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ABSTRACT

Traplining hummingbirds have been observed to change their foraging behavior in response to a change in resource availability. Generally, trapliners change to territorial behavior when presented with an economically defendable resource. I investigated the degree to which aggressive behavior increases by observing changes in behavior frequency in response to increased resources. I observed that trapliner species showed an increase in aggressive behavior and a decrease in the total frequency of traplining behavior following the introduction of increased resources. My study also supports that traplining hummingbirds could switch their foraging behavior to territoriality when resources become economically defendable.

RESUMEN

Se han observado colibríes que cambian su conducta de alimentación como respuesta al cambio de la existencia de recursos. En general, los ermitaños cambian su conducta al territorialismo cuando tienen un recurso que vale la pena defender. Yo investigué el aumento de conducta agresiva al observar los cambios en la frecuencia de conducta antes y después de aumentar los recursos. Yo observé que las especies de ermitaños aumentaron su conducta agresiva, y que todas las especies disminuyeron su conducta rutera después de que aumente la cantidad de recursos. Los resultados de esta investigación indican que los colibríes ermitaños pueden cambiar su conducta de alimentación al territorialismo cuando vale la pena defender los recursos.

INTRODUCTION

Hummingbirds (family Trochilidae) are important pollinators for many species of plants, particularly in the tropics, where they play an important role as facilitators of outcrossing between plant populations. They also help maintain genetic variability among neighboring plant populations (Feinsinger 1978) through their movement between different areas (Buono 2005) and their far-reaching flight capabilities. Several types of foraging behaviors have been observed among the species of hummingbirds found in Costa Rica, the two most prominent being "territoriality" and "traplining". Territoriality is a foraging strategy typically observed among the more aggressive species, such as the Purple-throated Mountain gem (Stiles and Skutch 1989). These birds fiercely defend an area of relatively dense resources against all competitors, conspecific or otherwise. The economic defendability of a resource (the value of defending the resource) depends on three main factors: resource quality and spatial distribution, temporal distribution of the resource, and competition for the resource (Davies and Houston 1984). In the case of territorial hummingbirds, it is more energetically efficient to vigorously defend an abundant resource as long as the benefits of the resource sufficiently outweigh the cost of its

defense. Traplining, on the other hand, is used principally by less-aggressive species that follow a specific route and visit multiple locations of different resources (e.g. Violet Sabrewings). The sites along the trapline are typically not adequate to justify defense as a primary resource. Therefore, the hummingbirds must visit more sites and expend more energy in foraging, which is ultimately the more energetically efficient option, as opposed to defending such a small territory. If the resource richness along the trapline changes to include higher densities (as in flowering peaks), some species will switch behaviors from traplining to territoriality (Fogden and Fogden 2005). However, the conditions under which behavior switching occurs are currently unclear.

A community-wide switch to territorial behavior could have seriously detrimental effects on the genetic health and variability of local plant populations. If a highly rich resource developed that allowed the local guild of hummingbirds to concentrate their foraging on a small territory, the plants contributing the resource could suffer from high rates of self-pollination. The pollination of heterospecific plants flowering simultaneously suffers due to the high rate of pollen loss that occurs when hummingbirds move indiscriminately between multiple species (Feinsinger 1978, Feinsinger and Tiebout 1991). However, studies indicate that many plants have evolved flowering peaks at different times to avoid competition for pollinators (Feinsinger 1978, Stiles 1977) and potential hybridization.

Behavior switching may also have significant consequences for pollination in terms of the reorganization of a local nectarivorous bird guild. One study observed that the dominance of one territorial hummingbird species was responsible, in large part, for determining the roles and foraging patterns of all other species in the study community (Feinsinger 1976). Subsequent changes in resource availability led to changes in the behavior of the dominant species, which then interfered with the foraging patterns of other nonterritorial species. Significant fluctuations in resource availability could have important implications for pollination and outcrossing.

The aim of this study is to determine the degree to which aggressive behavior changes (and under what conditions behavior switching occurs) by simulating a flowering peak through increasing resource availability. I hypothesize that traplining hummingbirds will switch their behavior to territoriality when presented with an economically defendable resource. I predict that the amount of aggressive behavior (Table 1) will be highest in the treatment that has the greatest quantity of resources due to the probable highest benefit—cost factor. I also predict that, in this treatment, the number of feeders visited along a trapline will decrease.

