PETRIE, M., T. HALLIDAY, AND C. SANDERS. 1991. Peahens prefer peacocks with elaborate trains. Anim. Behav. 41:323-331.
RANDS, M. R. W., M. W. RIDLEY, AND A. D. LELLIOT. 1984. The social organization of feral peafowl. Anim. Behav. 32:830-835.
SEARCY, W. A., AND M. ANDERSSON. 1986. Sexual selection and the evolution of song. Annu. Rev. Ecol. Syst. 17:507-533.
SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods, 6th ed. Iowa State Univ. Press, Ames.

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Consequences For Captive Zebra Finches of Consuming Tall Fescue Seeds Infected With the Endophytic Fungus *Acremonium coenophialum*

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Tall fescue (*Festuca arundinacea*) plants can be infected with the endophytic fungus *Acremonium coenophialum*. This fungus, which grows subcutaneously in leaves, stems, and seeds, does not undergo sexual reproduction or sporulate, and cannot survive outside the plant (Clay 1988). The fungus is passed from one generation to the next through infected seed. A mutualistic relationship exists between the grass and the fungus. The fungal endophytes produce ergopeptine alkaloids, notably ergovaline (Thompson and Stuedemann 1993), which makes the grass less palatable and more toxic to insect herbivores (Latch et al. 1985, Johnson et al. 1985) and nematodes (Kimmons et al. 1990). Because infected grasses are hardy (Arachevaleta et al. 1989) and resistant to insects, one infected cultivar (Kentucky 31) was widely planted before its infection was discovered. Hence, most of the plants grown on 14 million hectares of tall fescue pastures in the United States are infected (Shelby and Dalrymple 1987, Stuedemann and Hoveland 1988).

Consumption of large amounts of fungus-infected tall fescue (hereafter called infected fescue) can have a deleterious effect on livestock. Cattle grazing infected fescue, especially in hot weather, have exhibited lower food intake, lower daily mass gains, higher rectal temperatures, and a decrease in reproductive rates (Hoveland et al. 1983, Aldrich 1993, Schmidt and Osborn 1993). These problems, however, can largely be avoided by proper management, allowing infected tall fescue cultivars to still be recommended for pastures (Bouton et al. 1993).

Consumption of infected fescue can reduce the reproductive potential of laboratory rats (*Rattus norvegicus*; Zavos et al. 1986, Varney et al. 1987, 1988) and laboratory mice (*Mus musculus*; Zavos et al. 1987, 1988a, b, 1990, Godfrey et al. 1994). Reproductive rates decreased owing to reduced male fertility and because of delayed estruses, increased abortion rates, and poor lactation in females.

Whether avian seed predators that ingest infected fescue seeds suffer any ill effects is unclear. Zavos et al. (1993) reported a 10% reduction in fertility of Japanese Quail (*Coturnix japonica*) fed a diet of 45% infected fescue seed. It also is unknown whether birds find infected fescue seeds less palatable than uninfected ones, or whether they can discriminate between the two. In this study, we compared mass gains, reproductive rates, and mortality rates of Zebra Finches (*Taeniopygia guttata*) fed infected fescue *ad libitum* to those for conspecifics provided similar assess to uninfected fescue seed. Further, we tested whether these birds can discriminate between infected and uninfected seed.

Methods.—Experiments were conducted in 1992 and 1993 and lasted 18 months. Subjects were 20 pairs of Zebra Finches housed in Utah State University's Laboratory Animal Research Facility. Ambient temperatures were maintained between 21° and 23°C. Finch pairs were housed individually in 0.5 × 0.5 × 0.65 m cages that contained several perches and a straw basket that served as a nest. Each cage contained a water bowl and two feeding cups located 0.4 m apart. At the initiation of these experiments, a male and female finch were randomly paired together. If one died during the experimental period, it was replaced with an adult of the same sex.

Each finch pair was randomly assigned to either of two groups: (1) one received *ad libitum* tall fescue seed (K-31 cultivar) infected with *A. coenophialum* (hereafter called fungus finches); and (2) the other group received an *ad libitum* supply of uninfected fescue seed of the same cultivar (control finches). Approximately once every 10 days fungus finches were given for 48 h an *ad libitum* supply of sprouted infected fescue seed; control finches received similar access to sprouted uninfected seed. To supplement this diet, finches had access to Vita Finch Feed for 6 h each day. They also were allowed free access to water, calcium, and nesting material.

Each finch was weighed when the experiment be-

TABLE 1. Reproductive rates ($\bar{x} \pm$ SE) of Zebra Finches ($n = 10$ pairs) fed a diet containing fescue seeds infected with *Acremonium coenophialum* (fungus finches) or finches ($n = 10$ pairs) fed a diet with uninfected fescue seeds (control finches).

