WINTER FEEDING TERRITORIES IN THE TOWNSEND'S SOLITAIRE

By Roger J. Lederer

INTRODUCTION

The distribution of food resources is frequently the most important factor determining whether or not a species will maintain a territory (Brown and Orians, 1970; Orians, 1971). Intraspecific relationships among birds during the winter may be as significant in determining community structure and regulating population sizes as interactions during the breeding season (Fretwell, 1972; Gibb, 1956; Lack, 1966; Brown, 1969). Maintenance of territories serves to partition environmental resources, especially food in the winter. Thus food abundance and distribution, population sizes, and territoriality during the winter may be much more important to avian community structures or species during the breeding season than most current thinking reflects; this is likely due to a relative lack of winter field studies.

Townsend's Solitaires (*Myadestes townsendi*) are little-studied flycatcher-like thrushes (Turdidae). Recent observations of these birds during two winter seasons (Lederer, in press) demonstrated that they maintain intraspecific feeding territories but do no defend interspecific territories, even though Steller's (*Cyanocitta stelleri*) and Scrub jays (*Aphelocoma coerulescens*) and American Robins (*Turdus migratorius*), when present, feed heavily upon the solitaires' sole food resource, juniper berries. Solitaires minimize potential interspecific competition by utilizing different foraging behaviorisms.

This paper discusses the results of a winter study in 1976 and compares them with those of 1975. Information was collected in 1974, but not enough to make any quantitative comparisons.

STUDY AREA

The study area was a 12-hectare plot in an ecotone between the eastern Sierra Nevada Mountains and the Great Basin Desert at an elevation of 1,550 m. Western juniper (*Juniperus occidentalis*) was the most abundant tree. Jeffrey pine (*Pinus jeffreyi*) and Mountain mahongany (*Cercocarpus ledifolia*) were also present. The underbrush was sagebrush and scrub.

The mean daily temperature was $-3°$ to $10°$ C. Very little snow fell and snowcover was sparse.

METHODS

Over a two-week period in January 1976, 556 minutes were spent observing Townsend's Solitaires. Observations were made during all day light hours, with at least two total censuses of the study area made during a minimum of six hours in the field each day. Each solitaire seen was watched until it flew from view. For each observation, I recorded location in study area, height in vegetation, position in vegetation (top, periphery, middle of

foliage, next to trunk), species of vegetation, time spent in foraging or territorial maintenance activities (see Table 1 for categories), and interactions with others birds. Locations of robins and jays were also noted.

Territories were delimited by plotting on a map those areas where solitaires regularly foraged, sang, and called and where intraspecific encounters occurred. The boundaries are fairly accurate since I could accurately predict the presence of solitaires in particular areas after a week of censusing.

Continual mist-netting resulted in the capture of only two solitaires. One of these birds had been captured and banded in 1975 in the same place on the plot.

The numbers of berries were estimated in each territory by counting all the berries on sparse trees and on trees with abundant berries. Counting the berries in a section of the tree was accomplished by holding a one-meter square frame up to the foliage and counting all the berries that could be seen behind the frame. The height of the tree and radius of the lowest (and typically longest) branches were measured. Assuming the juniper is a cone, the number of berries on the tree was estimated by comparing the total volume of the tree with the volume of the sample section. Berry distribution on the juniper trees was not always uniform, so an average area of the tree was chosen as the sample section. Every tree in each territory was counted and its height measured with a rangefinder.

Tree and berry measurements were also taken in a 50 $\times$ 50 m sample plot outside of any territories.

RESULTS

Solitary behavior. Of all the categories of behavior, the most common was sitting, which accounted for 60.7% of all birds' activities (Table 1). Sitting, calling and singing accounted for 70.6% of their time.

Foraging behavior fell into one of four categories. The birds spent 25.7% of their total diurnal activity time searching for and eating berries. This 25.7% is the sum of (1) stationary tree gleaning (perching and picking berries; 6.7%), (2) stationary ground gleaning (picking up fallen berries; 14.3%), (3) aerial gleaning (picking a berry while hovering; 1.4%), and (4) searching (moving between branches or trees apparently looking for berries; 3.3%).

Junipers accounted for 62% of the trees in the study area. The average proportion of junipers in each territory was 57.2%, and the birds spent approximately 88.5% of their time in trees in junipers.

Interactions with other birds. Approximately 3.7% of the birds' time was spent in encounters with conspecifics and robins. Interactions were brief and typically consisted of one bird chasing another from the area. However, there were several instances in which two birds remained within a meter or two of each other and foraged with little or no interaction.

