTICIDE

The foraging model developed above provides a baseline description of this bird's position in the food chain. Because cowbirds are common inhabitants of prairie environments and consume large quantities of grasshoppers, and because grasshoppers are a frequently controlled pest in prairie environments, cowbirds could easily be impacted by a pesticide applied to control grasshoppers. How can the foraging model help assess potential impact?

Several realistic assumptions must be made to begin the analysis. First, assume that the pesticide is never applied at levels causing immediate toxic effects on the birds (i.e., acute effects are not important). This would make the pesticide's impact apparent and extreme. Second, assume that the pesticide is accumulated at greater concentrations in the grasshoppers than in seeds. This assumption is realistic because grasshoppers, as consumers of plants, may biologically amplify the pesticides that they ingest with the plants (or with the poison bait used to apply some grasshopper pesticides).

The chronic effects of a persistent pesticide can be viewed as an additional constraint added to the foraging model. This constraint will require knowledge of the amount of pesticide (or a derivative from environmental degradation) that must be accumulated in the bird before detrimental effects (i.e., reduced survival, reduced fecundity, etc.) will be observed. If different detrimental effects emerge as the accumulation of toxin increases, multiple constraints can be built into the model. However, for simplicity assume that the bird simply dies when a threshold level (T) of the toxin is accumulated (e.g., parts per million).

Accumulation of the toxin will depend upon:

1. the differential concentration (in parts per million) of the toxin in grasshoppers (L_g) and seeds (L_s),
2. the ability of the birds to degrade the toxin metabolically and excrete it (R: ppm/day), and
3. the life expectancy of a fledged bird in the absence of the toxin (E: days).

The constraint for the foraging model can be written as:

$$T/E + R \geq L_g G + L_s S \tag{2}$$

where the subscripts g and s, respectively, refer to grasshoppers and seeds. The term for life expectancy is restricted to fledged birds for several reasons. First, they feed themselves. Second, we are concerned with the population effects of the pesticide and, thus, the potentially reproductive individuals maintaining the population. Third, nestling mortality or failure to reproduce would be incorporated in a term converting food intake into nestling production.

The constraint for the persistent pesticide can be superimposed upon the foraging model (Figure 4). A conservative assumption (i.e., worst case) is that the bird will not avoid foods containing the toxic compound simply because they contain the toxin. This can be assumed because the toxin is not naturally occurring, as are plant secondary chemicals.[11] Therefore, natural selection would not have operated over time on the foragers to evolve an aversion or an ability to learn to avoid the food, and thus they will consume the contaminated foods. If the energy-maximizing diet now falls above the toxin constraint, the pesticide will exhibit a chronic effect on the birds.

The chronic effect of the pesticide will reduce life expectancy to a new level E':

$$E' = (T + R)/(L_g G + L_s S).$$

Depending upon whether T reduces reproduction or survival, the chronic effect of the pesticide could reduce population density, if the population is stationary, or population growth rate, if it is not stationary, by as much as E'/E. If both survival and reproduction are reduced, then population density or growth rate can be reduced by as much as $(E'/E)^2$.

The pesticide, however, will exhibit an effect on the foraging model in addition to its toxicity on the nontarget species. The pesticide will decrease the abundance of the pest
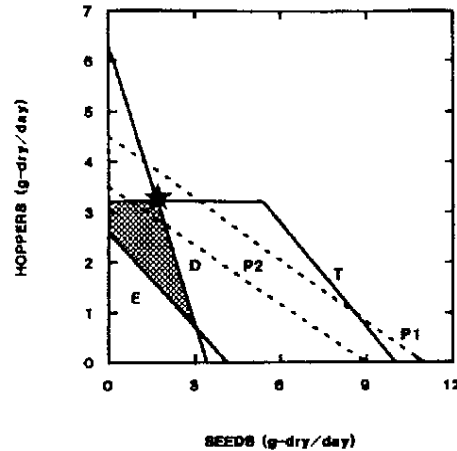
FIGURE 4.   The linear programming model of cowbird diet choice modified to include the toxic effects of a persistent pesticide in the food chain. The constraint equations and feasible region are denoted as in Figure 3, while the star only represents the energy-maximizing solution, as cowbirds appear to be energy maximizers. The toxin constraints are represented by the dashed lines, P1 and P2, and their mathematical formulation is presented in the text. In the case of P1, the toxin has no impact on the cowbird because the cowbird's diet (star) falls below the constraint. For P2, the toxin would affect the cowbird because the diet (star) falls above the constraint.