METHODS

STUDY SITE AND TREATMENTS

I performed this study at the Estación Biológica de Monteverde in an open clearing surrounded by forest edge. I chose four sites where I could easily hang multiple hummingbird feeders, with each feeder at least one meter below the supporting branch and at least one and one half meters above the ground. Each of the four sites was at least ten meters from the others, and arranged to be visible from a peripheral location (also at least ten meters from each site).

For the first treatment, one feeder was hung at each study site, filled with a 25% sugar solution (methods modified from McMahon 2005). The hummingbirds were given three days to discover the study site and to adjust their behavior before recording data.

For the second treatment, I added two feeders to each site, spaced at least one meter apart. The hummingbirds were allowed adapt to the new setup for two days before recording data.

DATA COLLECTION

Prior to observation, I predetermined seven behavior types (Table 1). From my observation point, I recorded behavior at each feeder site simultaneously for up to two hours per day. All observation periods took place between 8 am and 12 pm from October 25, 2007 to November 11, 2007. I recorded data for nine total hours during the first treatment and eight total hours during the second treatment.

At each site I recorded the number of each type of behavior per species (male and female combined). Observed species and feeding classification are listed in Table 2. If I was unable to identify an individual, I recorded the species as "Unknown" and included all unknown values in the territorial category of my analysis because all behaviors were typically aggressive during the first treatment, indicating a territorial species.

STATISTICAL ANALYSIS

For each treatment and type of behavior, I grouped all data together based on the feeding classification of each hummingbird species (territorial or traplining), combining all data from each site. I then standardized the data from each day into measurements of behavior per hour.

I used a Chi-squared Goodness of Fit test to compare values between Treatments 1 and 2 for both feeding classifications for each type of behavior.

RESULTS

I observed a total of seven hummingbird species, three considered to be territorial and four considered to be trapliners (Table 2).

In general, the behavior of traplining hummingbirds differed between treatments more often than that of territorial hummingbirds. Activity also generally increased from Treatment 1 to Treatment 2 in all observed behavior types. The recorded frequency of feeding behavior in traplining species increased between Treatments 1 and 2, but was not different for territorial species in Treatment 2 (Fig. 1). The same trend occurred for perching behavior (Fig. 2). However, both hummingbird classifications (traplining and territorial) showed increased frequencies of chasing, calling, and hovering behaviors (Figs. 3-5) between Treatments 1 and 2. The confronting behavior in traplining hummingbirds decreased between the two treatments, but territorial hummingbirds did not differ in confrontation from the first to the second treatment (Fig. 6). For total traplining behavior, fewer feeders were visited on a trapline in Treatment 2 (Fig. 7).

DISCUSSION

The purpose of this study was to observe the degree to which aggressive behavior changes due to an increase in resource availability. As predicted, the data indicate more frequent instances of aggression in the treatment with higher resource availability (Figs. 2-6). This is most likely due to the higher benefit—cost factor inherent in greater resource availability. A study on competition in caged hummingbirds found that increased aggressive behavior led to higher energetic success in terms of the maintenance of constant energy stores and body mass over 24 hours (Tiebout 1993). For this reason, hummingbirds could gain an energetic advantage by increasing aggressive behavior when resources are more abundant, as in Treatment 2.

Also as predicted, the total number of feeders visited along traplines per hour decreased from the first to the second treatment. Such a reduction of traplining behavior in a natural setting could severely alter the pollination of plant species, due to increased self-pollination, hybridization, and from the disruption of foraging strategies in traplining species (Feinsinger 1976 and 1978, Stiles 1977).

Although confronting behavior by traplining hummingbirds decreased between Treatments 1 and 2, this could be due to a higher rate of success at chasing away competitors. Confrontations were defined as an aggressive interaction in which one individual did not succeed in chasing the other away (Table 1). But if the trapliners were more successful at chasing in the second treatment, this would cause a decrease in confrontations and an increase in frequency of chasing behavior (Figs. 6 and 3).

The increase in the frequency of aggressive behavior of traplining species combined with the decrease in the number of feeders visited on traplines suggests that traplining hummingbirds may switch their behavior to territoriality when presented with an economically defendable resource. Despite the increased competition and energy expended from its defense, the benefits associated with greater spatial distribution of the resource outweigh the costs of aggressive behavior.

