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Avian seed preference and weight loss experiments: the effect of fungal endophyte-infected tall fescue seeds

Cynthia Wolock Madej and Keith Clay

Biology Department, Indiana University, Bloomington, IN 47405, USA

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Summary. The impact of endophytic fungus-infected seeds on seed predators is poorly understood. In this multiple trophic level investigation, seed preference experiments were conducted to determine whether five species of passerines (dark-eyed juncos, *Junco hyemalis;* American tree sparrows, *Spizella arborea;* song sparrows, *Melospiza melodia;* chipping sparrows, *Spizella pusilla;* and house sparrows, *Passer domesticus*) recognize and preferentially consume noninfected (NI) over infected (I) seeds of tall fescue *(Festuca arundinacea)*. We predicted that the birds would refrain from eating I seeds because those seeds contain high concentrations of fungal alkaloids. When given a choice of NI fescue seeds and control seeds (millet), all bird species showed a significant preference for millet. However, individuals of all species consumed some NI seeds. When given a choice of NI and I fescue seeds, all species except the chipping sparrow ate significantly more NI than I fescue seed and the chipping sparrow showed the same trend. Thus, birds were able to distinguish between the two seed types and preferred NI seeds in choice tests. Additional experiments investigated weight changes in dark-eyed juncos fed diets containing different proportions of millet, NI, and I fescue seed. Significant differences in weight loss were observed for the various diets. Juncos showed greater weight loss when the proportion of fescue seed, especially the proportion of I seed, in their diet was greater. The potential significance of the finding that abundant grass seeds are made unavailable to predators by fungal infection is discussed in relation to foraging and competition in avian communities.

Key words: Passerines – Fungal endophyte – Seed preference – Weight loss – Foraging behavior

Food availability and quality play crucial roles in the regulation of animal behavior and population and community dynamics. These factors can strongly influence behaviors such as diet choice (Pulliam 1985), foraging tactics (Werner and Hall 1974; Pulliam 1985; Holmes and Schultz 1988), aggression (Caraco 1979; Desy et al. 1990), and migration (Terrill 1987). In addition, consequences at the population and community levels include effects on territory (Stenger 1958; Lance 1978), group (Caraco 1980; Barnard 1981), and population sizes (Pulliam and Enders 1971), survival (Fretwell 1969), and competition within and between species (Pulliam 1985). While minimum threshold levels of food quality and quantity are necessary for maintenance and survival, the importance of these factors to consumers rapidly increases as quality and quantity decrease (Wiens and Johnston 1977; Morse 1980). During winter, for example, food availability decreases as seed predators deplete their "nonrenewable" resource. In addition, seed consumption is likely to deplete high quality seeds early in the season, thus reducing overall quality of foraging areas with time. This decrease in desirable, high-quality food can cause changes in diet choice and an increase in dietary overlap between species (Pulliam 1985).

In addition to depletion, the chemical composition of food can affect its quality. Plants containing chemical toxins, for example, have been shown to influence diet choice (Freeland and Janzen 1974; Sherbrooke 1974; Milton 1979; Rosenthal and Janzen 1979; Bryant and Kuropat 1980; Harborne 1982; Henderson 1990) and, if consumed, to cause a variety of dramatic physiological changes including narcosis, intoxication, and death (Hance 1876; Bailey 1903; Mantle 1969; Taper et al. 1986). In some grasses, toxins are produced by fungal endophytes. The fungus obtains nutrients from the host plant, while the plant receives benefits that can include protection from consumers (Clay et al. 1985; Hardy et al. 1985), increased survival and growth (Cheplick and Clay 1988), and increased competitive ability (Kelley and Clay 1987).

Endophytic, seed-borne, fungal infections occur in many cultivated and wild grasses (Clay 1989). In the United States, the mean percent infection of tall fescue

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Offprint requests to: C.W. Madej

(Festuca arundinacea) is 50% (Shelby and Dalrymple 1987), and an estimated 12–14 million hectares of tall fescue occur in the eastern half of the country (Siegel et al. 1985). This suggests that infected (I) tall fescue plants and seeds are encountered frequently by avian, mammalian, and insect herbivores and seed predators. From the perspective of a consumer, grasses containing a symbiotic, endophytic fungus are low quality foods relative to noninfected (NI) grasses. Consumption of I plant tissue has been shown to cause decreased food intake and decreased weight gain in grazing cattle (Hoveland et al. 1983) as well as decreased rates of survival, growth, and development in insects (Clay et al. 1985; Cheplick and Clay 1988).