(grasshoppers). This will decrease the rate with which birds encounter grasshoppers (functional response: Figure 1), which will change the feeding time constraint in the foraging model and the energy-maximizing diet. This could change the birds' diet; i.e., the consumption of grasshoppers will remain the same or decrease. If the consumption of grasshoppers declines enough, it is possible that the effects of chronic exposure to the pesticide may not materialize. Therefore, evaluating whether the pesticide will elicit chronic effects requires specific values for the toxin constraint, the baseline foraging model, and the reduction of prey via pesticide application.

NONTOXIC IMPACT OF THE PESTICIDE

The foraging model indicates that when both grasshoppers and seeds are available, cowbirds use all of their feeding time to consume only grasshoppers. This never changes unless grasshoppers are unavailable, which explains why cowbirds are considered to be such important avian predators on grasshoppers.[13] Because of this relationship, a general solution to the cowbird's energy-maximizing diet within the feasible region (Figure 3) can be written:

$$G = T_{gs}/C_g, \text{ and}$$

$$S = (D - G \, B_g/P_g)/(B_s/P_s),$$

where T_{gs} is the daily feeding time when grasshoppers and seeds are both available, C_g is the time required to ingest grasshoppers (grams of dry mass), D is the crop capacity, P. (* stands for either g or s) is the number of times the crop can be filled each day with food, and B. is the wet mass/dry mass of food.

The above result indicates that the energy-maximizing solution for cowbirds at a site will only depend upon C_g, which in turn is dependent on the abundance of grasshoppers and distribution of grasshopper body masses. Abundance affects the functional

response (Figure 1), and grasshopper body mass affects the functional response (Figure 1) and handling time (Figure 2). Given the cowbird functional response curves (Figure 1), changes in grasshopper abundance would dramatically change the feeding time constraint when grasshopper densities are below $10/m^2$, because the time to encounter a grasshopper increases dramatically when grasshopper densities fall below this value. When intermediate sizes of grasshoppers (100 to 400 mg) are abundant, the encounter rate declines even more, because these grasshoppers appear to be better able to avoid birds (Figure 1).[12]

In prairie environments, grasshoppers are considered pests when their total densities exceed $9.6/m^2$;[17] densities in the cowbird functional responses are expressed per square meter of vegetation, which would make the defined pest density approximately $16/m^2$ after bare ground is eliminated. A successful treatment with grasshopper pesticides at the usual application levels can reduce grasshopper densities by 70 to 90% with spray-applied pesticides (e.g., malathion), and 30 to 50% with bait-applied pesticides (e.g., carbaryl).[17] Therefore, when grasshopper densities are less than $50/m^2$ of vegetation and spray pesticides are applied, or less than $17/m^2$ of vegetation and bait pesticides are applied, the birds' intake of grasshoppers will decrease. This means that spray pesticides will generally impact the birds' diet selection, while bait pesticides will not.

To complicate the effects of pesticides on bird diets further, different pesticides and application methods differentially impact grasshopper species. This differential effect on grasshopper species may be related to body mass and taxon, which also influence a bird's ability to capture grasshoppers.[18] It appears that the grasshoppers more easily captured by birds (small and large body mass, and Oedopodinae)[18] may be further reduced by pesticides.[17]

Because cowbirds are energy maximizers prior to pesticide application, any reduction in their consumption of grasshoppers will result in the average bird ingesting less energy. Animals tend to be energy maximizers when their survival or reproductive success or both depend upon nutritional intake. Thus, pesticide-induced dietary changes should reduce survival and/or reproduction for the birds. This will ultimately reduce the population density of the birds. Given the foraging model, each gram of dry mass decrease in grasshopper consumption will reduce the bird's daily energy intake by nearly 14% (3.22 kcal/day).

