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REDWINGED BLACKBIRD FLOCK FEEDING BEHAVIOR IN RESPONSE TO REPELLENT STRESS

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The use of 4-Aminopyridine (Avitrol, a Phillips Petroleum trade-name, or AFCC 99, a name designated by Environmental Protection Agency) as an avian repellent when placed on agricultural crops has been reported upon (DeGrazio, et al., 1971, 1972; Stickley, et al., 1972, 1976); and its status in the United States and elsewhere has been recently reviewed (Bessek, 1976). Much more information has been collected; but unfortunately, it has not been made accessible in published form (see Besser, 1976). Thus, much of the information and opinions about this repellent material is anecdotal, and the scientific community must rely upon relatively sparse information in determining its overall efficacy. For this reason it is not altogether clear whether this "repellent" material and other such chemical compounds are useful in either ecological or economic senses, and much must be cleared up before such a control or management paradigm can be made creditable for either a scientific or a user audience.

The main problem is that published reports to date appear to be highly selected to put this work in its best possible light, and critical tests of the employment of avian repellents in agricultural ecosystems per se are lacking. We (the public) have been provided with "demonstrations" of efficacy in bird-corn crop associations, with broadly stated extrapolations to other crops; but there is not clear scientific evidence about whether this approach, let alone this particular chemical compound, is effective and how it relates to sound management practices of wildlife-oriented problems in agricultural ecosystems. For instance, Besser (1976) cited several unpublished reports supporting his case for continued or increased usage of 4-Aminopyridine and drew conclusions upon inference about why "conclusive data . . ." and anticipated protection were not achieved in two states. It was because "... of low bird pressure." Such statements cannot be accepted in attempting to present a case for or against the use of a management tool, simply because the reader is led to believe that scientific objectivity is lacking in the overall program.

In the above case one is led to wonder why we should worry about repellent stress being used at all when there were insufficient numbers of birds to make the control technique useful. Further, there is clearly a major difference of opinion emerging from the files of the researchers in the U.S. Fish and Wildlife Service that have worked with this strategy of management. Ingram (1976) pointed out how improper design of field work can be misinterpreted or misused in assessing perturbation treatments in ecosystems (the use of 4-Aminopyridine is a systems perturbation in the sense of Barrett, et al., 1976). Without such rigor in field programs, work of the nature discussed by Besser (1976) simply becomes a demonstration of what happened at that location at that time and can in no way help produce models to help predict what might be expected under extrapolation to new situations. This difference of opinion is further demonstrated by comparing the reports of testing of 4-Aminopyridine by Dolbeer, et al. (1976) in Ohio, Maryland, and New York with the statements of Besser (1976) and earlier demonstrations of effects in field corn reported by DeGrazio, et al. (1972). Thus, there is confusion about the use of this one material, at least as a repellent; and several facets that have not yet emerged must be examined in order to clarify the use of repellents or of 4-Aminopyridine.

It is patently obvious that several scientific steps in determining the use of this technique have either been overlooked or have gone unreported. This paper is then an initial step to deal with principles of decision making processes through testing of hypotheses formulated in a hierarchical fashion. It is through this series of relationships, or ones similar, that the proper questions can be asked of the nature of avian repellents in agricultural ecosystems.

Hierarchy of Hypotheses Related to Avian Repellents

The first criteria to be regarded are those related to function of repellents in some scheme of organization that forms a hierarchy. The scheme that should be considered follows those proposed by Rowe (1961) and DeWit (1970), both of whom have summarized concepts published by many others. One of the most important concepts to consider is that of von Bertalanffy (1950): "Reality, in the modern conception, appears as a tremendous hierarchical order of organized entities, leading in a super-position of many levels, from physical

and chemical to biological and sociological systems." Rowe (1961) and DeWit (1970) discussed levels of organization for biological systems, each expressing slightly differing positions of levels within the hierarchy. Importantly for this discussion, DeWit stated that in order to specify and discuss models of systems that represent behavior of the system at a given level, information must be conceptualized from testing of hypotheses from elements of the next lower level in the hierarchy. For dealing with reactions of birds to repellents placed in the ecosystem to keep them from food supplies, we must at the very least structure our analyses to obtain information in the following manner.

1. Organ physiology when perturbed by repellent chemicals, such as 4-Aminopyridine.
2. Behavior of the individual when subjected to a repellent.
3. Behavior of social units, up to and including populations.
4. Biological reactions in the biotic community.
5. Biological reactions and sociological outcomes in the local ecosystem (Rowe, 1961).
6. Biological reactions and sociological outcomes in the regional ecosystem (Rowe, 1961).

Other levels of organization higher than (6) are possible but of little consequence to this problem. In order to examine relationships within this hierarchical order it is necessary to pose a series of hypotheses, which, when studied at the appropriate level, will allow anyone interested in the subject to make objective decisions about the outcome of a repellent stress applied to avian feeding problems. The hypotheses in Table 1 present an attempt in this light. The hypotheses are posed in a null form so that if at any step in the hierarchy a hypothesis is accepted, there is reason to consider that the repellent treatment effect is not valid.

The main hypothesis, H_0 , has been addressed and answered in a satisfactory manner; birds do show the capability of responding to repellent stress placed on food supplies (see Rogers, 1974). H_1 and H_2 were addressed in early publications about 4-Aminopyridine and 4-nitropyridine-N-oxide (Goodhue and Baumgartner, 1965), and it was conclusively shown that application of these compounds disturbed both individuals and nearby social units. The level of social disturbance is noteworthy. Goodhue and Baumgartner (1965) reported that other birds within visual or auditory contact of the affected bird often reacted by vacating the area, thus the repellent nature of 4-Aminopyridine and 4-nitropyridine-N-oxide is dependent upon indirect effects to the chemically-unaffected individual through social communication. The effect was considered a "breakthrough" and elicited considerable research in U.S. Fish and Wildlife Service laboratories, with the first major report of crop repellent function by DeGrazio, et al. (1971) and follow-ups of similar work by DeGrazio, et al. (1972), Stickley, et al. (1972, 1976). Unfortunately this work skipped several levels within the hierarchical arrangement. Hypotheses 3, 3a,b,c were ignored; several of the studies regarded H_4 components to a limited degree, but most focused on H_5 in my arrangement. Thus, the major jump from analyzing components dealing with individuals to those dealing with ecosystems violates the precepts of several authorities cited earlier, but mainly that of DeWit (1970).

The remainder of this paper examines information about the use of 4-Aminopyridine to test hypotheses dealing with individual, population, and community responses (H_2 , H_3 , H_4) that have not been addressed before. From these tests come new assessments about the potential use of an avian repellent to protect crops.

METHODS AND MATERIALS

A 12-ha (ca. 30 acre) field of corn belonging to Bradley Farms located near the mouth of the Thames River, Kent County, Ontario was used for the experiment examining a "point" spatial location. Nine equal-sized plots were marked out in a 3 x 3 grid (Fig. 1); three of the plots (those along the diagonal) were treated with baits containing 3% 4-Aminopyridine (by weight) mixed 1:100 with normal cracked corn screened to sizes 6 and 7 by Tyler's scale. Approximately 2 kg ha⁻¹ were used at weekly intervals from August 5, 1966 to August 26, 1966, a period during which the corn ears were quite susceptible to Redwinged Blackbird (*agelaius phoeniceus*) damage. A small rotary spreader mounted on wheels was pushed by hand through the field on an every-other-row basis in the three treated plots.