Although the data indicate a change towards territorial behavior in traplining species as resources increased, a future study might investigate the change between three different treatments (the third treatment might include five feeders per site). While the hummingbirds may exhibit increased territoriality between the second and third treatments, they may conversely decrease their aggressive behavior in response to richness of the resource (McMahon 2005).

Another possibility for future study would be to observe traplining behavior in response to varying nectar concentrations. It would be interesting to compare the changes in foraging behavior based on fluctuating spatial distribution (number of feeders, this study) and resource richness (nectar concentration).

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Many people contributed greatly to the success of this project, and for that I owe them my deepest gratitude. I would like to thank the Estación Biológica de Monteverde, Tania Chavarría for all her avian and statistical savvy, Alan and Karen Masters for their enthusiasm and refinement of my study, Pablo Allen and Taegan McMahon for answering my endless questions, and my wonderful classmates for their continuous support and for making me laugh every day.

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TABLE 1. *A summary of standardized behaviors recorded at each site*.

Behavior	Description
Feeding	Each time an individual visits a feeder and feeds, regardless of how many times the bird inserts its beak into the feeder.
Perching*	Each time an individual perches near (within 3 meters of) the feeder site, for any length of time.
Chasing*	When one individual chases another away from the feeder site.
Calling*	Each time an individual calls, regardless of the duration of the calling sequence.
Hover*	When an individual hovers around a feeder but does not insert its beak. Also when one individual hovers around a feeding individual, but the latter does not respond.
Confront*	When two individuals engage in aggressive confrontations, but neither actually chases the other away for at least three seconds.
Traplining	When an individual consecutively feeds at two or more feeders (recorded all species together and analyzed all numbers as "Total Traplining")

*Denotes aggressive behavior

TABLE 2. *Observed species and feeding type classification.*

Common Name	Scientific Name	Feeding Behavior
Coppery-headed Emerald	*Elvira cupreiceps*	Trapliner
Green Violet-ear	*Colibri thalassinus*	Trapliner
Magenta-throated Woodstar	*Calliphlox bryantae*	Territorial
Purple-throated Mountain-gem	*Lampornis* (*castaneoventris*) *calolaema*	Territorial
Ruby-throated Hummingbird	*Archilochus colubris*	Trapliner
Striped-tailed Hummingbird	*Eupherusa eximia*	Territorial
Violet Sabrewing	*Campylopterus hemileucurus*	Trapliner