The impact of endophytic fungal infections on seed predators, however, is poorly understood. In many grasses, fungal endophytes are maternally transmitted through the seeds (Cheplick and Clay 1988). Due to a high concentration of alkaloids in the I seeds (Bush et al. 1982; Jones et al. 1983), predators would be expected to prefer NI seeds. When fed perennial ryegrass and tall fescue seed, flour beetles, *Tribolium castaneum,* exhibited reduced population growth on I seeds (Cheplick and Clay 1988), and laboratory rats fed I tall fescue seed responded with decreased food intake and growth rate (Neal and Schmidt 1985).

The purpose of this study was to investigate a multispecies interaction among fungal endophytes, grass seeds, and granivorous birds. Our objectives were to determine whether avian seed predators 1) avoid consuming seeds infected with an alkaloid-producing symbiotic fungus and 2) lose more mass when fed I seeds. We experimentally determined patterns of seed preference using five bird species and examined whether diets containing different proportions of NI and I seed caused changes in mass in dark-eyed juncos *(Junco hyemalis)*.

Materials and methods

Study organisms and general maintenance

Birds were caught at a variety of field sites in and around Bloomington, Indiana using mist nets and Potter traps. Dark-eyed juncos, American tree sparrows *(Spizella arborea)*, song sparrows *(Melospiza melodia)*, chipping sparrows *(Spizella pusilla)*, and house sparrows *(Passer domesticus)* were caught in the fall and winter of 1988–1989, and in the fall of 1989 for the seed preference experiment. For the weight loss experiment, dark-eyed juncos caught in early spring 1989 were used. Individuals of all bird species were captured in fields containing grasses infected with endophytic fungi, primarily tall fescue. Upon capture, flattened wing length and tail length were measured, and weight to the nearest tenth of a gram was determined using a pesola balance. For dark-eyed juncos and tree sparrows, we determined sex and age (see methods of Ketterson and Nolan 1976 and Heydweiller 1936, respectively), but sex and age were unknown for the other species. Birds were banded with either a U.S. Fish and Wildlife numbered leg band or a unique combination of color bands.

Birds were placed in identical individual cages measuring 29 cm × 26 cm × 22 cm and allowed to acclimate to captivity for 20–36 h. The cages were sheltered from rain and snow in an indoor aviary but were exposed to natural light, temperature, and wind. The arrangement of the cages prevented visual contact between the birds. At all times other than during experimental trials, birds received water and a standard diet of millet, cracked corn, and sunflower hearts ad libitum. NI and I tall fescue seeds were included in the standard diet so that all birds would have the opportunity to consume both types of grass seed. After trials were conducted, color bands were removed and birds were released where they were captured.

Tall fescue seed was chosen as the food supply because it is abundant in eastern North America and is often encountered by birds. Infected seeds contain the fungal endophyte *Acremonium coenophialum* as well as alkaloids (Jones 1983). NI seed lots contained less than 10% I seed, and I seed lots contained over 90% I seed. Tall fescue was also used in similar seed predation experiments with rats and *Tribolium* beetles (Neal and Schmidt 1985; Cheplick and Clay 1988). Millet was chosen as a control because it has relatively high nutritive value and captive birds readily consume it (Willson 1971).

Seed preference experiment

After acclimating, the birds were deprived of food overnight plus an additional 1–2 h in the morning to induce hunger. Deprivation occurred twice for each bird to allow observation of each of the following choices: NI fescue seed versus millet and NI versus I fescue seed. Petri dishes containing the seeds were placed at opposite ends of each cage, and birds were allowed to acclimate for approximately two minutes before observations began. Both the placement of the food dishes in the cage and the order in which birds received the choices were randomly determined. The number of seeds of each type eaten was recorded from a nearby blind for 30 min (binoculars were not necessary). An *a priori* limit of ten seeds consumed per trial was established for inclusion in the data set. After the first trial, birds were given the standard diet for the remainder of the day. In the evening they were deprived again, and the following morning the alternative choice was observed.