Bird feeding incidence and amount eaten on corn ears was measured before the start of treatments, then once every week for four weeks thereafter until the birds no longer fed in the field (after corn hardens, Redwings no longer are able to feed efficiently on the ears). Ten ears from five randomly selected plots were examined for feeding incidence, and estimates of the amount of grain eaten were made for each ear. Estimates of bird feeding levels on damaged ears were taken using the method of DeGrazio, et al. (1969) and Dyer (1967) by simply measuring the amount of corn removed from the tips of the ears. Estimates of corn loss owing to the feeding activity were obtained using empirical tables reported by DeGrazio, et al. (1969), as updated by Cutright (1973).

After the corn ears had matured, 10 ears from 10 locations in each plot (900 ears) were collected and taken to the University of Guelph for dry weight determination; total ear weights of damaged and undamaged classes were obtained. Subsequent statistical tests were conducted at Colorado State University.

A nested or hierarchical analysis of variance (ANOVA) (Snedecor and Cochran, 1967) was used to determine feeding levels for between treatment means (application of 4-Aminopyridine versus control), plots within treatments, replicates within plots using as parameters: 1) feeding incidence, 2) length of ear fed upon, 3) gross weight of the corn ear, and 4) gross weight plus estimated weight loss owing to bird feeding activity for damaged classes (Table 2). The basic model is $X_{ijk} = \mu + A_i + B_{ij} + \epsilon_{ijk}$, $i=1\dots a$, $j=1\dots b$, $k=1\dots n$, where A refers to treatment type and B is plot (Snedecor and Cochran, 1967:287). The ANOVA was used to test whether feeding intensity was uniform throughout the field. Regression techniques were used to report feeding rates in time throughout the experiment, and the amount of food removed per ear compared to the feeding incidence following the model suggested by Hayne (1946) and Dyer (1967).

The second set of data comes from an experiment conducted in Ohio in 1969 (Stickley, et al., 1976). Two study sites of 373 km² each constituting control and treatment areas were selected in which all field corn which could possibly be was studied. In the treatment area 4-Aminopyridine on corn baits was applied by aircraft at the rate of 3.5 kg ha⁻¹ to approximately 40% of each treated field. The dosage of 4-Aminopyridine was 3% by weight on cracked corn, which was then mixed at the rate of 1 part treated particles to 99 untreated. Several treatments were applied during the later summer period (see Stickley, et al. for further details). Data on feeding incidence and the amount of corn eaten per ear in row centimeters (Stickley, et al., 1976) were obtained, plotted, and analyzed for 57 control area fields, 57 treated fields in the treated area, and 33 untreated fields in the treated area. Regression analyses and tests of slopes of feeding rates in each of the three subject areas were computed. (Feeding rates are taken as the slope of the amount of food consumed per ear plotted against the incidence of feeding in each field location; the rate implies time-specific conditions which are a function of the numbers of birds feeding in a field during the 2- to 3-week period during which damage can occur.)

RESULTS

Ontario Field Plots

Feeding incidence in field. Feeding incidence, sampled during five periods, is shown as proportions of total ears damaged in each of the study plots (Table 3). (The field was sampled as a whole prior to the first 4-Aminopyridine bait treatment; thus there are no values for each replicate in each plot for either incidence or amount eaten, Tables 3, 4.) Summaries of all damage parameters in the control and 4-Aminopyridine plots are shown in Table 5. Feeding incidence progressed exponentially during the 5-week study period: the regression for the treated plots was $Y = 3.611 e^{0.105X}$, $r^2 = 0.791$; and for the control plots was $Y = 2.349 e^{0.121X}$, $r^2 = 0.628$; where Y = incidence of damage and X = time in days of experiment. Note that the slope for the treated plots was slightly lower than for the control, but the difference is not statistically significant ($F < 1.0$).

A simple way to test whether there were differences in the feeding incidence among the two treatments is to construct a 2 x 2 contingency table and determine the probability of damage proportions in each case (Table 6). X^2 for this determination is 0.69, a value that occurs with a probability = 0.447; thus there were no differences between the two treatments.

Amount of corn eaten. The amount of corn eaten per damaged ear in each of the two treatments, as estimated during the five sampling periods, is shown in Table 4. As noted for the incidence of damage, there are no differences for the length of damage on each ear and the estimated weight damaged between the two treatments, control, and 4-Aminopyridine treated plots ($F < 1.0$, Tables 7,8). The amount estimated eaten per day, according to a regression model, was $Y = 3.803 e^{0.078X}$, $r^2 = 0.801$ for the control plots; and $Y = 3.747 e^{0.077X}$, $r^2 = 0.821$; where Y = estimates of amounts eaten in grams and X = days of experiment.

Conversions have been made from the biomass data to determine the percentage of corn eaten from the damaged ears. (No estimates have been made of the percentage of the total crop consumed at each sampling period, because it was not possible to sample production levels in the maturing ears (Table 4).) Regressions in time show the following relationships: $Y = 1.924 e^{0.076X}$, $r^2 = 0.730$ for the control plots; and $Y = 1.940 e^{0.072X}$, $r^2 = 0.763$ for the 4-Aminopyridine treated plots; where Y = percent of each ear lost for damaged ears and X = days of experiment.

The relationship between the amount eaten on damaged ears plotted against incidence of feeding for each of the treatments has been estimated using two sources of data: 1) the estimates derived from the samples taken in time throughout the experiment, and 2) estimates

from the plots taken at harvest time when both the estimates of amount eaten and corn ear production values were measured. The regression relationships for the time series are: $Y = 2.549 e^{0.029x}$, $r^2 = 0.761$ for the control plots; and $Y = 2.421 e^{0.029x}$, $r^2 = 0.809$ for the 4-Aminopyridine treated plots. The harvest data show slightly different regressions. For the control plots $Y = 1.095 e^{0.030x}$, $r^2 = 0.762$; and for the 4-Aminopyridine treated plots, $Y = 1.003 e^{0.032x}$, $r^2 = 0.738$ where $Y =$ percent of total grain on damaged ears eaten by the birds and $X =$ Incidence of damage in percent. All of the above regressions show significant relationships ($P < 0.05$), but in neither case are either the slopes or intercepts between the 4-Aminopyridine and control plots different ($P > 0.1$).

Results of factorial analysis of variance. ANOVA results are presented for measurements of total damaged length (Table 7), for total estimated damage weight (Table 8), for total length of ears in undamaged and damaged classes (Table 9), for gross harvest weight of undamaged and damaged classes (Table 10), and for gross harvest weight plus estimated amount of corn removed by birds from ear (Table 11). ANOVA plus interactions are shown for the last three parameters (Tables 9, 10, and 11).

