Panama alone. Thus, the potential for female Tyrannidae to sing seems to be generalized. It is then surprising that among nonduetting tyrannids, only Eastern Phoebe (*Sayornis phoebe*) and Willow Flycatcher females are known to sing (Smith 1969, this study). Ritchison (1983) reported that breeding females of the Gray-capped Flycatcher (*Myiozetetes granadensis*) also sing. This was based on a description of the species' nesting behavior by Skutch (1953). I believe, however, that Skutch described duetting. Farabaugh (1982) included *M. granadensis* in her list of Panamanian duetters.

The songs of female flycatchers are identical to those of males (Smith 1969; Kroodsma 1984, 1985; this study). Such similarity, and the absence of sexual dimorphism in Tyrannidae, may explain the scarcity of reports of female singing in that family. Careful observations on birds of known sex will be required to determine the extent of female singing in tyrannid species.

Several hypotheses have been proposed to explain the occurrence of song in female birds (e.g. Armstrong 1963, Van Tyne and Berger 1976). All singing females I observed sang during simulated territorial encounters, suggesting that territorial defense is one function of female song in Willow Flycatchers. Singing by female Willow Flycatchers may also serve other functions. Detailed behavioral studies will have to be conducted to completely understand the functional significance of female singing by this species.

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Limitations of Tetracycline in Tracing Multiple Maternity

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A central assumption in many studies of monogamous birds is that kinship or parentage can be inferred reliably from patterns of parental care (Gowaty and Karlin 1984). However, offspring in a single clutch or brood may have multiple parentage (Andersson 1984, Gowaty and Karlin 1984, Harvey 1985). In such cases, estimates of the reproductive success of the putative parents may be affected considerably (Harvey 1985). Methods therefore are needed to identify eggs or young that belong to individuals other than the male or female attending the nest. Maternity and paternity exclusion based on electrophoretic protein variation has met with only limited success (see Gowaty and Karlin 1984, Scott and Tan 1985). A second approach has used nonintrusive markers that are fed or injected into an individual, and can be detected subsequently in the resulting eggs or offspring (Appleby and McRae 1983, Dickman et al. 1983, Scott and Tan 1985).

Haramis et al. (1983) proposed that tetracycline could be used as a marker to trace maternity. When injected intraperitoneally, tetracycline chelates with calcium ions in the forming eggshell and can be detected by a characteristic fluorescence when exposed to ultraviolet light. Haramis et al. (1983) used tetracycline to identify eggs of individual female Wood Ducks (*Aix sponsa*) in several different nests. They did not detect any adverse side effects of tetracycline, and suggested that it was a safe and effective marker. We report that tetracycline may have adverse effects on the egg-laying rate of nesting birds and therefore should be used with caution in estimating the reproductive success of individual females. We suggest some situations in which tetracycline nonetheless might be useful.

We conducted three experiments to assess the utility of tetracycline as an egg marker. In experiment 1, domestic hens were subjected to one of four treatments: (1) high-dosage injection of tetracycline (250 mg tetramycin suspended in 2.5 cc of distilled water; dose equals approximately 100 mg/kg bird), (2) low-dosage injection of tetracycline (125 mg of tetramycin suspended in 2.5 cc of distilled water = 50 mg/kg bird), (3) sham injection of 2.5 cc distilled water, and (4) control (no injection). The high dosage was equivalent to that used by Haramis et al. (1983). Egg laying by all birds was followed for 2 weeks before treatment and up to 30 days after treatment. All hens had been laying eggs for at least 1 week before the start of the experiment.

Tetracycline has been shown to interfere with calcium deposition and bone growth in humans, rats, and domestic chicks (Cleall et al. 1964, Demers et al. 1968). Tetracycline could inhibit egg laying in birds by interfering with calcium metabolism or deposition during egg formation. We tested this possibility in experiment 2. Domestic hens were assigned to one of three treatments: (1) low-dosage injection of tetracycline (as above), (2) low-dosage injection followed by an oral supplement of 600 mg calcium (dose = 250 mg calcium/kg using Calcite® tablets), and (3) control (as above). Experiment 2 was conducted 1 month after experiment 1 using new birds. Egg laying by all hens was followed for 2 weeks before treatment and 2 weeks after treatment.

In experiment 3, we injected 5 wild female Barrow's Goldeneyes (*Bucephala islandica*) with a dosage of 75–100 mg/kg tetracycline on a study area near 100 Mile House, British Columbia, Canada (description of study area in Eadie and Gauthier 1985). Goldeneye females were trapped on their nest midway through egg laying, injected with tetracycline, and released. We inspected each female's nest, along with all other nests within 1 km, every day or every other day and used a portable ultraviolet light to detect eggs labeled with tetracycline.

