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IMPACT OF CONSUMING TALL FESCUE LEAVES WITH THE ENDOPHYTIC FUNGUS, *ACREMONIUM COENOPHIALUM*, ON MEADOW VOLES

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Most of the 14 million hectares of pastures of tall fescue (*Festuca arundinacea*) planted in the United States are infected with the endophytic fungus, *Acremonium coenophialum*. I examined if grazing infected plants had an adverse impact on meadow voles (*Microtus pennsylvanicus*). Captive voles fed leaves from infected fescue plants (fungus-fed voles) gave birth and weaned as many offspring as voles fed leaves from uninfected plants of the same genotype of tall fescue (control voles). Mass and body temperatures of fungus-fed and control voles did not differ. When maintained at 21°C, mortality rates were similar, but when ambient temperatures were increased to 31°C, fungus-fed voles had significantly higher mortality rates than control voles. Naive voles did not discriminate between infected and uninfected leaves, but after a diet of fescue, voles preferred uninfected leaves.

Key words: *Microtus pennsylvanicus*, meadow voles, *Acremonium coenophialum*, endophytic fungus, *Festuca arundinacea*

Beginning in the 1940s, farmers in the eastern United States began planting a newly-discovered cultivar of tall fescue (*Festuca arundinacea*) called Kentucky 31 (Stuedemann and Hoveland, 1988). This cultivar was hardier and more productive than others. Unknown at the time, this cultivar was infected with the endophytic fungus, *Acremonium coenophialum*. By the 1970s, there were >14 million hectares of tall fescue pastures in the United States, and most were infected with this fungus (Shelby and Dalrymple, 1987; Stuedemann and Hoveland, 1988). This endophytic fungus, which grows subcutaneously in leaves, stems, and seeds, does not undergo sexual reproduction or sporulate and cannot spread contagiously; instead, it is seed-borne (Clay, 1988, 1993). The relationship between grass and fungus is mutualistic. Fungal endophytes produce ergopeptine alkaloids, notably ergovaline (Porter et al., 1981; Thompson and Stuedemann, 1993; Yates and Powell, 1988; Yates et al., 1985). The fungus makes grass less palatable and more toxic to herbivorous insects and nematodes (Johnson et al., 1985; Kimmons et al., 1990; Latch et al., 1985; Yates and Powell, 1988) and more hardy (Arachevaleta et al., 1989; Bacon, 1993).

Consumption of large amounts of fungus-infected tall fescue (hereafter called infected fescue) can have deleterious effects on cattle, including lower food intake, lower weight gains, higher body temperatures, reduced rates of conception, and suppressed milk production (Hoveland et al., 1983; Jackson et al., 1984; Schmidt and Osborn, 1993; Schmidt et al., 1982). Such problems, however, usually can be avoided by proper management, thus allowing continued use of infected cultivars of tall fescue for year-round grazing pastures (Bouton et al., 1993).

While it is possible to limit access of cattle to infected pastures, limiting access of free-ranging small mammals that live and graze in these pastures is not accomplished easily. It is unclear if small mammals suffer ill effects from grazing on infected fescue.

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Preliminary results indicated that deleterious impacts of consuming infected tall fescue may not be limited to cattle. Consumption of infected grass seed reduced reproductive potential of laboratory rats (*Rattus norvegicus*—Neal and Schmidt, 1985; Varney et al., 1987; Zavos et al., 1986) and laboratory mice (*Mus musculus*—Godfrey et al., 1994; Zavos et al., 1987*a*, 1987*b*, 1988*a*, 1988*b*, 1990).

Meadow voles (*Microtus pennsylvanicus*), the most widely distributed of North American voles, are herbivores that feed primarily on monocotyledons or dicotyledons depending on season and availability with seeds and fungi making <40% of their diet (Batzli, 1985; Keys and Van Soest, 1970; Lindroth and Batzli, 1984; Zimmerman, 1965). In this study, I compared reproduction and mortality rates of captive meadow voles fed leaves from infected tall fescue plants to those of voles fed leaves from uninfected plants of the same genotype.

MATERIALS AND METHODS

Experiments were conducted in 1992–1994 using meadow voles captured in Cache Valley, Utah. At the initiation of these experiments, 20 male voles were paired randomly with 20 female voles. If a member of a pair died during the experiment, it was replaced with an adult of the same sex. Each pair was housed separately in a 0.1- by 0.1- by 0.2-m cage about one-half filled with wood shavings. Water and rat chow were provided ad lib.