Often 6–8 individuals were observed on a given morning. The order in which birds were observed was determined randomly. Usually two individuals were observed simultaneously in order to maintain similar deprivation times among all individuals. Occasionally data for only one of the choice trials was obtained due to death or due to birds that chose to eat fewer than ten seeds.

To determine if there were significant differences in the number of NI and millet seeds eaten and/or the number of NI and I seeds eaten, data for each choice were analyzed using a nonparametric Wilcoxon signed-ranks test. This test compares the direction and magnitude of the differences for paired samples (Siegel and Castellan 1988) and was chosen based on the behavioral nature of the data and on sample size. While no prediction of the direction of preference was made for the NI vs. millet trials, we predicted that birds would prefer NI over I seeds. Thus, determination of p-values for the NI vs. millet trials used a two-tailed distribution while that for the NI vs. I trials used a one-tailed distribution. For summary purposes, the mean percentage of seeds eaten was calculated for each seed type for each bird species.

Weight loss experiment

Prior to the weight loss trials, juncos were housed in large aviary cages for approximately two weeks with water and a standard diet (see above) ad libitum in order that all individuals could accumulate similar amounts of fat. Twenty-five birds were then moved to the individual cages previously described. Both weight (to the nearest tenth of a gram) and subcutaneous fat levels (judged subjectively on a scale of 0–5; for methods, see Nolan and Ketterson 1983) were obtained at this time.

After acclimating for 24 h, birds were randomly assigned one of the following diets: 1) 100% millet, 2) 50% NI seed and 50% millet, 3) 50% I seed and 50% millet, 4) 100% NI fescue seed, or 5) 100%

I fescue seed. Two trials were conducted (approximately two weeks apart) with five individuals on each of the five diets (25 birds/trial). Each evening for five consecutive days, all seed was removed from each cage, and 5 g of the assigned diet was placed in the cage. The 5 g was chosen based on weight maintenance estimates for juncos (Caraco 1981; Terrill 1987). Birds were weighed each of these evenings at approximately the same time. These procedures were conducted in very low light to prevent excessive disturbance to the birds which could result in energy expenditure and weight loss. Birds whose weight reached a critical lower limit (approximately 15 g) were prematurely removed from the experiment and placed on the standard diet to prevent death. Following the trial all birds were placed on the standard diet for one to two days before being released.

Mann-Whitney U tests performed to assess deviations between trials revealed no significant differences in mean weight loss for any of the diets (p-values ranged from 0.1 to 1.0). Thus, data from the two trials were combined to provide a sample size of 50 birds with ten individuals/diet. One bird that ate no seed (including millet) was dropped from the analyses. The actual and percent of weight lost per day were averaged over the trial period for each bird. To determine if significant differences in either of these means existed for birds on different diets, data were analyzed using a Kruskal-Wallis one-way ANOVA. *A posteriori* comparisons (similar to Bonferroni tests; see Siegel and Castellan 1988, p. 213–214) were then made to determine which diets were significantly different from each other. While an attempt was made to equalize fat levels prior to the experiment, minor differences existed, and Spearman rank correlation coefficients were calculated to determine whether a significant correlation existed between initial fat level and mean weight loss.