There were no differences in the length of damage nor of the amount eaten between the 4-Aminopyridine-treated and control plots (Tables 7 and 8). However, there were differences between the plots within each of the two treatments, especially for the estimated amount eaten (Table 7). Some differences also existed between replicates within the plots (Table 7 and 8).

There were no differences for total length of ears, gross weight, and gross weight plus estimated weight eaten by the birds between the 4-Aminopyridine treated and control plots or among plots within treatments (Tables 9, 10, and 11). However, differences did show up among replicates. The main feature for these three parameters is the interaction among damaged and undamaged categories (Tables 8, 9, and 10). There were no interactions between damage and treatment for damage \times plot \times treatment, but there were two isolated interactions among replicates for length and gross harvest plus estimated amount eaten within one of the treated plots (Tables 9 and 11).

The interaction among factors of the two treatments and the damaged or undamaged categories for total length of ear and gross harvest weight are shown in Fig. 2. Ear length was uniformly greater for the 4-Aminopyridine treated than for the control plots, and was much greater for the damaged class compared to the undamaged class as reported previously (Dyer 1975). Gross harvest weight showed much the same picture; corn ears weighed more in the 4-Aminopyridine treated plots compared to the controls and were much heavier in the damaged class compared to the undamaged (Fig. 2), an important parameter also reported previously (Dyer, 1975).

Bird feeding patterns in treated and control areas. An assessment of the patterns in which the birds fed in the two treatments during the experiments is given in Table 12. For this analysis, damage incidence was taken at the time of harvest. Testing the damage-undamaged results in a X^2 contingency table, $X^2 = 45.18$, 11 d.f. ($p < 0.005$) for the control plots; $X^2 = 18.44$, 5 d.f., ($p < 0.005$) for the 4-Aminopyridine treated plots; and for the entire field, $X^2 = 64.15$, 17 d.f. ($p < 0.005$).

A second assessment of feeding patterns has been obtained from the ANOVA Information by using Tukey's "Q" test to determine which of the 9 plots in the field were most alike. Mean corn ear length plus length of damage data have been used for this determination. The results are shown in Fig. 3; plots that showed affinities are shaded the same. For the 4-Aminopyridine-treated plots, number 1 was isolated, and plots 5 and 9 grouped together; for the control, plots 2 and 3 grouped in one unit, while plots 4, 6, 7 and 8 formed another unit.

Assessment of feeding rate patterns: Ontario and Ohio. The feeding rates, i.e., a comparison of the amount of corn eaten from each ear compared to the incidence of feeding in each field, are presented in Fig. 4. The 1966 Ontario treated and control plot data from one field and the 1969 Ohio regional data comparing treated and untreated fields in a treatment area and control area fields show remarkable consistency in overall feeding rates. There was little difference between the repellent-treated plot feeding rates and those in the control plots for the 1966 Ontario field plots. Further, there was no statistical difference ($p > 0.10$) in feeding rates between the control or treated fields in the 1969 Ohio regional study. However, the feeding rates in the untreated fields within the treated area were significantly higher than either the control or treated fields ($p < 0.05$, using a pair-wise t-test of the slopes (B) of the three sets of data). The intercepts of the 1969 Ohio data were virtually identical and not significantly different.

DISCUSSION

The Redwinged Blackbird association with ripening corn in various parts of the corn belt is extremely topical and important. For several decades the Redwing has been defined as an agricultural pest because of the fact this species invades field and sweet corn fields and consumes what has been estimated to be large quantities of food destined for human or livestock consumption (Stone, et al., 1972).

As a result of being classified an agricultural pest, there have been intensive field and laboratory research and management programs carried out for many years by the U.S. Fish and Wildlife Service, as well as sporadic research and management programs in Ohio, New York, Delaware, New Jersey, and perhaps others to some degree, as well as work carried out by the Provinces of Ontario and Quebec and the Canadian Wildlife Service in Canada. Also, as a spin-off of the blackbird management, work has been carried out by U.S. AID abroad on several granivorous bird species. All of this adds up to a large time and monetary expenditure within the past decade and a half. Dollar values are not readily available, but total program costs could easily approach one million dollars a year in research and development (R & D) alone. These values are significant, for much of the work has gone into the development of repellents; and it is necessary to examine a benefit/cost (B/C) relationship to see whether such work ought to be continued in the future. U.S. Fish and Wildlife Service reports about the efficacy of repellents suggest that the B/C ratios are greater than 1 (the break-even point) (DeGrazio, et al., 1971; Stickley, et al., 1976), but the question must be asked, is this really true? Data presented in this paper cast doubt on that assumption.

The second reason that the Redwing-corn association is so important is because of inherent biological relationships about flocking feeding that are little understood. Since Redwings in many areas rely heavily upon corn in their diet during the summer (Hintz and Dyer, 1970) and since there is an excellent record of their feeding upon the corn ear and in plots and fields throughout a region (Hayne, 1946; Dyer, 1967), there is a unique opportunity available to study flock feeding patterns, a study little understood nor exploited to date with the exception of reports on Desert Finches (Cody, 1971), Waders (Goss-Custard, pers. comm.), and a few neotropical bird species (Moynihan, 1962). Thus I want to call attention to these two aspects dealing with Redwings in order to facilitate needed work in the field by capable researchers.

Does repellency work in avian populations feeding upon agricultural crops? The reports by DeGrazio, et al. (1971, 1972), Besser (1976), Stickley, et al. (1972, 1976) present both glowing accounts of the efficacy of repellents, specifically 4-Artnopyridine, and cautions about its use in agricultural ecosystems. Dolbeer, et al. (1976) and Ingram (1976) go farther and report either no efficacy or misuses of field data used to determine efficacy. Clearly, under these circumstances, the question of a favorable B/C ratio would be in doubt. What then is the potential for repellents?

In a manner of speaking, repellents are known in nature for many animal-plant associations. These mainly involve plant-insect interactions concerning the evolution of anti-herbivore defenses in plants and the strategies that insects evolve to cope with these defenses (Gilbert and Raven, 1975). Thus, "repellents" to natural herbivory are well known in nature and have important function in co-evolution of both the plant and the herbivore. However, there is an important distinction to make between nature and agriculture as far as repellents are concerned. In nature "repellents" cannot develop unless there is adaptation and a selection pressure favoring plants with certain secondary compounds, which means there must be a degree of herbivory. On the other hand, agriculture's attempts to develop the "perfect" repellent assume there will be zero feeding as a result of the repellent treatment, a level that probably cannot be achieved, since few if any such repellent perturbations result in an animal starving to death in front of a potential food supply. It is possible to construct tests of these conditions in laboratory experiments using noxious materials (Rogers, 1974), but there is considerable doubt about being able to do this in either agricultural or natural systems. It is conceivable that "pre-adaptation" involving random associations of plants and animals could provide for efficient repellency when those combinations come together; but the event is unlikely, and I cannot develop arguments for or against this potential here.

What then is the pertinent evidence available from this study to apply to the question of repellency? In the review I stated the argument that, since this is an ecosystem level problem, then in order to understand the overall consequences there must be several levels of inputs in the form of a set of hypotheses in hierarchical order to consider. If at any point in the testing of such hypotheses certain premises are rejected or violated, then there is doubt about the overall effects of the series of tests being made.