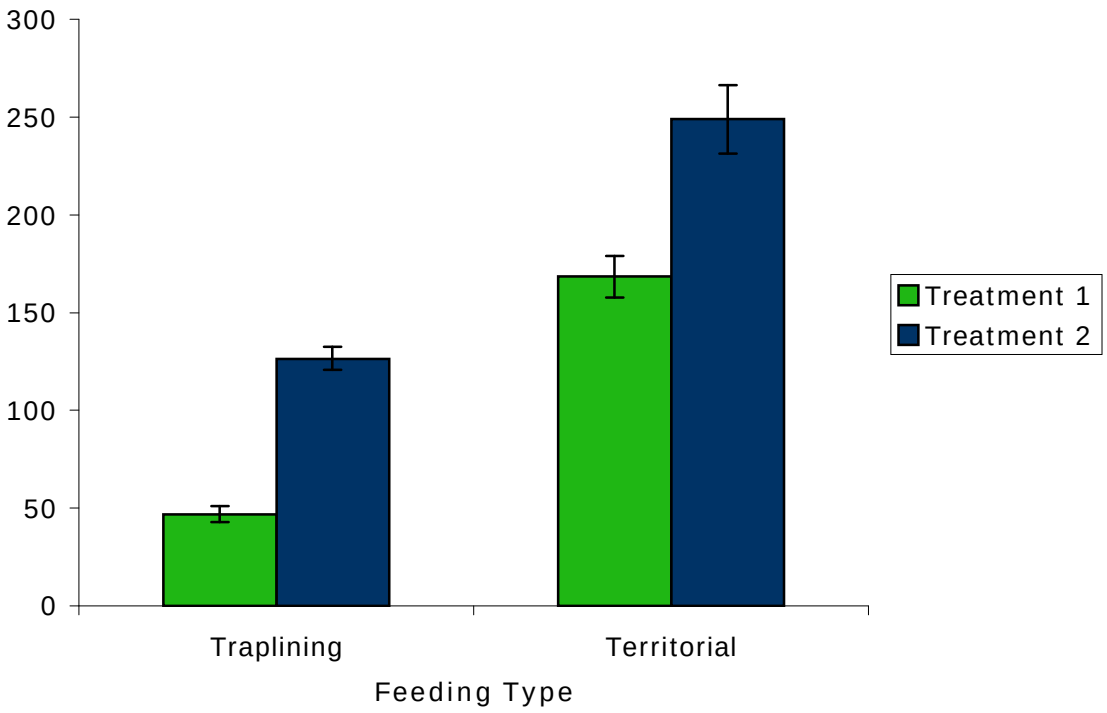

FIGURE 1. Instances of feeding for traplining species increased significantly between Treatments 1 and 2 ($X^2 = 12.17$, df = 1, P = 0.0005). Trends for territorial species indicate an increase in the number of behavior from Treatment 1 to 2 ($X^2 = 0.022$, df = 1, P = 0.881), though not significant.

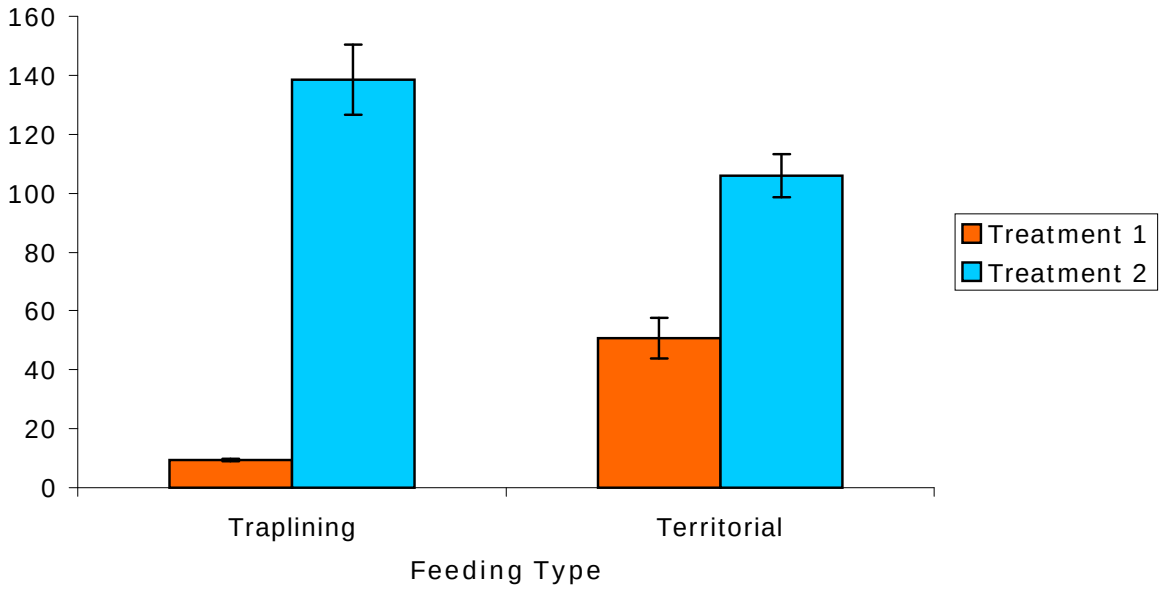

FIGURE 2. Traplining species exhibited a significant increase in perching from Treatment 1 to Treatment 2 ($X^2 = 69.90$, df = 1, $P < 0.0001$). The observed numbers of perching behavior per hour did not differ significantly between treatments for territorial hummingbirds ($X^2 = 3.83$, df = 1, $P = 0.05$).