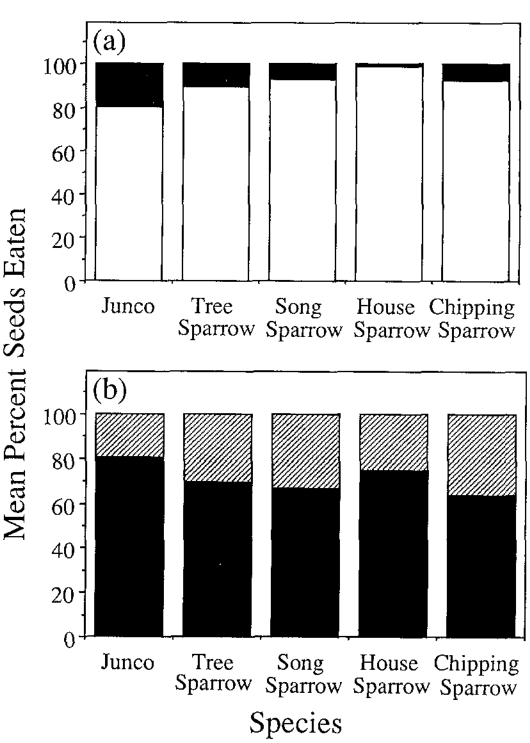

Fig. 1. Summary of species preferences. a) Percentage of seeds eaten by birds when given a choice of millet (□) and noninfected fescue seed (■). Standard errors range from 1.2 to 5.8. b) Percentage of seeds eaten when given a choice of noninfected fescue seed (■) and infected fescue seed (▨). Standard errors range from 5.7 to 9.4

Results

Seed preference experiment

All five bird species showed a significant preference for millet when given a choice of millet and NI fescue seeds (Fig. 1a, Table 1). Probability values ranged from $p = 0.0002$ for song sparrows to $p = 0.0162$ for tree sparrows. However, individuals of all species consumed some NI seeds with one individual eating 72.8% NI seeds in a 30 min trial (Table 1).

All species significantly preferred NI over I fescue seeds (p-values ranged from 0.0010 to 0.0391), except the chipping sparrow, whose preference, while nonsignificant, was 2 NI:1 I (Fig. 1b, Table 1). Thus, birds were able to distinguish between NI and I grass seeds and preferred NI seeds. The percentage of NI seeds eaten in NI vs. I trials ranged from 5.3% to 100% and the percentage of I seeds eaten ranged from 0% to 94.7%. While the number of I seeds eaten per trial was variable (Table 1), the vast majority were consumed at the start of the trial when birds were presumably determining the contents of each dish. The few individuals that did eat a substantial amount of I seed (as high as 144 seeds per 30 min trial) had difficulty walking and maintaining their balance as if drugged (onset of symptoms occurred by the end of the trials).

The total number of seeds eaten per 30 min trial ranged from 0 to 251. For both choice experiments (millet vs. NI and NI vs. I), the number of each type of seed eaten varied both within and among species (Table 1). While there is some variability, a preference for millet over NI seeds and a preference for NI over I seeds were

Table 1. Range, in number of seeds eaten per trial, and statistical summary of choice trials

Species	Millet	vs.	Noninfected		Noninfected		vs.	Infected
	Millet range	NI range	p-value*	N[a]	NI range	I range	p-value**	N[a]
Dark-eyed junco	21–120	0–89	$p = 0.00054$	18	11–192	0–58	$p = 0.0010$	17
Tree sparrow	11–163	0–67	$p = 0.0162$	12	6–126	2–43	$p = 0.0391$	8
Song sparrow	21–248	0–41	$p = 0.0002$	13	2–172	2–69	$p = 0.0061$	13
House sparrow	37–236	0–20	$p = 0.0078$	8	51–116	9–84	$p = 0.0156$	7
Chipping sparrow	49–207	0–38	$p = 0.0156$	7	10–114	3–144	$p = 0.1484$	7

* Two-tailed probability, Wilcoxon signed-ranks test for number of seeds eaten

** One-tailed probability, Wilcoxon signed-ranks test for number of seeds eaten

[a] Individuals were given both Millet vs. NI and NI vs. I seed tests. Sample sizes wary within species due to death or due to birds that chose to eat fewer than ten seeds

observed both within and among species, demonstrating the general effect of endophyte infections on seed preference.

Weight loss experiment

Mean weight loss and mean percent weight loss differed significantly for the juncos fed the five diets containing different proportions of NI and I seeds (Fig. 2; $p \ll 0.001$, Kruskal-Wallis test). Mean weight loss per bird ranged from 0.08 to 2.5 g per day, a substantial amount for the average 19 g bird, and mean percent of weight lost per bird ranged from 0.8 to 11.2% per day. Because one-way ANOVAs indicate only if significant differences exist among treatments, multiple *a posteriori* comparisons were performed to assess which treatments differed (see Siegel and Castellan 1988, p. 213–214). Significant differences in weight loss were found for approximately half of the diet comparisons (Fig. 2). Diets containing all or some millet were not significantly different from each other (p-values≥ 0.15), while most other comparisons were significantly different (p-values< 0.025). Mean weight loss for juncos on the 100% NI and 100% I diets were not significantly different, although the difference was in the predicted direction.