In order to understand the question of avian repellents in ecosystems then, I have chosen to integrate and restate the hypotheses as shown in Fig. 5. According to this scheme, if a repellent is to be efficacious, any of three possibilities will allow a favorable outcome. For this analysis there are three important axes: (1) events in time, (2) the incidence of feeding in time and space, and (3) the amount eaten per feeding bout in time and space. The dependent scale of amount eaten is set in terms of "one unit of consumption."

The theoretical function is this. If a repellent stress and the animal have a historical association, either in evolutionary time in terms of the behavioral repertoire within the species, or in terms of individual behavior within recent time as a result of previous experience, a repellent-treated resource will not be touched if the repellent has a high degree of efficacy (H_1 , Fig. 5). But if repellency is less than perfect, then birds will tend to feed at some locations where the resource is distributed; and in a statistical sense this feeding level will be at unity in terms of the time and feeding incidence axes (H_2 , Fig. 5). However, it might be that the avian population is large in size and that there will not be a level of unity in feeding incidence; rather there will be a linear increase in the feeding rate in space and time. Thus H_3 (Fig. 5) is a consequence. Notice that at each subsequent level in the three hypotheses there is less and less efficacy of the repellent. The important feature finally is that the amount being consumed will be drastically affected, and the sought-after outcome is a saving of the resource to which the repellent is applied. With significant savings made from the standpoint of the amount being consumed, then the repellent can be judged to be truly efficacious.

What is the interpretation of the results stemming from experiments introduced in this paper? The 1966 Ontario within-field result summarized in Fig. 6 and the results of the feeding rates shown in Fig. 4 predict what will occur in local or regional ecosystems.

Hypothesis 1 (Fig. 5) is rejected because it is apparent that birds fed within the treated field. Thus, it is plain to see there was little or no evolutionary or individual experience having to do with this type of repellent that precluded the birds from the field.

Hypothesis 2 (Fig. 5) is rejected because the Redwings did not confine their feeding incidence to unity in either the control (open circles, dashed line) or the treated (open triangles, solid line) plots within the field (Fig. 6).

Hypothesis 3 (Fig. 5) is rejected for two reasons. First of all, there was not a linear increase in the incidence of feeding in time and space (the increase follows the predictions of Hayne (1946) and Dyer (1967)). Secondly the amount of consumption increased throughout the entire experiment. Furthermore, there was virtually no difference in the amounts being eaten in the treated (closed triangles, solid line) and the control (closed circles, dashed lines) plots (Fig. 6, see ANOVA results, Tables 7-11). Thus, there is ample evidence that within this field, the repellent failed to meet objectives spelled out for it.

As exists in nearly all studies of its type, it is extremely difficult to extrapolate such information to the level of an ecosystem. However, a connection exists. The feeding rates become important, because it is this process that dictates the final level of depredation that is commonly analyzed after the fact within an ecosystem. Stated differently, without the increasing levels of the independent effect of damage incidence and the dependent effect of the amount eaten per unit of damage incidence, there is no depredation. Thus, it makes as much sense to study these effects as it does to attempt to measure the amount of corn Redwings eat within each field. One of the main reasons it makes sense to concentrate upon studies of the process rather than the effects of the process is that estimates of depredation stemming from field surveys have little reliability. Intensive estimates reported by Stone, et al. (1972) show standard deviation values larger than the mean; thus the confidence in these values is very low. But, if we can accept a biological process, such as the relationship between amount eaten and incidence of damage, for which there is good information in the literature (Hayne, 1946; Dyer, 1967) and in this report, then it is possible to predict what may happen in a region or ecosystem.

From a statistical standpoint, the "goodness of fit" values obtained from the 1966 Ontario plots and the 1969 Ohio fields are sufficient to place a considerable amount of confidence in this approach (see Fig. 4). In short, the regression values all fall within very close proximity to one another, and from that a strong tie can be made from the field plots to the regional picture. The interpretation is this. At the outset of the feeding process, i.e., when a flock of Redwings enters a field or a region, the amount of corn available for food is essentially infinitely large. The birds, upon the encounter of a repellent stress, can simply move to another locality to feed. If the new location is untreated, they can feed with impunity until the resource is exhausted; or if it is treated, they can move to another, and another, and so on. As the birds continuously "sample" the resource, they automatically increase the incidence of feeding in the field or region. But,

as they do so, according to the predictions made by Hayne (1946) and Dyer (1967), they increase the total amount of consumption under normal conditions. The choice facing the birds in the treated areas is to feed on the treated resource, or move out. Apparently many move out, witness the curve shown for the untreated fields in the treatment area in the Ohio experiment (Fig. 4) and the analysis by Stickley, et al. (1976).

Using parametric statistics, the analyses suggest that the overall effect of the 4-Aminopyridine treatment was to decrease the overall feeding level in the treated regions in contrast to every other area. However, as the level of feeding in the field or region increases, the available resource becomes less than infinitely large and, under some circumstances, quite limited. At this point, the repellency potential breaks down. In other words, when resources, either the preferred of the bird or less preferred alternative food supplies, are large, repellents can have efficacy. But, when resources become more limited, there would be more competition for these limited food supplies; and eventually the birds must either choose to feed in repellent stressed areas or starve. Under these conditions the model predicts that repellents will be of little use.

The information I need to back up this prediction comes from the feeding rates. Nowhere are there field data to suggest that feeding rate, basic to the entire argument about agricultural depredations, is different between treated and untreated plots or fields. On the contrary, the information I present suggests the rates are equivalent. Further, the rates of feeding in untreated fields adjacent to treated fields suggest that the transfer of bird foraging to nearby untreated areas could be more disastrous than what would occur by simply leaving the system alone.

These functions involved with displacement of feeding identify a series of "feedbacks" in this agricultural ecosystem; and these "feedbacks" are based in interactions between components of the system such as avian behavior, competition for food resources, crop production, and the amount of alternative food resources. On the basis of logic alone, one ought to expect a series of such reactions to emerge during such ecosystem perturbation (e.g., the application of a repellent). The final outcome of the practice of using repellents against Redwings, and perhaps other birds, is: Under the potential of severe depredation pressure, repellents work best when they are not needed, i.e., when the cost of depredation is insignificant, and are likely not to work at all when they are needed most, i.e., when depredation is extremely high. In either case, any benefit/cost ratios are less than 1.0. Thus, I argue that on the whole Redwing repellents are of little use, and it is possible this situation exists for many other species as well.

The question has been posed to me, am I insisting all the reports to date about high repellency efficacy are wrong? This point may be valid, but to consider it this simply is a misjudgement. I am not suggesting the reports per se are wrong; and even if they were, I am in no position to state the field work was inadequately carried out. What I am saying, however, is that the right questions have not always been asked, and in light of this the right hypotheses have not been posed. If this is the case, then we must consider the reports of recommended field use of 4-Aminopyridine, and perhaps other avian repellents, with considerable caution, especially if the continued use is expensive to individuals and to society through the support of governmental R and D. I am not prepared to "dig into" each report about avian repellents and judge its merits on the basis of what was actually done, but I am making the point there should be critical thought given to why that work was done that way in the first place.