TABLE 1

Percent of time spent in different activities

Activity	1975	1976
Searching	2.9	3.3
Aerial gleaning	3.7	1.4
Stationary gleaning	1.95 (ground) .65 (tree)	14.3 (ground) 6.7 (tree)
Hawking	0.02	0
Sitting	79.3	60.7
Calling	5.5	9.0
Singing	0.5	0.9
Interactions with other individuals	5.5	3.7

Only one robin was in the area. It maintained a territory that overlapped that of a solitaire. Aggressive encounters between the two were common, but were short and of low intensity. One Steller's Jay was frequently seen, but I did not observe it to encounter the solitaires. No Scrub Jays were present in 1976.

Food availability. Juniper berries were the only food item available in any quantity to robins and solitaires. Pine nuts may have been utilized by the jays. Insects, other berries, and any other food resources that all these birds could utilize were either very scarce or absent. (Stomach analyses of 4 solitaires, 2 robins, and 1 Scrub and 1 Steller's jays in 1975 yielded only juniper berries).

The number and density of berries varied between territories from 60,000 (5.1/m^2) to 1.4 million (165.5/m^2) (Table 2).

Territories. I was able to plot the boundaries of nine solitaire territories, although portions of some boundaries were not well defined. The average territory size was 10,885 m^2, the largest being 13,416 m^2 and the smallest 8,520 m^2 (Table 2). There is a negative correlation between the density of berries and the size of the territory ($P < .05$).

Territory establishment begins in late September, and territories are defended until April. No significant shifts in sizes or boundaries of territories occur during this time although the intensity of defense seems to wane in March. All solitaires seen were territorial; there was no evidence of transient birds.

COMPARISON WITH 1975 RESULTS

Information gathered in 1975 is discussed in a previous paper (Lederer, in press), so the comparison here is brief.

Solitary behavior. Sitting was a more frequent behavior in 1975, whereas stationary gleaning was more common in 1976 (Table 1).

Interactions with other birds. In 1976, there were fewer birds of all species and interactions were less frequent (Table 1).

TABLE 2
Territory size and berry crop

Territory size (m^2)	No. berries/m^2
1975	
2,255	8.86
1,356	7.37
1,368	13.0
1,879	15.9
2,616	11.4
1,474	20.3
1,627	13.6
1,651	14.5
1,879	19.1
1,150	28.0
1,923	11.4
1,467	12.3
4,215	2.37
2,616	15.38
1,518	19.4
1,348	7.4
1,172	8.5
1,194	20.6
4,827	3.13
3,685	5.69
3,405	5.13
6,957	1.44
1,430	6.99
2,690	3.71
1,857	6.46
1976	
11,388	14.5
11,076	21.4
10,452	26.1
13,416	26.7
10,920	20.9
8,580	165.5
11,700	5.11
11,856	68.3
8,520	58.2

Food availability. Berry densities in 1976 were approximately twice those of 1975 (Table 2).

Territories. Territory sizes in 1976 were 3 to 5 times as large as those in 1975 (Table 2). A though there was no significant correlation between berry density and territory size in 1975, there was an indication of an inverse relationship.

Weather. In 1975, the temperatures ranged somewhat lower (-10 to $+10°$ C) and there was occasional rain and snow. Snow covered most of the study area.

DISCUSSION

Territoriality and food supply. Townsend's Solitaires maintain intraspecific territories thus insuring a source of juniper berries (Lederer, in press). The relationship between berry density and territory size confirms the frequently accepted idea for many species

that territory sizes are closely related to the density and distribution of food sources (Pitelka et al., 1955; Stenger, 1958; Schoener, 1968; Orians, 1971) although there are apparently some exceptions (Brown and Watson, 1964; Lack, 1966).

Territory sizes in 1976 were larger than those in 1975. Larger territory sizes may be due either to a reduction in competitors (Lack, 1964; MacArthur and Pianka, 1966; Fretwell and Lucas, 1969; Morse, 1976) and/or differences in food denisty (Orians, 1971; Schoener, 1971; Gill and Wolf, 1975). Berry densities in 1976 were twice that of 1975. There were fewer potential competitors because only nine solitaire territories were found in 1976 compared to 25 in 1975. The influence of robins and jays in 1976 was minimal (perhaps negligible) in comparison to 1975, since in 1975 robins were numerous and frequently chased solitaires. An increase in berry density should induce smaller territories whereas a decrease in competitors should create larger territories. In this case these opposing forces resulted in larger territories. Does this indicate that interactions are more important factors than food density? Perhaps, but there are other considerations.