Perhaps most important was a trend toward greater weight loss on diets with higher proportions of fescue seed and greater amounts of I seed (Fig. 2). On average, birds on the control diet (millet) lost rather than maintained weight, although daily weight gains were recorded for some individuals. Weight loss for birds on the 100% I diet resulted from both the low food quality and a behavioral inhibition of feeding. Although seed consumption was not directly measured, some birds refrained from eating rather than eat I seed, and all birds lost weight when eating I seed.

No correlation between initial fat level and mean weight loss was found ($p = 0.275$) indicating that the slight differences in initial fat levels did not influence the outcome.

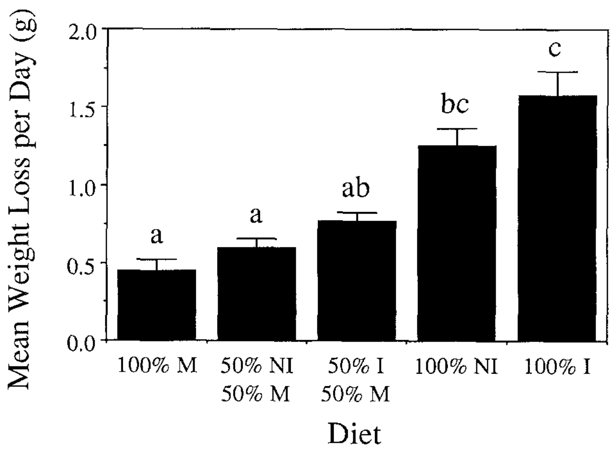

Fig. 2. Mean weight loss (with standard error bars) for dark-eyed juncos on diets containing different proportions of millet, noninfected (NI), and infected (I) fescue seed. $N = 10$ birds per diet. Bars with the same letters are not significantly different. (e.g. 100% Millet and 50%I/50% Millet are not significantly different whereas 100% Millet and 100% NI are.)

Discussion

Results of this study suggest that birds are able to distinguish between NI and I tall fescue grass seeds and refrain from consuming I, alkaloid-containing seeds. This preference was consistent both within and among various bird species. Birds consuming diets containing large proportions of I seed lost substantial amounts of weight. This indicates that the presence of the alkaloid-containing fungus influenced body mass. In addition, when I seed was consumed in large quantities, it produced behaviors indicative of physiological changes. Possible explanations for weight loss on the control diet include stress of captivity, insufficient nutrient content of millet, and an insufficient quantity of seed. Increased weight loss with increasing amounts of NI grass seed in the diet suggests that our assumption that equal weights of millet and NI fescue seeds provided equal nutrition was incorrect.

The consumption of NI fescue seeds by all species supports the hypothesis that fescue seeds are consumed by these birds in nature. Evidence from diet studies (Baumgartner 1937; Baumgras 1943) indicates that birds consume seeds of plant species that are known to have infected populations (Clay 1989) providing additional evidence that these foraging choices occur in nature. Tall fescue is also extremely widespread and abundant (Siegel et al. 1985) and a large proportion of tall fescue is infected (Shelby and Dalrymple 1987). Thus, foragers are likely to encounter tall fescue seed and endophyte infections frequently.

While the mechanism of seed choice was not determined, taste is the most likely candidate. Supporting this mechanism of discrimination are the identical appearance of NI and I seeds (to humans), and the fact that birds sampled both types of seeds before rejecting one, indicating their inability to judge the seeds visually. Birds possess taste receptors (Berkhoudt 1985) and have the ability to discriminate between bitter, sweet, sour, and salty substances (Kare et al. 1957; Duncan 1960). Cedar waxwings *(Bombycilla cedrorum)* used gustatory as well as tactile and visual cues to discriminate between fungus-free and moldy fruits (Buchholz and Levey 1990). Birds have also been shown to avoid insects and other arthropods that contain bitter compounds (Yang and Kare 1968; Brower 1969). Thus, birds may be using the bitter taste of the alkaloids as a cue for the presence of infection.