	Fungus finches	Control finches	t^a
Mean egg mass	8.1 ± 0.3	8.7 ± 0.2	1.33
Eggs·pair^{-1}·year^{-1}	21.5 ± 3.8	22.7 ± 2.2	0.27
Chicks·pair^{-1}·year^{-1}	4.5 ± 1.2	4.7 ± 1.1	0.12
Fledglings·pair^{-1}·year^{-1}	3.4 ± 1.2	2.1 ± 0.7	0.92

[a] All $P > 0.05$.

gan and every four months thereafter. Every six months, body temperature of the finches was taken using a rectal probe. Numbers of eggs and chicks in each nest were checked weekly. We considered a chick fledged when it was three weeks old.

Mass and body temperatures of fungus finches were compared to those of control finches using repeated-measures ANOVAs (Myers 1972, Hintze 1990) to test for statistically significant differences ($P < 0.05$). Males and females were analyzed separately unless otherwise noted. If the consumption of infected fungus does not increase finch mortality rates, fatalities should be evenly distributed between control and fungus finch groups. We tested our data against this null hypothesis using the Fisher exact probability test.

Egg size of fungus and control finches were compared by collecting a sample of 125 eggs within 48 h of laying and weighing them. The mean mass of each female's eggs was then determined, and this value for fungus females was compared to that of control females, using a one-way ANOVA.

To assess whether finches preferred uninfected to infected seed, we conducted a one-choice feeding test every four months. During this test, the finches were allowed simultaneous access to infected and uninfected seed for at least an 8-h period. For this test, one of the two feeding cups in each cage was randomly selected and infected seed of known mass was placed in it; uninfected seed was placed in the other. At the end of the period, the seed was reweighed and consumption was defined as the loss in seed mass after any spillage was replaced.

Four times a year, a no-choice feeding test was conducted by recording the amount of fescue seed each fungus bird and control bird consumed during a four- to seven-day period during which their normal routine was maintained. We calculated the mean amount of fescue seed consumed per day for each bird and compared the consumption rates of fungus and control birds using an unpaired t-test.

At the completion of the experiments described above, ambient temperatures were raised over a period of six weeks to 31°–34°C and then maintained for four months. During this period, nests were checked weekly for eggs, chicks, and fledglings. Data on mass and body temperatures were collected in the same manner described above. A one-choice test was conducted (but not a no-choice test). Results from this period were analyzed separately from those collected in the earlier period.

Results.—During the 18-month period, when ambient temperatures were 21°–23°C, one control finch and four fungus finches died. This difference in mortality rates was not statistically significant ($P = 0.5$).

Mean mass of fungus males (12.9 g) and control males (12.9 g) did not differ significantly ($F = 0.02$, df = 1 and 18, $P = 0.90$) during the course of these feeding trials. Not surprisingly, there was a significant season effect ($F = 4.99$, df = 5 and 90, $P < 0.001$) given that males gained mass during the first eight months and maintained it thereafter. Likewise, the mean mass of fungus females (13.6 g) was identical to that of control females (13.6 g) during the course of this experiment; again, there was a seasonal effect ($F = 8.13$, df = 5 and 90, $P < 0.001$) in that females also gained weight during the first eight months.

Body temperature of males ($\bar{x} = 41.8° \pm$ SE of 1.4°C) and females ($\bar{x} = 41.8° \pm 1.4$°C) did not differ ($F = 0.14$, df = 1 and 18, $P = 0.71$). Consequently, temperature data for both sexes were analyzed together. Body temperatures of fungus finches ($\bar{x} = 41.7° \pm 1.5$°C) and control finches ($\bar{x} = 41.8° \pm 1.4$°C) were not significantly different ($F = 0.29$, df = 1 and 38, $P = 0.60$). Moreover, egg mass of fungus finches was similar to control birds (Table 1). Egg, chick, and fledgling production rates were similar between the two groups (Table 1).

Initially, both fungus and control finches exhibited a preference for infected seed when given a choice of fungus infected and uninfected seed (Table 2). After being on a fescue diet for four months, however, both control and fungus finches exhibited a preference for uninfected seeds, a preference that persisted for the entire experiment. Likewise in the no-choice tests, fungus finches given access to infected seed consumed less of it than control finches given uninfected seed (Table 3).

After the temperature was raised to 31°–34°C, 13 fungus finches died (7 males and 6 females), as did 1 control finch (a female). This difference between mortality rates of fungus finches and control finches was statistically significant ($P = 0.016$). The mean body temperature of fungus finches (42.3°C) did not differ from that of control finches (42.2°C). Body mass was

TABLE 2. Results of one-choice feed trials in which Zebra Finches (n = 20 pairs) given access to two feeding trays: (1) one containing tall fescue seeds infected with *Acremonium coenophialum* and (2) the other with tall fescue seeds that were fungus-free.