Each pair of voles was assigned randomly to either of two groups: one group received tall fescue leaves infected with *A. coenophialum* ad lib (hereafter called fungus-fed voles) and the other (control voles) received uninfected fescue leaves ad lib. Leaves were harvested from one of eight fescue plots located at Utah State University's Green Canyon Ecology Center. All plots were planted with the same infected genotype (CN-15) of the Kentucky 31 cultivar. However, the grass in one-half of the plots was uninfected because the seed used in these plots was first heated in a water bath at 58°C for 17 min to kill the fungus (Siegel et al., 1984; Williams et al., 1984). Microscopic examination of leaves from those plants indicated that the treatment was effective in killing the fungus; infection rates were <10% in uninfected plots but >80% in infected ones. Fresh fescue was fed to voles during spring, summer, and fall; during winter, voles were fed fescue that had been harvested earlier and frozen. After 12 months, diets of the voles were switched so that those that had been receiving infected leaves, received uninfected leaves and became the control group; the control group then received infected leaves. This feeding regime continued for 10 months.

During the fifth and sixth month of the trial, young from cages of control and fungus-fed voles were paired and placed in their own cages to form an F_1 generation (20 F_1 pairs each of fungus-fed voles and control voles). Young were not paired with their siblings or cousins. Control voles from the F_1 generation were maintained on uninfected fescue from birth, but fungus-fed voles were fed infected fescue. Unlike the parent generation, F_1 voles were maintained on the same diet throughout the experiment.

Each vole was weighed when the experiment began and every 3 months thereafter. Cages were checked daily for fatalities. Numbers of young in each cage were checked weekly, and young were weaned when they were 3–4 weeks of age. After collecting data on the F_1 generation for 8 months and on their parents for 14 months, I gradually increased ambient room temperature from 21°C to 31°C over 6 weeks and then maintained it at the higher temperature for a 4-month period after which it was again lowered to 21°C for an additional 4 months. During the high-temperature period, a rectal probe was used monthly to record body temperatures of voles.

I conducted a feeding test every 4 months to assess if voles preferred uninfected or infected leaves. For this test, voles were allowed simultaneous access to a bundle of infected leaves and a bundle of uninfected leaves for a 2-h period. A metal wire secured each bundle in the middle. Leaves in all bundles were cut to a uniform length. Consumption was measured by weighing each bundle before and after the 2-h test. Consumption was corrected for water loss by subtracting from it the decrease in mass of bundles placed in unoccupied cages.

Statistical analyses.—Mass and body temperatures of fungus-fed voles were compared to those of control voles using repeated measures analysis of variance (Little and Hills, 1978).

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TABLE 1.—*Reproductive rates of meadow voles* (n = *20 pairs) fed a diet containing tall fescue leaves infected with* Acremonium coenophialum *(fungus-fed voles) or voles* (n = *20 pairs) fed a diet of uninfected tall fescue leaves (control voles) during a 14-month period when they were maintained at 21°C and a 4-month period at 31°C.*

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Ambient temperature (°C)	Dependent variables	Fungus-fed voles		Control voles			
		$\bar{X}$	*SE*	$\bar{X}$	*SE*	*z*	*P*
21	No. born/pair/year	8.7	2.8	6.2	3.2	1.49	0.14
	No. weaned/pair/year	7.7	2.7	4.9	2.6	1.08	0.28
31	No. born/pair/year	4.2	1.2	7.2	2.4	0.32	0.75
	No. weaned/pair/year	3.0	1.0	5.4	1.7	0.05	0.96

Males and females were analyzed separately unless statistical tests showed no sexual differences. Numbers of young born or weaned to control and fungus-fed pairs were compared using *z* statistic of the Mann–Whitney *U* tests. Mortality rates were compared between fungus-fed and control voles using a chi-square test. Similar tests were used to compare F_1 voles to the parent generation. Results were considered significant if $P < 0.05$.

RESULTS

Birth rates for the F_1 generation ($\bar{X}$ number born/year ± SE = 7.5 ± 3.3) and the parent generation (8.9 ± 3.7) did not differ significantly ($z = 0.43$, $P = 0.67$). Weaning rates for the F_1 generation (6.4 ± 2.9) and the parent generation (6.4 ± 2.4) were similar ($z = 0.55$, $P = 0.58$). Mortality rates also were similar ($z = 0.43$, $P = 0.51$). Hence, I combined data on F_1 and parent generation voles for all further analyses so that samples were 20 pairs of fungus-fed voles and 20 pairs of control voles.