Territories may be held to protect a minimum amount of food (Gibb, 1956; Brown and Watson, 1964; Gill and Wolf, 1975), but as competition lessens it may be the distribution of food within a territory that becomes more important than the amount of food, i.e., clumped food sources may increase foraging efficiency (Royama, 1970) and the birds should forage where expectation of yield is greatest (Tullock, 1971; MacArthur, 1972). Great Tits apparently maximize their food searching behavior by discriminating between profitable and unprofitable feeding areas (Smith and Sweatman, 1974). Thus an increase in territory sizes may be the solitaires' strategy to maximize foraging efficiency rather than to gain a larger food (berry) source, because a larger territory may contain patches of more concentrated or more accessible berries.

Foraging behavior. Of the four categories of foraging behavior that I considered, only stationary gleaning differs notably between the two years (Table 1). Almost four times as much time in 1976 was spent in gleaning. The time spent gleaning in 1976 was almost all stationary, whereas in 1975 more relative and absolute time was spent in aerial gleaning.

Aerial gleaning allows the solitaires to forage on the most abundant berry sources while partially avoiding competition from other berry-eating species (Lederer in press). The most concentrated berry source is the area of fallen berries around a juniper, so this is where the solitaires should spend the majority of their foraging time, all else being equal. Although ground gleaning takes less energy than aerial gleaning and occurs in the area of greatest berry density, it greatly diminishes the bird's effectiveness in defending its territory. So it seems to follow that a reduction in competition in 1976 led to an increase in ground gleaning, apparently the most profitable method of foraging. Insufficient data were gathered on feeding rates to make any generalizations, but in 1975 solitaires generally picked up 2-3 berries while ground

gleaning before returning to an aerial perch. In 1976 they picked up 18-20 berries before flying and on two occasions I saw a solitaire regurgitate a berry after it had returned to the top of a tree. Apparently they were satiating themselves as quickly as possible and then returning to an exposed perch. The greater density of solitaires in 1975 apparently required too much time in defense activities for the birds to become satiated before they resumed defense activities.

Another consideration obfuscates this discussion: the density of berries on the ground. A higher density of berries would probably lead to more time being spent on the ground. Berry density on the ground could not be compared between the two years because of intermittent snowfall in 1975. Accessibility of berries on the ground varied with snowfall and snow melts which were sometimes only hours apart.

In 1975, 85.3% of the solitaires' daily activity was devoted to passive territorial maintenance—sitting on treetops, calling, and singing; 5.5% was used in aggressive encounters. In 1976, 70.6% was used in passive defense and 3.7% in active defense. Larger territories may be beneficial, but they require a greater expenditure of time and energy than smaller territories, unless competition is weak enough to allow an increase in territory size without any significant increase in energy expenditure. In fact, energy expended in defense decreased. But the solitaires still spent most of their time sitting on tree tops, an activity that I believe is a passive, subtle form of territorial maintenance. Morse (1968) observed that conspicuousness may play a role in warbler territory maintenance and Wolf and Hainsworth (1971) found that hummingbirds (*Eulampis jugularis*) announce their territory by sitting on exposed perches. Leck (pers. comm.) suggests that sitting may just be resting. In many observations of numerous species of birds, sitting is probably synonomous with resting. But in the solitaires situation, sitting on treetops in cold, windy, and often wet weather does not appear to be restful. It costs less energy than activity requiring much movement, but is more costly than sitting in a sheltered portion of the vegetation. Treetop-sitting is probably a compromise between active territorial defense and not defending a territory.

Walsberg (pers. comm.) has studied winter territoriality of Phainopeplas (*Phainopepla nitens*) in the Sonoran Desert and found a similar type of territorial advertisement. He adds that this kind of advertisement may be most effective in relatively open habitats.

Foraging and territorial defense may be modified by winter weather. Grubb (1975) demonstrated that numerous woodland birds foraged differently under cold windy conditions to reduce their exposure to the wind. My original assumptions were that solitaires needed to eat approximately 50 berries per day and that each territory contains many more berries than a solitaire would need (Lederer, in press). Recent information on other berry-eating birds (Walsberg, 1975) has indicated to me that I may have severely underestimated the cost of a solitaire's diurnal activity.