Month from start	Grams consumed/day ($\bar{x} \pm$ SE) Infected seed	Uninfected seed	t
0	1.38 ± 0.27	0.67 ± 0.14	2.41*
4	1.00 ± 0.12	1.97 ± 0.30	2.65*
8	0.86 ± 0.27	1.93 ± 0.31	3.63**
12	0.50 ± 0.10	1.59 ± 0.30	3.44**
16	0.79 ± 0.10	1.00 ± 0.13	1.28
20	0.47 ± 0.07	0.85 ± 0.16	2.09*

*, $P < 0.05$; **, $P < 0.01$.

TABLE 3. Results of no-choice feed trials in which Zebra Finches (n = 10 pairs) on diet of fescue seeds infected with *Acremonium coenophialum* were given access to infected seeds *ad libitum*, while other finches (n = 10 pairs) on diet of uninfected seed were given similar access to uninfected seeds.

Month from start	Grams consumed/day ($\bar{x} \pm$ SE) Infected seed	Uninfected seed	t
0	1.57 ± 0.10	1.66 ± 0.11	0.52
3	0.30 ± 0.14	0.78 ± 0.14	3.23**
6	0.55 ± 0.07	1.47 ± 0.37	2.47*
12	0.37 ± 0.10	1.25 ± 0.10	4.08**

*, $P < 0.05$; **, $P \leq 0.01$.

similar for fungus finches (females = 14.0 g, males = 13.0 g) and control finches (females = 13.7 g, males = 13.0 g). Reproductive data during the high-temperature period were not analyzed because they were confounded by the high mortality among fungus finches.

Discussion.—In our experiments, the reproductive performance of Zebra Finches was not affected by their consumption of fescue seed infected with *Acremonium coenophialum* when ambient temperatures were 21°–23°C. This contrasts with findings of Zavos et al. (1993), who reported that Japanese Quail suffered a 10% decrease in reproductive performance after eating infected fescue seed. We also found that consuming infected seeds did not affect the ability of Zebra Finches to increase or maintain body mass. Similar findings have been reported by Madej and Clay (1991).

When ambient temperatures were 21°–23°C, consumption of infected fescue seeds had little impact on Zebra Finches, but at higher ambient temperatures, it caused an increase in bird mortality. Likewise, many of the adverse symptoms livestock experience from grazing infected fescue are temperature dependent and only occur in hot weather. Such occurs because alkaloids produced by the fungus, especially ergovaline, inhibit the ability of livestock to lose excess heat (Aldrich et al. 1993, Schmidt and Osborn 1993). The same may be true in avian species. In our experiments, Zebra Finches that consumed infected grass exhibited a slight, but nonsignificant, increase in body temperature over the control group.

Upon first exposure to fescue, Zebra Finches preferred consuming infected over uninfected fescue seed, but this preference reversed after the birds had consumed fescue for four months. Furthermore in no-choice tests, finches given infected seed consumed less than those given uninfected seed. Likewise, birds captured in fields containing infected fescue (we assume that these birds had foraged on tall fescue seeds in the past) exhibited a preference for uninfected tall fescue seeds over infected ones (Madej and Clay 1991). While alkaloids often have a bitter taste, the experimental birds' initial preference for infected seed and their delay in developing an aversion to it indicates that this aversion may be based on postingestion feedback. Creation of such an aversion should help protect avian species from the adverse impacts of infected fescue. It also suggests that birds will be most vulnerable either before they have developed an aversion or in situations where alternate foraging opportunities are limited.

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LITERATURE CITED

ALDRICH, C. G., J. A. PATERSON, J. L. TATE, AND M. S. KERLEY. 1993. The effects of endophyte-infected tall fescue on diet utilization and thermal regulation in cattle. J. Anim. Sci. 71:164–170.

ARACHEVALETA, M., C. W. BACON, C. S. HOVELAND, AND D. E. RADCLIFFE. 1989. Effect of the tall fescue endophyte on plant response to environmental stress. Agron. J. 81:83–90.

BOUTON, J. H., R. N. GATES, D. P. BELESKY, AND M. OWSLEY. 1993. Yield and persistence of tall fescue in the southeastern coastal plain after removal of its endophyte. Agron. J. 85:52–55.

CLAY, K. 1988. Fungal endophytes of grasses: A defensive mutualism between plants and fungi. Ecology 69:10–16.

GODFREY, V. B., S. P. WASHBURN, E. J. EISEN, AND B. H. JOHNSON. 1994. Effects of consuming endophyte-infected tall fescue on growth, reproduction and lactation in mice selected for high fecundity. Theriogenology 41:1393–1409.