There were no significant differences in number of young born to control and fungus-fed voles regardless of whether ambient temperature was 21°C or 31°C (Table 1). There also were no significant differences between control and fungus-fed voles in number of young that were weaned.

During the 14-month period when room temperature averaged 21°C, 10 fungus-fed voles died (four males and six females). This was not significantly different ($\chi^2 = 0.67$, $\bar{X} = 0.41$) from the seven control voles (three males and four females) that died during the same period. However, when room temperature was increased to 31°C, 25 fungus-fed voles (11 males and 14 females) died as did 13 control voles (five males and eight females); this difference was significant ($\chi^2 = 7.22$, $P = 0.007$). When room temperature was returned to 21°C, fatalities among control voles (one male and four females) and fungus-fed voles (no males and four females) were similar ($\chi^2 = 0.13$, $P = 0.72$).

Mean masses of fungus-fed males (43.2 g) and control males (40.7 g) did not differ significantly ($F = 0.64$, *d.f.* = 1,34, $P = 0.43$) when voles were maintained at 21°C, but there was a time effect ($F = 4.09$, *d.f.* = 2,68, $P = 0.02$) because most fungus-fed and control males gained mass during the experiment. Mean masses of fungus-fed females (34.5 g) and control females (39.6 g) did not differ ($F = 2.74$; *d.f.* = 1,30, $P = 0.11$), but there was a time effect ($F = 17.79$, *d.f.* = 3,90, $P < 0.001$).

At 31°C, mean masses of fungus-fed males (44.2 g) and control males (42.2 g) were similar ($F = 0.32$, *d.f.* = 1,27, $P = 0.58$). Mean masses of fungus-fed females (36.3 g) and control females (38.4 g) also were similar ($F = 0.30$, *d.f.* = 1,20, $P = 0.30$). However, there was a time effect for males ($F = 3.91$, *d.f.* = 5,135, $P = 0.002$), because they continued to gain weight, but not for females ($F = 0.83$, *d.f.* = 5,100, $P = 0.53$).

The difference in mean body temperature of males (37.8°C) and females (38.2°C) was

TABLE 2.—*Results of feeding trials in which meadow voles were given access simultaneously to two feeding trays: one containing tall fescue leaves infected with* Acremonium coenophialum *and the other containing tall fescue leaves that were uninfected.*

Month from start	Temperature (°C)	Grams consumed/day				t	P (one-tailed)
		Infected leaves		Uninfected leaves			
		$\bar{X}$	*SE*	$\bar{X}$	*SE*		
1	21	1.25	0.33	1.73	0.43	0.88	0.19
4	21	7.85	1.03	9.80	1.10	3.54	0.001
8	21	7.24	0.54	8.04	0.42	1.41	0.09
18	31	4.87	0.30	5.93	0.25	3.57	0.001
20	21	7.01	0.57	8.04	0.54	1.51	0.07

significant (F = 9.23, *d.f.* = 1,78, P = 0.003). So data on body temperature were analyzed separately for each sex. Mean body temperatures for fungus-fed males (37.7°C ± 0.1° *SE*) and control males (37.9°C ± 0.1°) did not differ (F = 1.50, *d.f.* = 1,38, P = 0.23). Body temperatures for fungus-fed females (38.1°C ± 0.1°) and control females (38.3°C ± 0.1°) also did not differ (F = 0.48, *d.f.* = 1,38, P = 0.49).

Feeding preferences (mass of uninfected grass consumed minus mass of fungus-infected grass consumed) of fungus-fed voles and control voles were never statistically different during choice tests. Consequently, data from control and fungus-fed voles were combined for all analyses for feeding preference experiments. In the initial choice test, naive voles consumed similar amounts of uninfected and infected grass (Table 2), but rates of consumption were low. Thereafter, voles consumed more uninfected than infected grass in all choice tests; differences were significant half of the time.

DISCUSSION

Consumption of leaves from infected tall fescue had no impact on body mass of voles when subjects were maintained at either 21°C or 31°C in my experiments. Zavos et al. (1990) also found no difference in average daily weight gains between mice fed a diet of infected seeds of tall fescue and those fed uninfected seeds during a 50-day period. In contrast, laboratory rats fed infected seeds of tall fescue had slower growth rates or reduced body mass (Neal and Schmidt, 1985; Varney et al., 1987, 1988). Many studies have found that cattle on a diet of infected fescue had lower weight gains than animals on uninfected diets (Schmidt and Osborn, 1993).