CONCLUSIONS

Townsend's Solitaires hold intraspecific territories, the size of the territories being correlated with the density and perhaps distribution of juniper berries and the number of conspecifics in nearby areas. Time and energy budgets vary with food accessibility and competitors. To clarify the situation further, more data on time budgets have to be collected and laboratory measurement of energy utilization and food assimilation would be desirable.

Another aspect that needs investigation is the possible nutritive and caloric differences in berries. If the food quality of some berries is higher than others and the solitaires are able to make a distinction, then foraging behavior and territory size could perhaps be explained somewhat differently. (Perhaps aerial gleaning is used to reach more nutritive berries on the branch ends).

ACKNOWLEDGMENTS

I sincerely appreciate a second year's financial support from the Frank M. Chapman Memorial Fund of the American Museum of Natural History. California State University, Chico allowed the use of its Eagle Lake Field Station during the course of the study. Alanna Pass and Jennifer Goulding provided considerable field assistance. My thanks go to Steve Bailey and Glen Walsberg for helpful comments on the manuscript.

LITERATURE CITED

BROWN, J. L. 1969. Territorial behavior and population regulation in birds. *Wilson Bull.*, **81**: 293-329.

BROWN, J. L., AND G. H. ORIANS. 1970. Spacing patterns in mobile animals. P. 239-262 *in* Annual review of ecology and systematics, Vol. 1.

BROWN, L. H., AND A. WATSON. 1964. The Golden Eagle in relation to its food supply. *Ibis*, **106**: 78-100.

FRETWELL, S. D. 1972. Populations in a Seasonal Environment. Monographs in population biology 5. Princeton, N.J., Princeton University Press.

FRETWELL, S. D., AND H. L. LUCAS, SR. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoret.*, **19**: 16-36.

GIBB, J. 1956. Food, feeding habits, and territory of the rock pipit, *Anthus spinoletta*. *Ibis*, **98**: 506-530.

GILL, F. B., AND L. L. WOLF. 1975. Economics of feeding territoriality in the Goiden-winged Sunbird. *Ecology*, **56**: 333-345.

GRUBB, T. C., JR. 1975. Weather-dependent foraging behavior of some birds wintering in a deciduous woodland. *Condor*, **77**: 175-182.

LACK, D. 1964. A long-term study of the Great Tit (*Parus major*). *J. Anim. Ecol.*, **33**: 159-173.

———. 1966. Population Studies of Birds. Oxford, Clarendon Press.

LEDERER, R. J. Winter territoriality and foraging behavior of the Townsend's Solitaire. *Am. Midl. Nat.*, in press.

MACARTHUR, R. H. 1972. Geographical Ecology. New York, Harper and Row.

MACARTHUR, R. H., AND E. R. PIANKA. 1966. On optimal use of a patchy environment. *Amer. Nat.*, **100**: 603-609.

MORSE, D. H. 1968. A quantitative study of foraging of male and female spruce wood warblers. *Ecology*, **49**: 779-784.

———. 1976. Variables affecting the density and territory size of breeding spruce-woods warblers. *Ecology*, **57**: 290-301.

ORIANS, G. 1971. Ecological aspects of behavior. P. 513-546 *in* Avian Biology Vol. I. D. S. Farner and J. R. King, eds. New York, Academic Press.

PITELKA, F. A., P. G. TOMICH, AND G. W. TREICHEL. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. *Ecol. Monogr.*, **25:** 85-117.

ROYAMA, T. 1970. Factors governing the hunting behavior and selection of food by the Great Tit (*Parus major* L.) *J. Anim. Ecol.*, **39:** 619-668.

SCHOENER, T. W. 1968. Sizes of feeding territories among birds. *Ecology*, **49:** 123-141.

———. 1971. Theory of feeding strategies. P. 369-404 *in* Annual review of ecology and systematics. Vol. 2.

SMITH, J. N. M., AND H. P. A. SWEATMAN. 1974. Food-searching behavior of titmice in patchy environments. *Ecology*, **55:** 1216-1232.

STENGER, J. 1958. Food habits and available food of ovenbirds in relation to territory size. *Auk*, **75:** 335-346.

TULLOCK, G. 1971. The coal tit as a careful shopper. *Amer. Nat.*, **105:** 77-79.

WALSBERG, G. E. 1975. Digestive adaptations of *Phainopepla nitens* associated with the eating of mistletoe berries. *Condor*, **77:** 169-174.

WOLF, L. L., AND F. R. HAINSWORTH. 1971. Time and energy budgets of territorial hummingbirds. *Ecology*, **52:** 980-988.

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