If we do ask such questions, I feel the scientific community ought to reconsider the use of repellents. If such reflection shows that chemical repellent programs are of little value, then we must turn our somewhat limited R and D resources to management programs where more success can be guaranteed. On the other hand, if new tests of the hypotheses presented here, plus stringent tests of new hypotheses, favor continued use of chemical repellents, management can then proceed without doubts about the value of avian chemical repellents, something that is not now possible.

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TABLE 1. Hypotheses presented in a hierarchy of relationships to examine the efficacy of a chemical, 4-Aminopyridine, as a repellent stress to birds feeding in a corn dominated agricultural ecosystem. Brackets suggest relationships between hypotheses and overlaps between levels of organization.

Level of Organization	Hypotheses
Individual Physiological Response	H ₀ : Birds are refractory to chemical repellent stimulus when placed on food.
	H ₁ : 4-Aminopyridine is ineffective in eliciting repellent response from individual blackbirds subjected to stress from this chemical.
Individual and Population Behavioral Response	H ₂ : 4-Aminopyridine is ineffective in eliciting repellent response from foraging groups of blackbirds subjected to stress from this chemical.
	H ₃ : 4-Aminopyridine, placed on food supplies, does not alter feeding behavior of blackbird flock units within small plot areas.
	H _{3a} : 4-Aminopyridine does not alter feeding incidence within any given plot.
	H _{3b} : 4-Aminopyridine alters feeding incidence, but does not alter amount eaten in any given plot.
	H _{3c} : 4-Aminopyridine alters neither feeding incidence nor amount eaten in any given plot.
Community Response	H ₄ : Use of 4-Aminopyridine in large plots or fields does not result in decreased total consumption of corn grain by blackbirds.
	H _{4a} : Levels or rates of avian consumption on corn grains are not different in repellent-treated and normal or untreated plots or fields.
	H _{4b} : Levels or rates of avian consumption on corn grains are not different in plots or fields adjacent to fields treated with 4-Aminopyridine repellent stress.
Ecosystem Response	H ₅ : Use of 4-Aminopyridine in large plots or fields does not result in economically feasible decreases in total consumption of corn grain by blackbirds.

TABLE 2. Statistical design for analysis of bird feeding incidence and estimated amount eaten in 4-Aminopyridine-treated corn field. Design is for analysis of harvest data taken after end of depreddation period.

Source of Variation	d.f.
Treatment	1
Plot (Treatment)	7
Plot (4-aminopyridine)	2
Plot (control)	5
Replicates (Plot (Treatment))	9
Replicate (Plot(4-aminopyridine))	
Replicate 1	1
Replicate 5	1
Replicate 9	1
Replicate (Plot (Control))	
Replicate 2	1
Replicate 3	1
Replicate 4	1
Replicate 6	1
Replicate 7	1
Replicate 8	1
Reminder	575
TOTAL	592

TABLE 3. Feeding Incidence (proportion ears fed upon) in treated and untreated plots by date in 4-Aminopyridine-treated field, Bradley Farms, Paincourt, Ontario 1966.

Treatment	Plot	Rep	Incidence of Feeding by Date				
			5 Aug	13 Aug	19 Aug	26 Aug	Sep 1 Harvest
4-Aminopyridine	1	a	-	0.02	0.39	0.52	0.86
		b	-	-	-	-	0.70
	5	a	-	0	0.22	0.34	0.56
		b	- 0.058	-	-	-	0.64
	9	a	-	0.06	0.30	0.50	0.60
		b	-	-	-	-	0.48
Control	2	a	-	0	0.36	0.30	0.88
		b	-	-	-	-	0.76
	3	a	-	0	0.38	0.74	0.80
		b	-	-	-	-	0.62
	4	a	-	0	0.46	0.50	0.66
		b	-	-	-	-	0.67
	6	a	- 0.058	0.02	0.14	0.48	0.45
		b	-	-	-	-	0.66
	7	a	-	0.02	0.16	0.18	0.66
		b	-	-	-	-	0.68
	8	a	-	0.06	0.20	0.24	0.44
		b	-	-	-	-	0.48

Comparison of treatment means, $F = 0.01$; 1, 43 d.f.

TABLE 4. Estimated amount (g) eaten per ear by date in 4-Aminopyridine-treated field, Bradley Farms, Paincourt, Ontario, 1966.

Treatment	Plot	Rep	Grass Consumed by Date				
			5 Aug	13 Aug	19 Aug	26 Aug	Sep 1 Harvest
4-Aminopyridine	1	a	-	5.2	29.12	24.75	35.46
		b	-	-	-	-	29.69
	5	a	-	0	5.21	24.15	17.04
		b	- 4.45	-	-	-	13.16
	9	a	-	4.17	17.79	11.51	20.12
		b	-	-	-	-	17.02
Control	2	a	-	0	16.51	22.13	32.36
		b	-	-	-	-	26.60
	3	a	-	0	33.91	26.73	25.20
		b	-	-	-	-	34.94
	4	a	-	0	19.18	13.50	21.55
		b	-	-	-	-	19.01
	6	a	- 4.45	0	8.10	21.62	14.32
		b	-	-	-	-	17.64
	7	a	-	4.2	7.25	39.73	24.86
		b	-	-	-	-	11.94
	8	a	-	4.17	30.90	26.35	21.35
		b	-	-	-	-	16.96

Comparison of treatment means, $F = 0.09$ 1, 43 d.f.

TABLE 5. Summary of results of feeding incidence, total estimated amount of corn consumed, and percent total consumed on damaged ears for control and 4-Aminopyridine-treated plots. Kent County, Ontario, 1966.

Sample Date	Day of Experiment	SUMMARY OF DAMAGE LEVELS					
		Control Plots		4-Aminopyridine Treated Plots		Total	
		Feeding Incidence (%)	Amount Eaten (g ear ⁻¹)	Total Damage (% of grain)	Feeding Incidence (%)	Amount Eaten (g ear ⁻¹)	Total Damage (% of grain)
Aug 5	1	5.84	4.45	2.54	5.84	4.45	2.54
Aug 13	9	1.33	4.70	1.93	2.67	4.65	2.02
Aug 19	15	28.33	21.26	10.54	30.00	19.50	8.97
Aug 26	22	40.67	23.37	11.17	38.67	21.15	10.44
Sep 1 (Harvest Date)	26	67.17	23.15	11.70	64.20	23.30	10.89

TABLE 6. Bird feeding incidence in a Kent County, Ontario corn field classified by damaged or undamaged conditions in control and 4-Aminopyridine-treated plots.

	TREATMENT		
	4-Aminopyridine-Treated	Control	TOTAL
Damaged ears	192	400	592
Undamaged ears	107	197	304
TOTAL	299	597	896

$$\chi^2 = 0.69, 1 \text{ d.f. } p = 0.447$$

TABLE 7. Results of ANOVA for estimated damage length of ears for 4-Aminopyridine-treated and control plots in field corn, Kent County, Ontario, 1966.