In all cases, eggs of domestic hens injected with tetracycline were easily distinguished from eggs of sham or control females when examined under ultraviolet light. There were no qualitative differences in the degree of fluorescence between the high- and low-dosage groups. In some females, tetracycline was detected in eggs up to 20 days after injection. These results show that tetracycline can be used to mark eggs of individual females, consistent with the findings of Haramis et al. (1983).

However, tetracycline reduced the egg-laying rate of injected females. In experiment 1, both high- and low-dosage females had a significantly lower rate of egg laying than did sham or control females (all $P < 0.05$, Mann-Whitney U-test; Table 1A). There was no significant difference between sham and control females, nor between high- and low-dosage females. Moreover, we found no significant relationship between egg-laying rate and mass-specific dosage ($r = 0.14$, $P > 0.10$, $n = 15$). Thus, the depression in egg laying was not due to handling stress and did not appear to be dependent on dosage for the range tested.

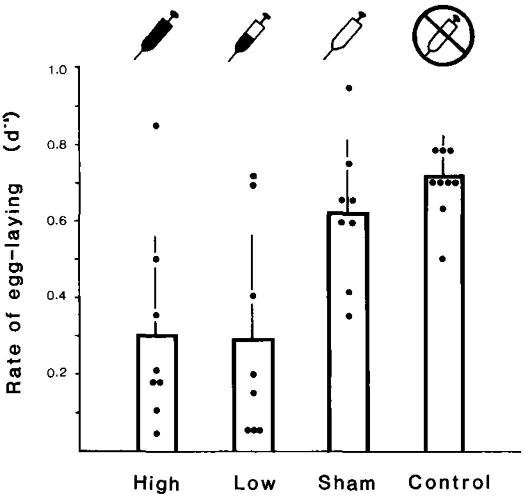

Fig. 1. Variation in egg-laying rates of domestic hens injected with a high or low dosage of tetracycline compared with sham injected and control females. Histograms represent means, lines are 1 SE.

Injection of tetracycline produced a cessation of laying by females. High- and low-dosage females laid a mean of 3.5 eggs after injection and then did not resume laying until 16 days, on average, after treatment (Table 1A). In contrast, sham and control females laid 6–8 eggs in the 10 days following the injection date, and there was no apparent delay in the resumption of laying. Number of eggs laid after the injection date and number of days to resume laying differed significantly between tetracycline (high- and low-dosage) and nontetracycline (sham and control) females, but did not differ significantly within these groups (Mann-Whitney U-tests; Table 1A). There was, however, considerable variation among females in each treatment group (Fig. 1). Egg-laying rates of some of the females treated with tetracycline were not affected; 3 of 8 (37%) high-dosage females and 3 of 8 low-dosage females laid eggs at a rate and pattern comparable to sham and control females (Fig. 1). We do not know the reason for this variation.

Females treated with tetracycline and a calcium supplement exhibited a higher rate of egg laying compared with females injected with tetracycline only

TABLE 1. The effects of tetracycline on the egg laying of domestic hens. Values are means ± 1 SE.

Treatment (n)	Dosage (mg/kg)	Bird mass (kg)	Laying rate (eggs/day)	No. of eggs laid[a]	No. of days to resume laying
A. Tetracycline treatment					
High (8)	120 ± 10	2.2 ± 0.1	0.30 ± 0.26	3.6 ± 0.8	16.1 ± 5.0
Low (8)	50 ± 10	2.4 ± 0.1	0.29 ± 0.28	3.5 ± 0.9	16.3 ± 5.2
Sham (8)	0	2.3 ± 0.1	0.62 ± 0.19	6.3 ± 0.8	0.8 ± 0.2
Control (9)	0	—	0.71 ± 0.09	8.8 ± 0.3	0.2 ± 0.2
B. Tetracycline + calcium					
Tetra (4)	50	—	0.11 ± 0.04	1.0 ± 0.4	—
Tetra + Ca (4)	50/250	—	0.42 ± 0.14	3.8 ± 0.1	—
Control (4)	0	—	0.72 ± 0.11	6.5 ± 1.0	—

[a] Number of eggs laid in the first 10 days after injection.

(Mann-Whitney U-test, $P = 0.057$; Table 1B). Both groups of females treated with tetracycline had a lower rate of egg laying than did control females, although this difference was significant only for the females without a calcium supplement (tetracycline-only vs. controls: $P < 0.014$; tetracycline + calcium vs. controls: $0.05 < P < 0.10$; Table 1B). Although sample sizes were small, this experiment suggests that tetracycline inhibits egg laying in birds by interfering with calcium metabolism or deposition. Administration of a calcium supplement partially mitigated these effects.