The baseline model was constructed for an observed grasshopper density of $18.6/m^2$ of vegetation, slightly above the USDA/APHIS (Animal and Plant Health Inspection Service) definition of pest levels. Assume that cowbirds do not substitute other arthropod prey for grasshoppers when pesticides reduce grasshopper densities, or the pesticide indiscriminately reduces all arthropod prey for the bird, which is likely. The application of a spray pesticide would reduce the cowbird's energy intake above maintenance by 74%, and the bait pesticide would reduce surplus energy by 39%. It is this surplus energy that should be related to cowbird reproductive output and survival over the winter and hence population density. If surplus energy is monotonically related to survival and reproduction, these declines in energy intake could have dramatic effects on the bird population.

Birds that are feeding time minimizers also may experience reduction in survival and reproduction via pesticide application. This would occur if more time is required to acquire a minimum intake of grasshoppers, and feeding increases vulnerability to predators and leaves less time for care of young. If cowbirds were feeding time minimizers, the application of a spray pesticide would increase feeding time by only 19% above baseline, while grasshopper densities decline by 80%. Therefore, the baseline foraging model indicates that there would be less effect on feeding time minimizers.

Data comparing bird populations in areas treated with grasshopper pesticides and

nontreated controls[19] provide some indication that bird populations decline in the treated areas. However, whether the population decline reflects the death and reproductive failure of birds from either exposure to the pesticide or reduction in food, or their movement to areas where grasshopper densities are higher, cannot be ascertained. Also, the controls are not necessarily comparable to the treated areas (i.e., areas with grasshoppers at pest densities are treated, while the control areas never had pest densities).

If the bird encounters toxic effects of the pesticide, even at the reduced prey densities, the new relative population density or growth rate might be as low as $(E'/E)^2(1 - M)$, where M is the reduction in energy intake due to pesticide application. This portrays a worse-case scenario, assuming the pesticide effects are linearly related to survival and reproduction. However, this estimate would at least provide an *a priori* limit to expected occurrence with pesticide application. A better understanding of how reductions in food intake affect survival and reproduction, and how changes in survival and reproduction in turn affect population growth rate or density or both, would lead to more accurate estimation of the pesticide effects.

USING THE FORAGING MODEL FOR INTEGRATED PEST MANAGEMENT

The above analysis indicates how the foraging model can be used to address the impact of pesticide use on a nontarget species. The first avenue is through chronic exposure to toxic effects of a persistent pesticide that is transmitted through the food chain and accumulated by the nontarget species. The second way is through the reduction via pesticide of the pest that is a food resource for the nontarget species. One can argue that neither of these effects is environmentally acceptable. Nonetheless, the control of pests at times may be economically and politically mandated, and pesticides are often the most effective means of control. However, pesticide use may be moderated by the use of integrated pest management; pesticide use might actually increase the effectiveness of the avian predator as a control agent. The cowbird-grasshopper example developed above may illustrate how this can be envisioned.

Using the cowbird functional response curves (Figure 1), the foraging model for cowbirds can be solved for different hypothetical distributions of grasshopper abundances and body sizes. These solutions show ways in which the model can be used to predict how the bird's diet changes in different environments by varying the feeding time constraint.

For pest management, diet changes themselves are not critical; rather, it is the number of grasshoppers consumed per day relative to grasshopper abundance. Even without knowing the area covered by the bird in its foraging, or bird density, the ratio of grasshoppers consumed per bird to grasshopper abundance will indicate the environmental conditions (grasshopper abundance and relative abundance of body sizes) in which each bird will have the greatest predatory impact (Figure 5a). An individual bird has the greatest impact at low grasshopper densities and when grasshoppers of small body size are relatively the most abundant.