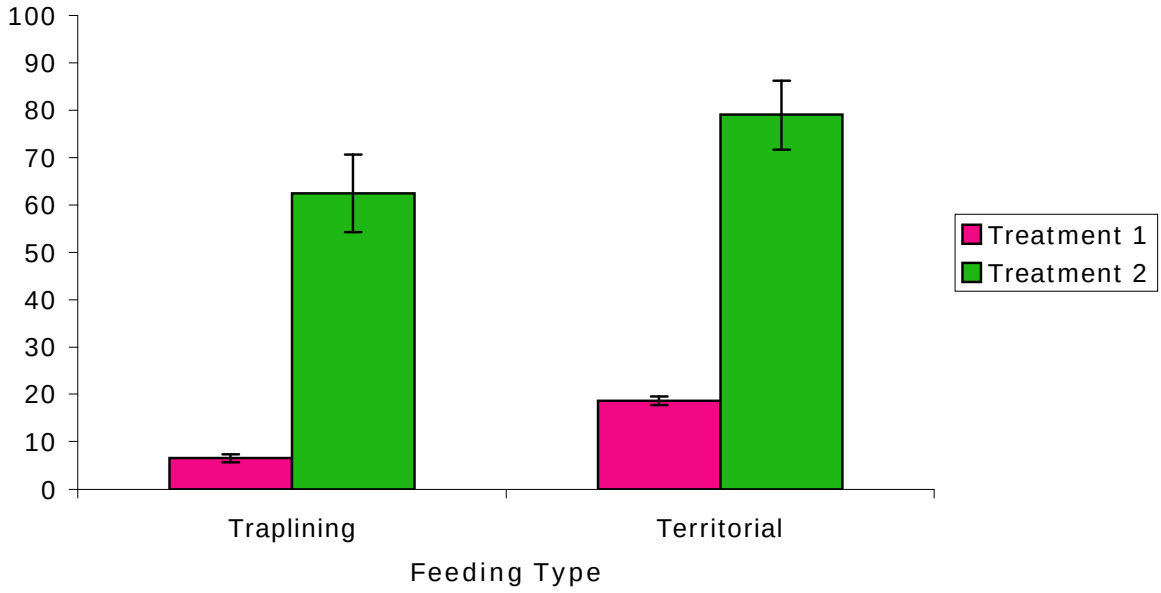

FIGURE 3. The recorded instances of chasing behavior per hour increased significantly between treatments for both traplining ($X^2 = 26.89$, df = 1, $P < 0.0001$) and territorial ($X^2 = 17.74$, df = 1, $P < 0.0001$) species of hummingbirds.