Source	d. f.	F	P
Tot	1	.007	.9357
Plot (T)	7	4.441	.0211*
Plot (t)	2	8.083	.0098**
Plot (c)	6	2.954	.0734
Rep [P(T)]	9	2.027	.0344*
Rep [P(t)]			
Rep (1)	1	1.954	.1616
Rep (5)	1	.599	.4035
Rep (9)	1	.184	.6681
Rep [P(c)]			
Rep (2)	1	1.483	.2238
Rep (3)	1	4.326	.0390*
Rep (4)	1	.390	.5325
Rep (6)	1	.602	.4391
Rep (7)	1	7.373	.0068**
Rep (8)	1	1.223	.2692
Residual	575		
TOTAL	582		

* = $p < 0.05$
 ** = $p < 0.01$

TABLE 8. Results of ANOVA for estimated damage weight per ear (using damage weight assessment of Cutright, 1973).

Source	d. f.	F	P
Trt	1	.000	1.0000
Plot (T)	7	4.812	.0164*
Plot (t)	2	8.076	.0098**
Plot (c)	5	3.507	.0491*
Rep [P(T)]	9	1.996	.0376*
Rep (1)	1	1.739	.1878
Rep (5)	1	.612	.4344
Rep (9)	1	.349	.5549
Rep (2)	1	1.840	.1755
Rep (3)	1	5.159	.0235*
Rep (4)	1	.305	.5810
Rep (6)	1	.396	.5294
Rep (7)	1	6.907	.0088**
Rep (8)	1	.654	.4190
Remainder	575		
TOTAL	592		

TABLE 9. Results of ANOVA for total length of ears for damaged and undamaged classes in 4-Aminopyridine-treated and control plots in field corn, Kent County, Ontario, 1966.

Source	d. f.	F	P
Treatment	1	3.337	.1021
Plot (Trt)	7	.816	.5968
Plot (trtd)	2	1.231	.3368
Plot (untrd)	5	.890	.6143
Rep [Plot(trt)]	9	2.482	.0094*
Rep (1)	1	4.422	.0358*
Rep (5)	1	6.790	.0093*
Rep (9)	1	3.056	.0805*
Rep (2)	1	.222	.6376
Rep (3)	1	.202	.6532
Rep (4)	1	3.603	.0563
Rep (6)	1	.011	.9165
Rep (7)	1	3.793	.0518
Rep (8)	1	.164	.6956
Damage	1	102.644	.0000*
D * T	7	.871	.3817
D * P(T)	7	.098	.5461
D * P(t)	2	.533	.6043
D * P(c)	5	1.044	.4186
D * R[P(T)]	9	.902	.5228
D * R(1)	1	.010	.9204
D * R(5)	1	2.173	.1408
D * R(9)	1	4.638	.0315*
D * R(2)	1	1.134	.2872
D * R(3)	1	.713	.3987
D * R(4)	1	2.403	.1216
D * R(6)	1	.023	.8795
D * R(7)	1	.572	.4497
D * R(8)	1	.031	.8603
Remainder	860		
TOTAL	896		

*p < 0.05

TABLE 10. Results of ANOVA for gross harvest weight of corn ears for damaged and undamaged classes in 4-Aminopyridine-treated and control plots in field corn, Kent County, Ontario, 1966.

Source	d.f.	F	P
Trc	1	1.307	.2774
Plot (Tt)	7	.393	.8842
P(c)	2	.120	.8993
P(c)	5	.502	.7682
Rep [P(T)]	9	2.790	.0031*
Rep (1)	1	.775	.3789
Rep (5)	1	4.728	.0290*
Rep (9)	1	6.140	.0134*
Rep (2)	1	1.095	.2957
Rep (3)	1	.012	.9128
Rep (4)	1	1.078	.2994
Rep (6)	1	.104	.7472
Rep (7)	1	6.616	.0103*
Rep (8)	1	4.558	.0330*
Damage	1	19.190	.0001*
D * T	1	.018	.8970
D * P(T)	7	1.524	.2122
D * P(c)	2	2.319	.1541
D * P(c)	5	1.206	.3193
D * R[P(T)]	9	.022	.9959
D * R(1)	1	.107	.7437
D * R(5)	1	.001	.9746
D * R(9)	1	3.242	.0721
D * R(2)	1	.270	.6025
D * R(3)	1	2.069	.1507
D * R(4)	1	.193	.6605
D * R(6)	1	.908	.3409
D * R(7)	1	.293	.5816
D * R(8)	1	.315	.5742
Residual	860		
TOTAL	895		

TABLE 11. Results of ANOVA for gross harvest weight plus estimated amount of corn removed from each ear (Cutright, 1973) in 4-Aminopyridine-treated and control plots in field corn, Kent County, Ontario, 1966.

Source	d.f.	F	P
Trc	1	1.452	.2274
Plot (T)	7	.550	.7786
Plot (c)	2	.354	.7112
Plot (c)	5	.629	.6830
Rep [P(T)]	9	2.301	.0148*
R(1)	1	1.318	.2513
R(5)	1	3.793	.0640*
R(9)	1	7.003	.0083*
R(2)	1	.614	.4325
R(3)	1	.216	.7227
R(4)	1	.779	.3777
R(6)	1	.266	.6062
R(7)	1	3.420	.0644
R(8)	1	3.440	.0637
Damage	1	126.223	.0000*
D * T	1	.017	.8999
D * P(T)	7	1.062	.4554
D * P(c)	2	.362	.7125
D * P(c)	5	1.345	.2600
D * R[P(T)]	9	1.016	.4251
D * R(1)	1	.350	.5490
D * R(5)	1	.041	.8396
D * R(9)	1	3.595	.0487*
D * R(2)	1	.058	.7543
D * R(3)	1	.032	.8306
D * R(4)	1	.342	.5588
D * R(6)	1	1.303	.2540
D * R(7)	1	1.529	.2166
D * R(8)	1	.675	.4116
Residual	860		
TOTAL	895		

*p < 0.05

TABLE 12. Contingency table data for final Incidence of damage in 4-Aminopyridine-treated and control plots, field corn, Kent County, Ontario, 1966.

	Plots and Replicates												TOTAL
	A ² B	A ³ B	A ⁴ B	A ⁶ B	A ⁷ B	A ⁸ B							
A. Control Plots													
Damaged	44	38	39	41	53	32	22	33	33	34	22	29	400
Undamaged	6	12	10	9	17	17	27	17	17	15	20	21	197
TOTAL	50	50	49	50	50	49	49	50	50	50	50	50	597
$\chi^2 = 45.18, 11 \text{ d.f.}, p < 0.005$													
	Plots and Replicates						TOTAL						
	A ¹ B	A ⁵ B	A ⁹ B										
B. 4-Aminopyridine-Treated Plots													
Damaged	43	35	28	32	30	24	192						
Undamaged	7	15	22	18	19	26	107						
TOTAL	50	50	50	50	49	50	299						
$\chi^2 = 18.44, 6 \text{ d.f.}, p < 0.005$													
C. Control and 4-Aminopyridine-Treated Plots													
$\chi^2 = 64.15, 17 \text{ d.f.}, p < 0.005$													

1 4-AP	4 C	7 C
2 C	5 4-AP	8 C
3 C	6 C	9 4-AP

ANOVA:

Source of Variation	df
Treatment	1
Plot (Treatment)	7
Plot (4-aminopyridine)	2
Plot (Control)	5
Replicates (Plot (Treatment))	9
Replicate (Plot (4-aminopyridine))	
R-1	1
R-5	1
R-9	1
Replicate (Plot (Control))	
R-2	1
R-3	1
R-4	1
R-6	1
R-7	1
R-8	1
Remainder	575
Total	592

Fig. 1. Field design of experiment where efficacy of a chemical repellent was tested in Southwestern, Ontario (C = control plots, 4-AP = repellent-treated plots).