These results indicate tetracycline should not be used in studies that require an accurate assessment of the reproductive success of individual females. Clutch sizes of treated females will be depressed significantly. However, tetracycline may be useful in studies where it is not necessary that marked females lay a full clutch. For example, Haramis et al. (1983) tested the hypothesis that Wood Ducks lay eggs parasitically if they have lost their own clutch. They injected nesting hens with tetracycline, removed the clutches of these females, and then traced further egg laying using the ultraviolet fluorescence. In this experiment, it was necessary only that marked females lay at least some eggs after being treated with tetracycline. One female laid up to 6 eggs after treatment. Our experiments show that domestic hens laid 3-4 eggs after an injection of tetracycline, and some females laid as many eggs as control hens (Fig. 1).

We repeated the experiment with a sample of wild Barrow's Goldeneyes. For 3 of the 5 females tested, we removed the entire clutch of eggs from the nest (range 3-6 eggs) immediately following injection. We removed only part of the clutch (1 of 8 eggs and 4 of 9 eggs) from the nests of two other females. We did not find tetracycline-labeled eggs in any nest on the study area for 3 of these females. The remaining 2 females laid one egg each after injection, and in both cases the eggs exhibited the characteristic fluorescence. Interestingly, these females were the two suffering only a partial nest loss, and both laid the labeled egg in her original nest, incubated the remaining eggs, and successfully hatched the clutch. The tetracycline-treated eggs hatched in these nests, and the resulting young did not differ in size or apparent behavior from their nest mates.

Tetracycline appears to be a useful marker under some circumstances, and does not appear to affect the viability of the eggs or the survival of the female. Further research is needed to examine the effects of tetracycline and other egg markers on egg-laying rates in wild birds. Until such studies are carried out, these methods should be used with caution.

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It Is Expensive To Be Dominant

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Many animals spend long periods in groups. The advantages of being a group member, compared with solitary living, include improved predator avoidance and increased feeding efficiency (Pulliam and Caraco 1984). However, the costs and benefits involved may differ among the group members. The results of individual contests are usually heavily biased in favor of the dominant individuals, who generally obtain more food, enjoy a more protected position within the group, and enjoy improved chances of survival than do their subordinates (Baker and Fox 1978, Kikkawa 1980, Morse 1980, Baker et al. 1981). By allocating time to aggression, dominant individuals may increase their chances of daily survival (Pulliam and Caraco 1984), even if they risk being hurt. The benefits of dominance can be diminished, however, by more frequent involvement in aggressive encounters (Järvi and Bakken 1984). An increase in the metabolic rate, due to more frequent aggressive encounters and mediated through hormone levels, could represent one proximate pathway of meeting the costs of dominance (cf. Røskaft et al. 1986). Based on the functional relationship that exists between endocrine activity and metabolism (Silver et al. 1979, Hänssler and Prinzinger 1979), one would predict that a relationship should exist between the metabolic rate and the social status of each group member, and that a change in social status will entail changes in the metabolic rate, especially among the dominants. I tested these predictions by manipulating the composition of free-ranging, winter flocks of Willow Tits (*Parus montanus*).

The Willow Tit is a highly sedentary European species. Breeding pairs remain in their exclusive areas throughout the year. During the winter these areas are defended by small, non-kin flocks, formed as the roaming yearlings become sedentary and join the adults during the late summer and autumn. Once established, stable hierarchies are maintained in these flocks during the winter.

I studied Willow Tits living in a subalpine mixed forest in central Norway. The social rank order of six members of each of six such winter flocks, and oxygen-consumption rates of each bird, were studied. All birds were caught in mist-nets or feeder-traps during August-October 1984. They were individually color-banded, aged, and their wing lengths were measured. The dominant-subordinate relationships within each flock were determined by observation of the outcomes of behavioral interactions at feeders placed in the center of the territory of each of the flocks studied (Hogstad 1987).

The experiments were made between November 1984 and January 1985. Oxygen-consumption rates were measured by using a manometric respirometer (with a 20% KOH solution as CO_2 absorber) connected to a compensatory chamber (Dixon 1934). Constant pressure was maintained by injecting pure oxygen into the respirometer chamber, and the amount of oxygen injected equaled the amount of oxygen consumed. All values are given in STP conditions. The measurements were made between 1100 and 1300 at an ambient temperature of 5°C. The birds were caught 1-12 min before the experiments started, and were kept in the dark during the experiments. The body mass of each bird was recorded before the start of each experiment. Immediately after measuring their oxygen-consumption rates, all birds, except the most dominant one in three flocks and one of the subordinates in the three other flocks, were released in their original territories. A week later, the oxygen-consumption rates of the five birds released in each flock, and their present social rank order within the same flocks, were redetermined.

The initial oxygen-consumption rates of the individual birds varied considerably, ranging from 9.7 to 12.6 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ (Table 1). This variation could be due to differences in body size, age, sex, or dominance status. The intercorrelations among these factors are given in Table 2. A multiple regression anal-