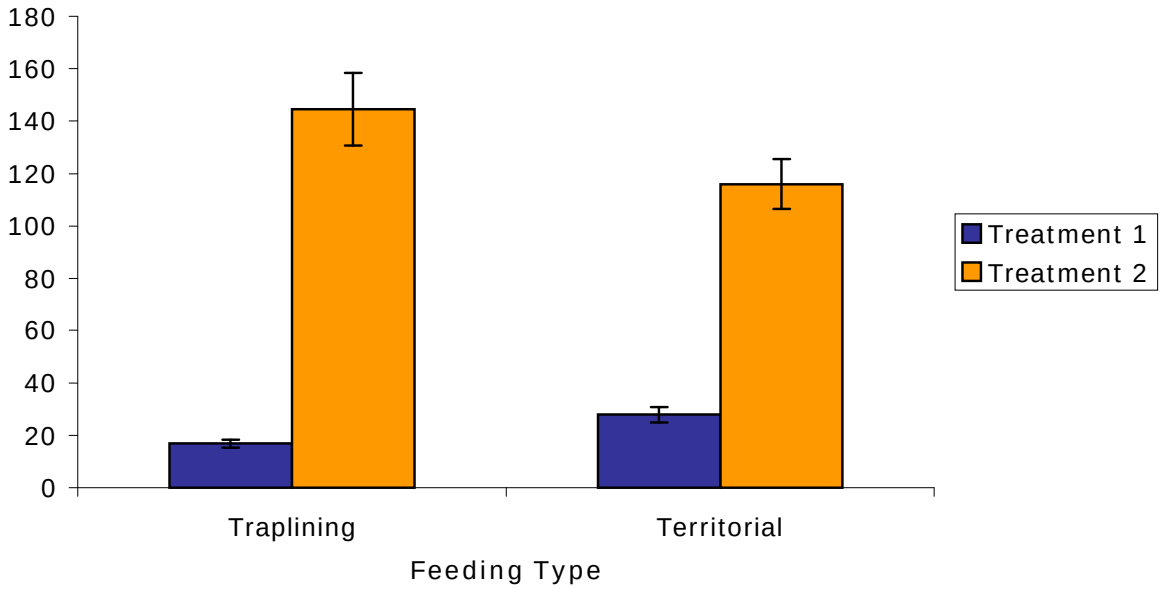

FIGURE 4. The observed calling behavior per hour increased significantly between Treatments 1 and 2 for both traplining ($X^2 = 58.76$, df = 1, $P < 0.0001$) and territorial ($X^2 = 25.33$, df = 1, $P < 0.0001$) feeding classifications.

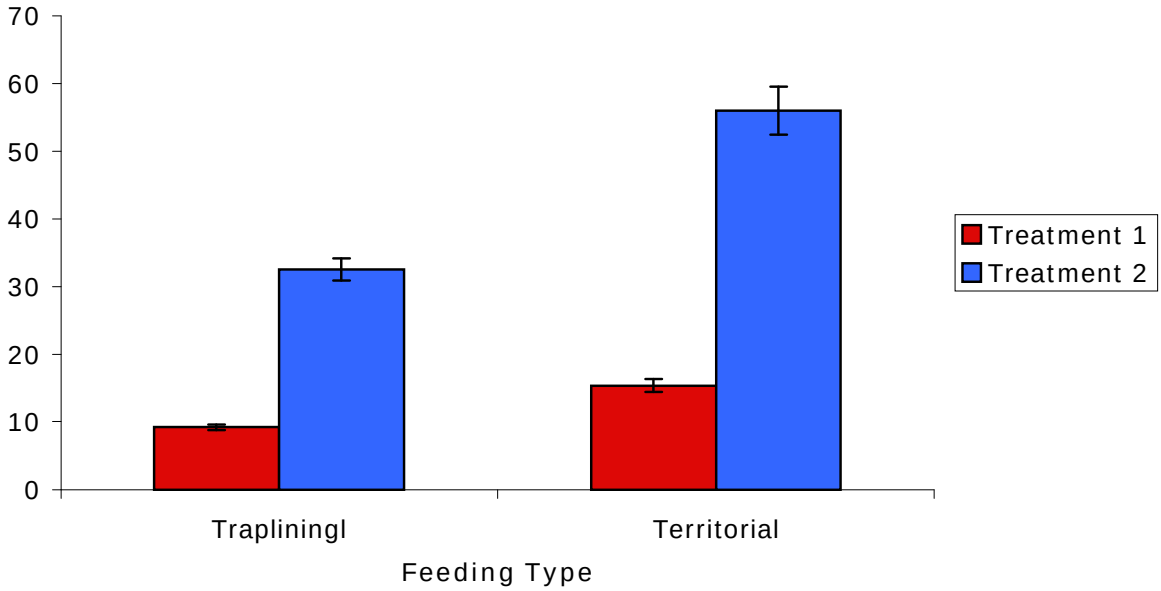

FIGURE 5. The recorded numbers of hovering per hour increased significantly from Treatment 1 to Treatment 2 for both traplining ($X^2 = 5.62$, df = 1, $P = 0.018$) and territorial ($X^2 = 10.18$, df = 1, $P = 0.0014$) species of hummingbirds.