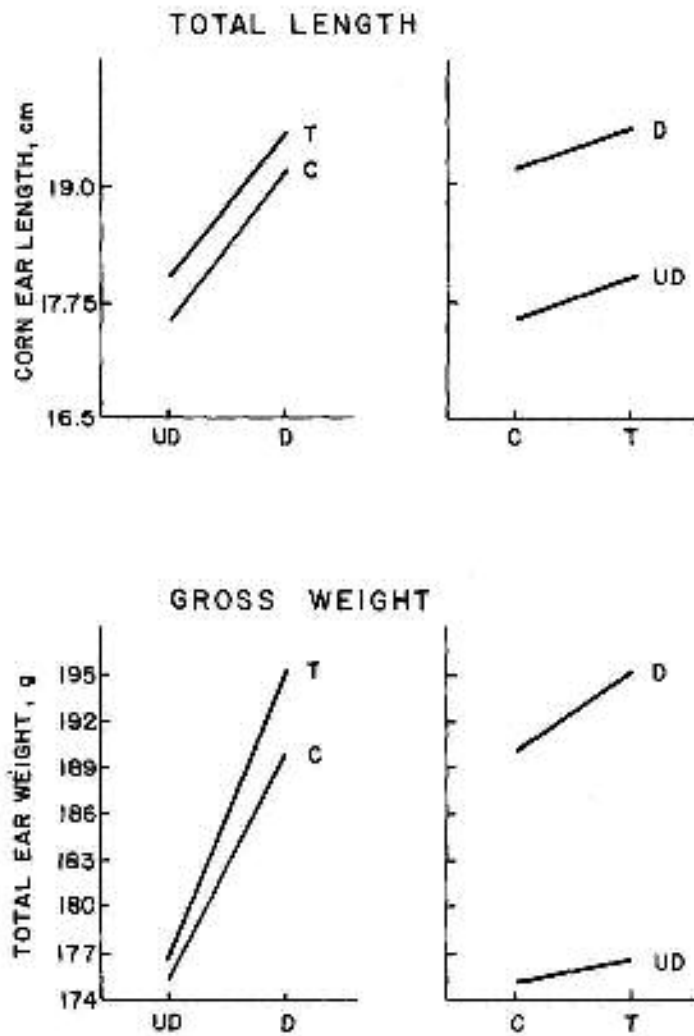


Fig. 2. Interactions between treatment type and damage class for field corn, Kent County, Ontario. (T = 4-Aminopyridine treated plots, C = control plots, D = damaged classes, UD = undamaged classes).

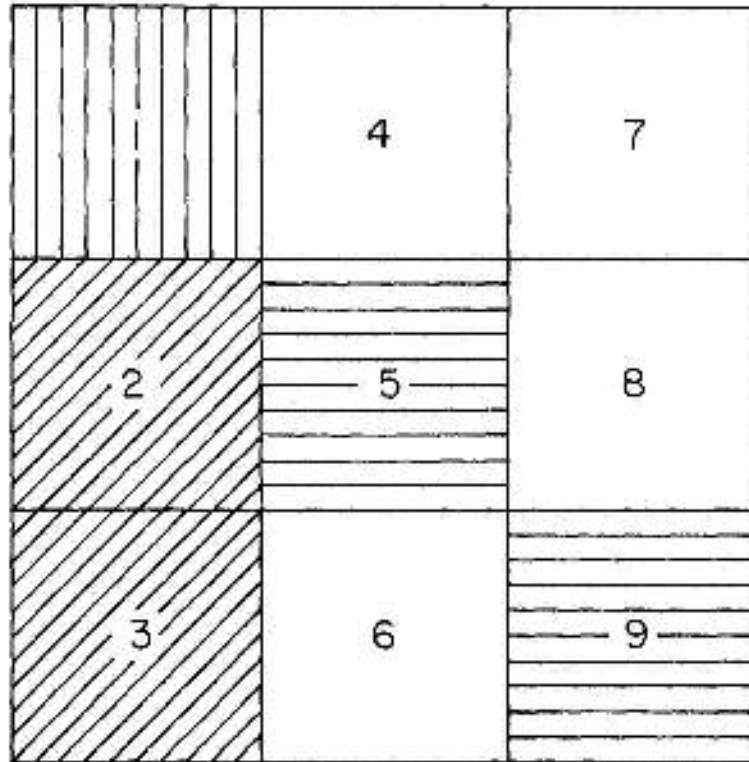


Fig. 3. Pattern of bird feeding activity (measured by estimated amount eaten per ear) in 4-Aminopyridine-treated plots (1, 5, and 9) and control plots (2,3,4,6,7, and 8) in field corn, Kent County, Ontario, 1966. Relationships are determined by Tukey's "Q" test.