The predatory impact of an individual bird in different environments (functional response) is not the sole determinant of the impact on the pest; predator density is also important (numerical response). Assume that energy intake above metabolic requirements limits the bird's reproductive success and survival, which limits population density. This is likely for cowbirds, because as with domestic chickens, they continuously lay eggs as long as their nutritional level is above a minimum.[20] The same assumption may be valid for bird species that are not nest parasites, as survival of their young may
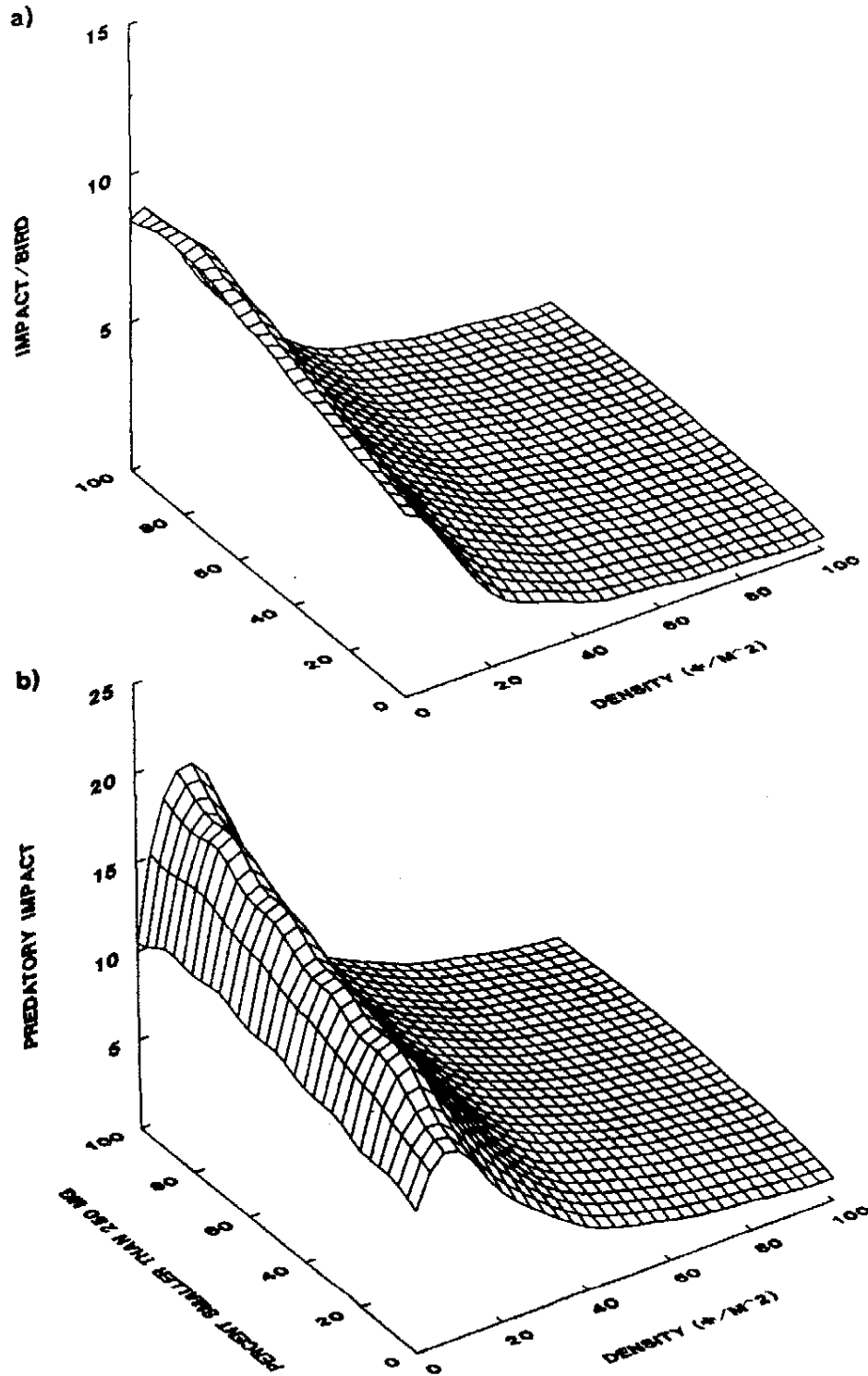
a)

b)

FIGURE 5. The linear programming model of cowbird diet choice used to estimate the predatory impact of the bird on grasshoppers at different densities and with different relative abundances of body sizes: (a) the impact of an individual bird, and (b) the impact of the entire population at different grasshopper abundances. The values of predatory impact are indices (see text) that reflect relative values at different grasshopper abundances. Therefore, the graphs only indicate under what conditions the birds will have the greatest predatory impact.

be a function of the parents' ability to provide food to the young. Therefore, the numerical response is proportional to energy intake above requirements, and this can be computed for different environments (grasshopper abundances and relative abundances of body sizes) using the foraging model.