Consumption of leaves from infected tall fescue had no effect on rectal temperatures of voles when ambient temperatures were 31°C. Steers on infected and uninfected fescue diets at 21°C exhibited similar body temperatures; at 32°C, rectal temperatures were higher for steers on an infected fescue diet, but their surface temperatures generally were lower, due presumably to vasoconstrictive properties associated with the endophyte (Schmidt and Osborn, 1993). Laboratory rats on a diet of uninfected seeds of tall fescue had lower body temperatures than rats on an infected diet (Neal and Schmidt, 1985).

When fed seeds from infected tall fescue, laboratory rats (Varney et al., 1987, 1988; Zavos et al., 1986) and laboratory mice (Godfrey et al., 1994; Zavos et al., 1987*a*, 1987*b*, 1988*a*, 1988*b*, 1990) experienced a decrease in their reproductive rates because of reproductive problems such as reduced fertility in males and delayed estruses, lower pregnancy rates, increased abortion rates, smaller litters, and poor lactation in females. In my experiments, consumption of infected leaves did not affect reproductive performance of voles.

I found that fungus-fed voles suffered

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higher mortality than control voles, which was temperature-dependent. Differential mortality between fungus-fed and control voles did not occur until after room temperature was raised from 21°C to 31°C. Likewise, many of the debilitating effects of consumption of infected fescue are manifested in cattle only when temperatures exceed 31°C (Hemken et al., 1981; Schmidt and Osborn, 1993), because alkaloids produced by the fungus cause peripheral vasoconstriction and inhibit an animal's ability to shed excess body heat.

Voles preferred uninfected leaves over infected ones when given a choice. This appeared to be a learned aversion because it was not expressed by naive voles. However, preference for uninfected leaves was manifested equally by control and fungus-fed voles. Thus, experience with a diet of tall fescue was more important than experience with the fungus. Similar learned aversions to infected fescue have been observed in Canada geese (*Branta canadensis*—Conover and Messmer, 1996*a*) and zebra finches (*Taeniopygia guttata*—Conover and Messmer, 1996*b*). Cattle also exhibit a preference for grazing uninfected tall fescue (Schmidt and Osborn, 1993; van Santen, 1992).

Despite ill effects that cattle suffer when grazing fungus-infected fescue, farmers still like to plant it in pastures because infected grass is hardier, more resistant to insects, and outproduces uninfected pastures. Because of those beneficial qualities, infected fescue also is used increasingly for lawns (Funk et al., 1993). Fortunately, problems that cattle face when grazing infected fescue largely can be avoided by proper husbandry that consists of limiting intake of infected fescue by cattle. Consequently, infected cultivars of tall fescue are still used for year-round grazing pastures (Bouton et al., 1993). Unfortunately, it is not as easy to control forage intake of free-ranging small mammals. My results indicate that consumption of fescue leaves infected with *A. coenophialum* may have little impact on meadow voles at 21°C, but it can cause an increase in mortality when they are stressed by higher ambient temperatures.

To date, most research on infected tall fescue has centered on its impact on cattle. Considering that there are 14 million hectares of tall fescue pastures in the United States and most are infected (Shelby and Dalrymple, 1987; Stuedemann and Hoveland, 1988), it is important to determine the impact of these grasses on native mammalian herbivores and animals that feed on them. Several factors may reduce negative consequences of consumption of infected fescue on free-ranging voles. First, after voles develop an aversion to infected fescue, their consumption of it probably will be reduced. Second, free-ranging voles would have a more varied diet than my subjects. Third, free-ranging voles could modify their behavior to reduce exposure to high ambient temperatures (e.g., by reducing their activity during the day). However, Coley et al. (1995) compared abundance of small mammals in three plots with infected fescue to three other plots with uninfected fescue. Although samples (three pairs) were small, they reported that small mammals were less common in the infected plots. Unfortunately, soil types also varied among plots, which made results hard to interpret.

Many wildlife species cause problems that can be serious, including damage to agricultural crops, deer–car or bird–aircraft collisions, and diseases vectored by wildlife (Conover, 1994; Conover and Decker, 1991; Conover et al., 1995). Some losses could be prevented if there were an unpalatable ground cover that could be used to keep problem animals from foraging in areas where they are likely to cause serious problems (Conover, 1985, 1991). Perhaps fungus-infected fescue is such a ground cover.

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