Endophytic fungal infections decrease both food quality and effective food availability. Food quality is reduced simply by the presence of the potentially detrimental compounds associated with the infection. Studies of I plant and seed consumption have demonstrated numerous negative effects including decreased survival, growth, and development (Cheplick and Clay 1988), and decreased weight gain and food intake (Hoveland et al. 1983; Neal and Schmidt 1985). Feeney (1975) and

Rhoades and Cates (1976) described a range of plant chemical defenses and indicated that the more poisonous toxins limit the range of available prey types for consumers. Consider seed types that vary in toxicity. Seeds that contain small quantities of toxins may be consumed by predators with few consequences. Seeds of intermediate toxicity may be consumed when a benefit such as high caloric content or a required nutrient is present in the seeds, or when the availability of other seeds is low. If, however, seeds contain toxins that are more poisonous, the food source becomes an unavailable alternative (Stephens and Krebs 1986). Alkaloids produced by endophytic fungi apparently make I seeds low-quality, essentially unavailable alternatives for the bird species studied.

Endophytic fungal infections could have two temporal effects on effective food availability for seed predators. Within a winter, seed availability generally decreases with time because seeds are a nonrenewable resource. The depletion of NI seeds would be equivalent to the depletion of all fescue seeds because I seeds are low quality food alternatives (due to toxicity). Thus, the number of I seeds would remain nearly constant while their proportion in the seed pool increased due to preferential consumption of NI seeds. An increase in the number of I seeds in the seed bank could lead to higher recruitment of I plants in subsequent years, effectively lowering the availability of NI seeds in the following winters. In addition, this increase in I seed numbers across winters would be expected to cause an increase in the frequency of infection as populations aged. Evidence indicates that infection does increase with population age (Clay 1986a), sometimes up to 100% (White 1987; Latch et al. 1987). Finally, because infection is associated with increased vegetative vigor (Clay 1984, 1986b; Kelley and Clay 1987), I plants would have a competitive advantage over NI plants and the probability of I plant survival would increase, again causing lowered effective food availability across winters. Thus, the fungal symbiont provides the plant with protection from seed predators and herbivores, generating expansion of I seed and plant populations, which in turn causes lowered food availability and resource limitation for foragers.

Since both food quality and effective food availability are lowered by the presence of endophytic fungal infections, the role of infection in regulating the behavior and ecology of seed predators must be considered. During winter, sparrows are ground foragers whose diets consist predominantly of seeds. Birds must find one seed every 2–5 s (excluding handling time) to survive an average winter day (Benkman and Pulliam 1988). This is a difficult task given that seeds are often small and cryptic. Compounding this problem is the potential for infection of seeds by endophytes. Thus, seed selection may be based not only on the evaluation of variables such as seed size (Hespenheide 1966; Willson 1971; Henderson 1990), caloric/nutrient content (Willson 1971; see review by Pyke et al. 1977; Thompson et al. 1987; Henderson 1990), and handling time (Kear 1962; Hespenheide 1966; Willson 1971; Grant 1981), but also on toxicity due to fungal infection.

When foraging occurs in fields containing populations of endophyte-infected grasses, high quality resources will be depleted faster compared to fields with noninfected populations. Avian seed predators in such an environment are likely to move to another foraging locale, although dense bird populations, predator avoidance, habitat spatial heterogeneity, or a variety of other factors may constrain movement. Our results suggest that when confined to such an environment, seed predators should either refrain from foraging entirely or should consume a small number of I seeds. The few birds that consumed a substantial number of I seeds would be likely to suffer physiological and behavioral changes due to the alkaloids produced by the fungus, which could increase their susceptibility to predators.

While foragers may prefer to exclude infected species from their diets, the likelihood of this declines as food supplies decrease and as the probability of encountering I seeds increases (due to preferential consumption of NI seeds). In addition, excluding these seed species from the diet would limit food resources further, causing an increase in dietary overlap between individuals and between species (Pulliam 1985). This, in turn, is likely to intensify aggression and competition, altering population and community structures among seed-feeding birds.

Conspecific seeds are not always perceived as equal by consumers. Future seed preference studies should consider the presence of fungal endophytes as probable influences on diet choice in granivorous species. The direct effects of endophytes on food availability and foraging behavior as well as the indirect consequences at the population and community levels should also be considered.

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