HINTZE, J. L. 1990. Number cruncher statistical system. NCSS, Kaysville, Utah.

HOVELAND, C. S., S. P. SCHMIDT, C. C. KING, JR., J. W. ODOM, E. M. CLARK, J. A. MCGUIRE, L. A. SMITH, H. W. GRIMES, AND J. L. HOLLIMAN. 1983. Steer performance and association of *Acremonium coenophialum* fungal endophyte on tall fescue pasture. Agron. J. 75:821-824.

JOHNSON, M. C., D. L. DAHLMAN, M. R. SIEGEL, L. P. BUSH, G. C. M. LATCH, D. A. POTTER, AND D. R. VARNEY. 1985. Insect feeding deterrents in endophyte-infected tall fescue. Appl. Environ. Microbiol. 49:568-571.

KIMMONS, C. A., K. D. GWINN, AND E. C. BERNARD. 1990. Nematode reproduction on endophyte-infected and endophyte-free tall fescue. Plant Dis. 74:757-761.

LATCH, G. C. M., M. J. CHRISTENSEN, AND D. L. GAYNOR. 1985. Aphid detection of endophyte infection in tall fescue. N. Z. J. Agric. Res. 28:129-132.

MADEJ, C. W., AND K. CLAY. 1991. Avian seed preference and weight loss experiments: The effect of fungal endophyte-infected tall fescue seeds. Oecologia 88:296-302.

MYERS, J. L. 1972. Fundamentals of experimental design. Allyn and Bacon, Boston, Massachusetts.

SCHMIDT, S. P., AND T. G. OSBORN. 1993. Effects of endophyte-infected tall fescue on animal performance. Agric. Ecosystems Environ. 44:233-262.

SHELBY, R. A., AND L. W. DALRYMPLE. 1987. Incidence and distribution of the tall fescue endophyte in the United States. Plant Dis. 71:783-786.

STUEDEMANN, J. A., AND C. S. HOVELAND. 1988. Fescue endophyte: History and impact on animal agriculture. J. Prod. Agric. 1:39-44.

THOMPSON, F. N., AND J. A. STUEDEMANN. 1993. Pathophysiology of fescue toxicosis. Agric. Ecosystems Environ. 44:263.

VARNEY, D. R., C. J. KAPPES, S. L. JONES, R. NEWSOME, M. R. SIEGEL, AND P. M. ZAVOS. 1988. The effect of feeding tall fescue seed infected by *Acremonium coenophialum* on pregnancy and parturition in female rats. Comp. Biochem. Physiol. C Comp. Pharmacol. 89:315-320.

VARNEY, D. R., M. NDEFRU, S. L. JONES, R. NEWSOME, M. R. SIEGEL, AND P. M. ZAVOS. 1987. The effect of feeding endophyte infected tall fescue seed on reproductive performance in female rats. Comp. Biochem. Physiol. C Comp. Pharmacol. 87:171-175.

ZAVOS, P. M., A. H. CANTOR, R. W. HEMKEN, R. J. GROVE, D. R. VARNEY, AND M. R. SIEGEL. 1993. Reproductive performance of Japanese Quail fed tall fescue seed infected with *Acremonium coenophialum*. Theriogenology 39:1257-1266.

ZAVOS, P. M., B. SALIM, J. A. JACKSON, JR., D. R. VARNEY, M. R. SIEGEL, AND R. W. HEMKEN. 1986. Effect of feeding tall fescue seed infected by endophytic fungus (*Acremonium coenophialum*) on reproductive performance in male rats. Theriogenology 25:281-290.

ZAVOS, P. M., M. R. SIEGEL, R. J. GROVE, R. M. HEMKEN, D. R. VARNEY. 1990. Effects of feeding endophyte-infected tall fescue seed on reproductive performance in male CD-1 mice by competitive breeding. Theriogenology 33:653-660.

ZAVOS, P. M., D. R. VARNEY, R. M. HEMKEN, M. R. SIEGEL, AND L. P. BUSH. 1988a. Fertilization rates and embryonic development in CD-1 mice fed fungal endophyte-infected tall fescue seed. Theriogenology 30:461-468.

ZAVOS, P. M., D. R. VARNEY, J. A. JACKSON, R. W. HEMKEN, M. R. SIEGEL, AND L. P. BUSH. 1988b. Lactation in mice fed endophyte-infected tall fescue seed. Theriogenology 30:865-875.

ZAVOS, P. M., D. R. VARNEY, J. A. JACKSON, M. R. SIEGEL, L. P. BUSH, AND R. W. HEMKEN. 1987. Effect of feeding fungal endophyte (*Acremonium coenophialum*)-infected tall fescue seed on reproductive performance in CD-1 mice through continuous breeding. Theriogenology 27:549-559.

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