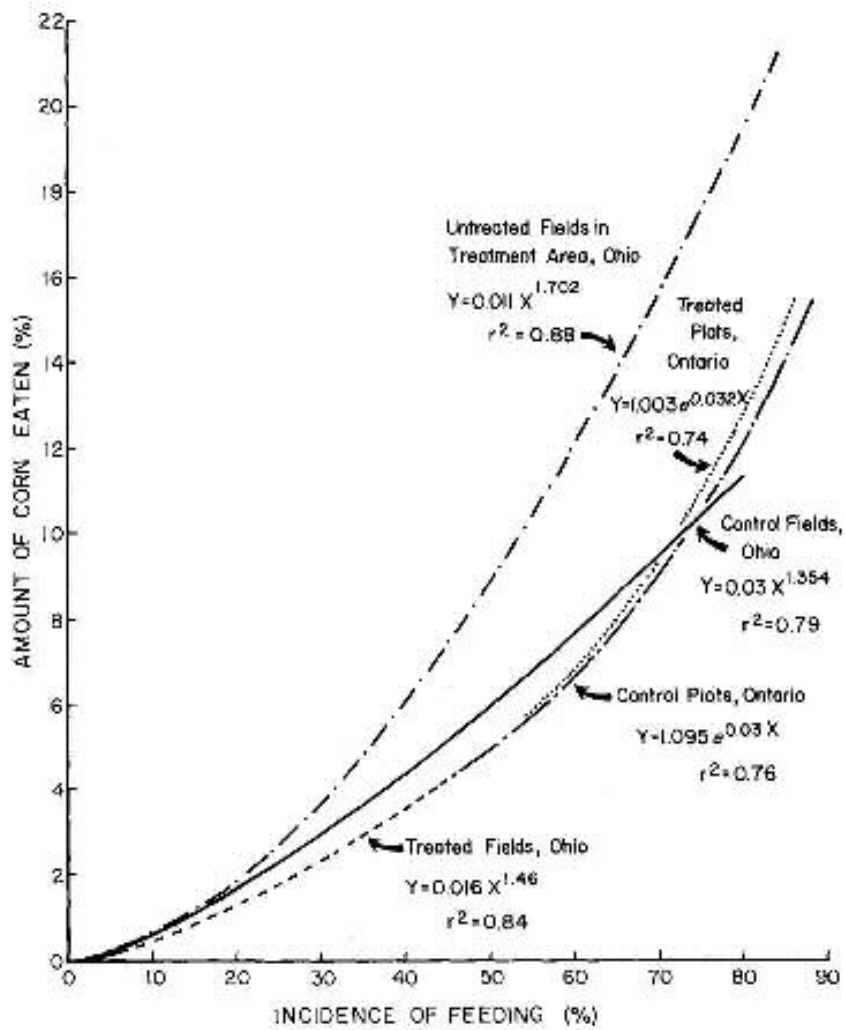


Fig. 4. Feeding rates of Red-winged Blackbirds in field corn; Ontario, 1966 and Ohio, 1969. The relationship plotting the amount of corn eaten against the incidence of feeding follows the models of Hayne (1946) and Dyer (1967). Note that the lower limb of the two Ontario curves meet the upper limb of the treated-fields curve from Ohio.

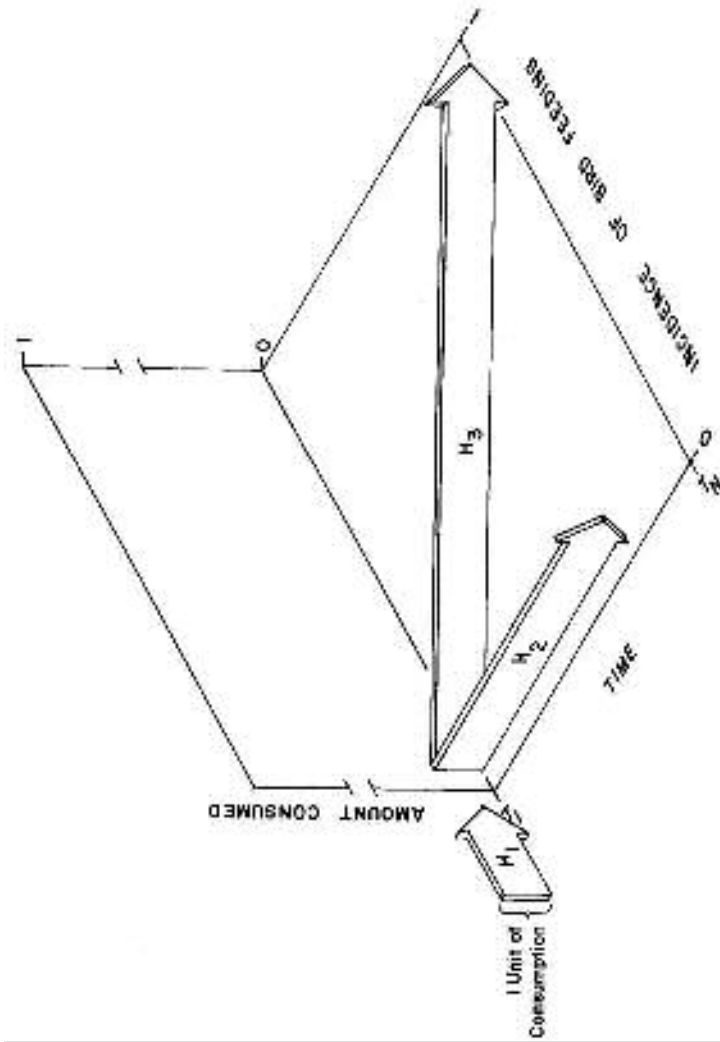


Fig. 5. Three hypothetical relationships concerning the testing of the efficacy of chemical repellents in avian feeding systems.

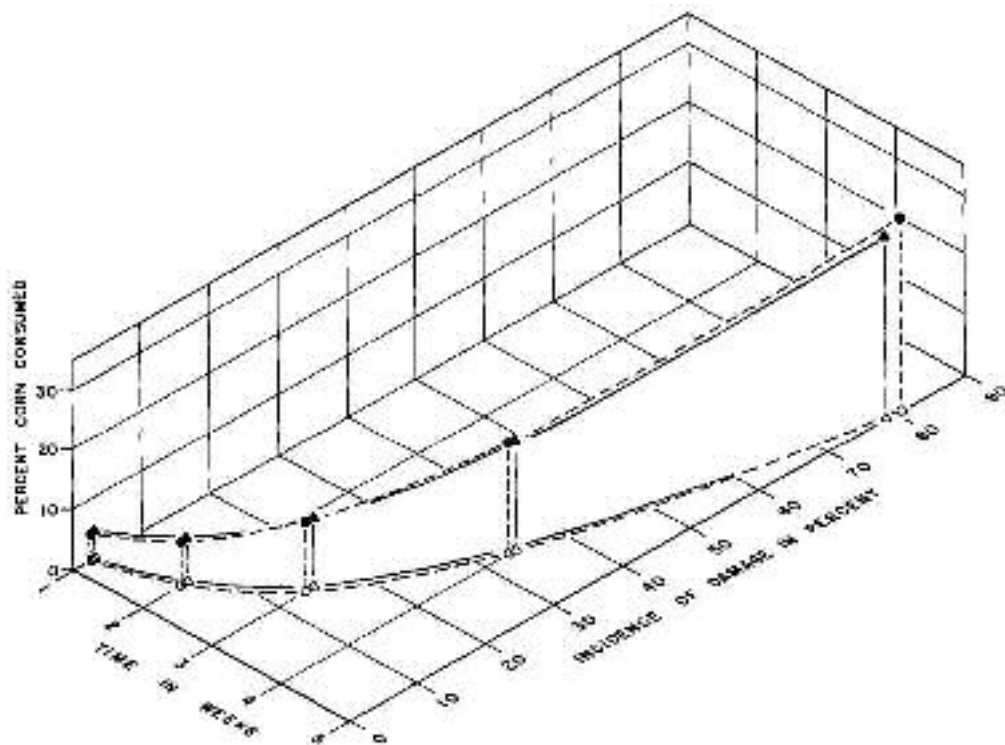


Fig. 6. Integrated results of 4-aminopyridine testing program in a 12 ha field in Kent, County, Ontario, 1966. Open circles and broken line show results of feeding incidence in control plots; open triangles and solid line show the same in treated plots. Closed circles and broken line show the amount of corn consumed in control plots; closed triangles and solid line show the same for treated plots. Neither feeding incidence nor amount eaten are statistically different for the two treatments (4-aminopyridine and control plots). Thus it is apparent that Red-winged Blackbirds did not respond to the treatment and that the repellent was ineffective throughout the entire experiment.