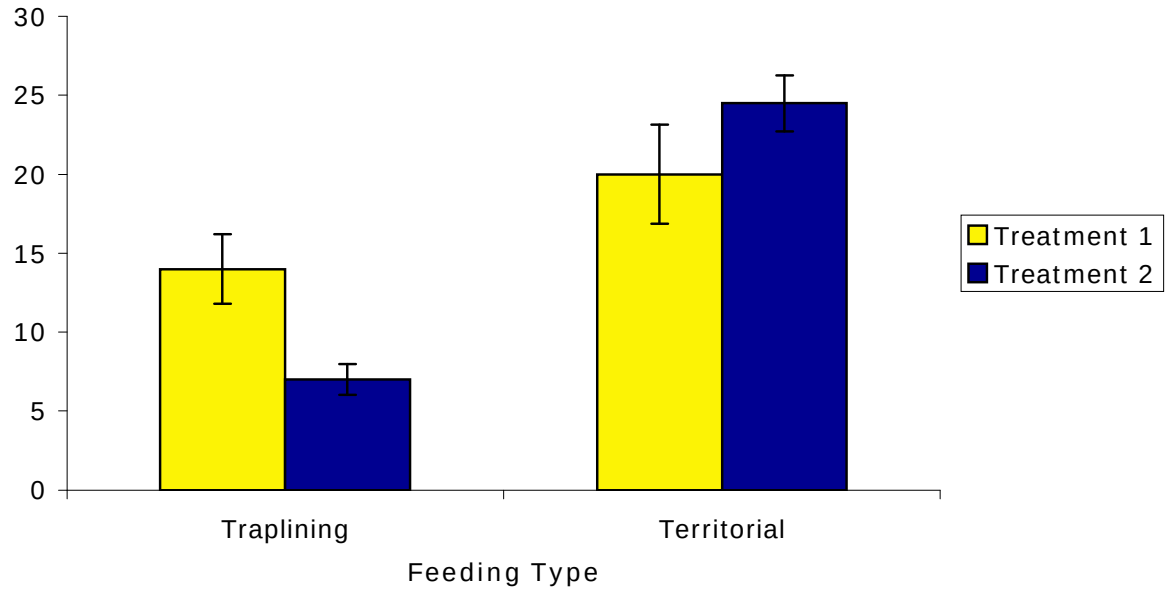

FIGURE 6. Confronting behavior in traplining species decreased significantly from Treatment 1 to Treatment 2 ($X^2 = 6.22$, df = 1, P = 0.013). Confronting behavior per hour in territorial species did not differ significantly between treatments ($X^2 = 0.453$, df = 1, P = 0.501).

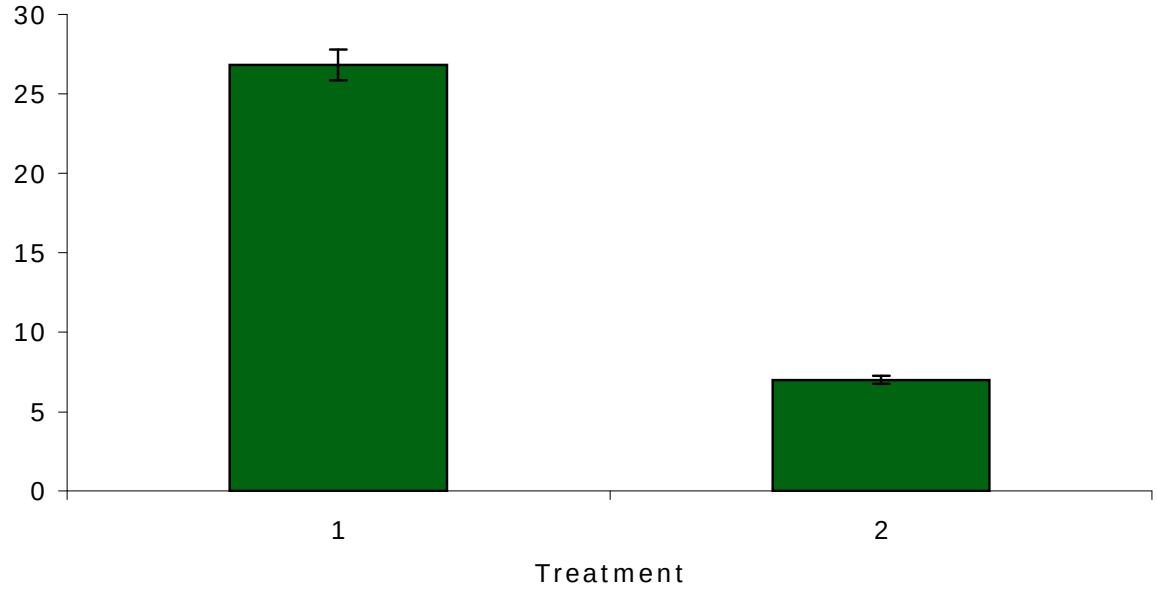

FIGURE 7. The total number of feeders visited (by both traplining and territorial species) on a trapline per hour decreased significantly from Treatment 1 to Treatment 2 ($X^2 = 5.26$, df = 1, P = 0.022).