The product of the functional and numerical response provides the overall predatory impact of the bird. Assuming that the grasshoppers eaten relative to their abundance is proportional to the functional response, and energy intake above requirements is proportional to the numerical response, one can compute the predatory impact from the foraging model, as presented in Figure 5b. The bird would have the greatest potential impact on grasshoppers at moderate densities ($5/m^2$ of vegetation) and when the grasshoppers are represented by species of small body size. Therefore, birds are unlikely to reduce grasshoppers at pest levels ($16/m^2$ of vegetation), and when the grasshoppers are dominated by large species. Furthermore, as grasshopper densities increase, the predatory impact of birds rapidly becomes negligible.

While birds may not reduce grasshoppers from outbreak levels, they may be able to prevent them from achieving outbreak densities. This would occur in environments in which the grasshoppers generally are at densities near the level at which birds could have a large predatory impact (low to moderate densities), and the conditions that permit the grasshoppers to exceed these densities and achieve pest status occur infrequently.

More importantly, birds may be used in an integrated pest management plan. This might be useful for regions where grasshoppers frequently achieve densities greater than those where birds have an appreciable predatory impact and the rate at which grasshoppers are able to increase is high. Here, the application of pesticides or other control agents (e.g., fungal pathogens) could be used to reduce the grasshopper densities to levels at which birds have a potential predatory impact. In this way, further reduction of the grasshoppers and retardation of their return to outbreak densities could be achieved by the birds. Integrating bird predation with the application of control agents would reduce the level and frequency of application, which would reduce the deleterious environmental impact from pesticides as well as costs.

Because predator effectiveness depends upon functional and numerical responses, the analysis presented in Figure 5b will not be adequate to develop an integrated pest management plan, if the plan uses a pesticide that is persistent in the food chain and causes chronic toxic effects on the bird. In this case, the pesticide's chronic effect could reduce the bird's numerical response and predatory impact on the pest by as much as $(E'/E)^2$. Therefore, Figure 5b must be recomputed with the toxin constraint included in the foraging model and its effect on population dynamics incorporated. The bird's reduced numerical response might negate the use of integrated pest management or require a reduced use of pesticide; the option chosen will depend upon the effectiveness of pesticides and avian predation, economic costs, and environmental hazards.

The foraging model illustrates for pest control that the ability of birds to limit grasshopper densities depends upon initial grasshopper densities, the relative abundance of grasshoppers of different body sizes, and the ability of grasshopper populations to increase. This is evident from studies of the impact of avian predation on grasshoppers that illustrate the presence of predatory impact,[19,21] and the absence of impact.[18,22] Therefore, one should not expect a single statement about the ability to use birds as a control agent for grasshoppers (e.g., birds limit grasshopper densities). Rather, the potential to use birds, and how to use them in an integrated fashion with other control measures, will vary between environments.

CONCLUSION

Optimal foraging models, such as the one developed here for a cowbird, using the mathematical technique of linear programming, may provide useful insights into understanding the potential impacts of pesticides on birds and how birds may be integrated into pest control programs. Evident from the analysis presented here, the models do not provide answers in the absence of detailed biological data. However, they aid in defining the critical elements of information that need to be supplied. Given the model and parameter values, projections can be made to assess the impact of pesticide application: toxic effects of persistent pesticides that are amplified in the food chain and their effect on the bird through reduction of potential prey. Finally, the model can be used to define the environmental conditions under which the bird may be built into an integrated control program for pests, thereby reducing the use of costly and potentially environmentally hazardous pesticides.

ACKNOWLEDGMENTS

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