

WINTER TERRITORIALITY OF TOWNSEND'S SOLITAIRES (*MYADESTES TOWNSENDI*) IN A PIÑON-JUNIPER- PONDEROSA PINE ECOTONE

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Townsend's Solitaires (*Myadestes townsendi*) are poorly-known thrushes (but see Sibley 1973) inhabiting western North America from central Mexico to Alaska. Typically, they breed in mixed conifer forests but winter in piñon-juniper woodlands or other habitats that provide berries for food (Munro 1919, Johnston 1943, Bent 1949). In Arizona, they are summer residents of high mountains in the north, but they winter in berry-producing Upper Sonoran woodlands and well-wooded Lower Sonoran canyons throughout much of the state (Phillips et al. 1964). Their migration is apparently both altitudinal and latitudinal. During the breeding season, they forage like flycatchers, and their diet consists mostly of insects. During the winter, they eat mainly fruit (Beal 1915, Bent 1949).

The solitaires' habit of singing and their aggressiveness throughout the fall and winter (Mailliard 1926, Skinner 1928, Lockerbie 1939, Roest 1957) indicate that they probably maintain winter territories. Winter territoriality has been reported for a number of North American birds including Mockingbirds (*Mimus polyglottos*, Hailman 1960), Plain Titmice (*Parus inornatus*, Dixon 1956) and Red-headed Woodpeckers (*Melanerpes erythrocephalus*, Kilham 1958) and for some Palearctic migrants wintering in the tropics (Elgood et al. 1966, Medway 1970, Nisbet and Medway 1972). Pearson (1972) noted that warblers wintering in Uganda spent more time on winter territories than on breeding territories.

With such a large amount of time being spent on wintering grounds, natural selection should operate to produce adaptations promoting survival during the winter, especially for birds (such as Townsend's Solitaires) which frequently winter in cool or cold environments. Winter territoriality may be such an adaptation. If so, then such behavior should impart some selective advantage to territorial individuals which permits them to survive better until the breeding season relative to non-territorial conspecifics.

In this study, we wanted to determine if Townsend's Solitaires are territorial in winter. Secondly, we examined the mechanics of the solitaires' territorial system, i.e., how territories are defended, what features of the territory are important to solitaires, and how changes in those features affect the territorial system. Finally, we attempted to determine what selective advantages individuals gain by being territorial.

Using Brown and Orians' (1970) definition of territory, it was necessary to show that individuals defend relatively fixed areas which become exclusive (or nearly so; Brown 1975) with respect to rivals, and that defensive behavior evokes escape or avoidance in rivals.

STUDY AREA AND METHODS

The study was conducted in a piñon-juniper-ponderosa pine ecotone about 24 km NNE of Flagstaff, Coconino Co., Arizona in the fall and winter seasons of 1973-74 and 1974-75. The study area, about 35 ha, was located on a gently sloping plateau between 2,082 and 2,106 m elevation. It is bordered to the east and southeast by a series of high (2,400-2,700 m) volcanic cinder cones and to the southwest by the San Francisco Peaks (3,801 m). These landforms effectively limit the mid-winter day on the study area to about 9 h. The substrate is a volcanic soil.

The understory consisted of a number of species of herbs and shrubs (Laudenslayer 1973), but it was not utilized by the Townsend's Solitaires. The overstory was composed of ponderosa pine (*Pinus ponderosa*), piñon pine (*Pinus edulis*), *Juniperus monosperma*, *J. deppeana*, and *J. scopulorum*. The most common juniper was *J. monosperma*, the one-seed juniper, which produced a berry crop during the summer of 1973. No additional berries were produced by any species during the rest of the study. The junipers, piñons, and small ponderosas formed a uniform stratum averaging 4 m high. Taller ponderosa pines up to 12 m high occurred occasionally, and a very few widely scattered ponderosas (referred to as tall ponderosas) attained heights up to 23 m.

Between 18 November 1973 and 20 February 1974, 150 cm of snow fell on the study area; between 26 October 1974 and 19 February 1975, 135 cm of snow fell. The mean weekly temperatures were about the same for both winters with mean lows between -12 and -6°C, means between -4 and 1°C, and mean highs between 2 and 9°C. The lowest temperature in 1973-74 was -16°C and that for 1974-75 was -21°C. Daytime temperatures in late January and

February 1975 averaged about 5°C higher than in 1974. All climatic data were collected on the study area. Temperatures were recorded with a maximum-minimum thermometer checked at least three times a week. Snow depth was recorded by measuring the depth of new snow with a metric ruler soon after every snowfall.

In the fall of 1973, seven Townsend's Solitaires observed singing and chasing other solitaires were captured and color-banded for individual recognition. Birds were lured into a mist net by playing a tape recording of a Townsend's Solitaire's song recorded on the study area early in October 1973. Four of the birds disappeared within one week after banding, but an additional bird was banded in January 1974. Thus, a total of four birds were observed during a large part of 1973-74. In October 1974, three new birds were banded. One disappeared, but one of the birds banded in 1973 returned to the study area, so three birds were observed in 1974-75.

The ages of all banded birds were determined on the basis of interior mouth color. In juveniles and sub-adults this region is yellow, but at approximately one year of age it turns pink. We did not determine the sex of the banded birds at the time of capture. Instead, in 1973-74, once it became clear that Townsend's Solitaires were territorial, we obtained and sexed six unbanded individuals in a similar habitat about 2 km from the study area. These birds responded to the tape-recorded song and to other solitaires with the same behavior as did the banded birds. The banded birds of 1974-75 were collected and sexed at the end of the study. Also, five birds showing no evidence of territorial behavior in response to the recorded song were collected and sexed. A response to the tape recording was considered positive (indicative of territoriality) if the subject sang and/or actively searched for the source of the recorded song by flying to-and-fro around the speaker. If neither singing nor searching occurred, the response was considered negative.

For both years, territorial boundaries were determined by plotting locations where each banded bird was seen on a scaled map of the study area using a method similar to that of Odum and Kuenzler (1955). Conflicts involving banded solitaires were observed very carefully and their locations plotted on the map. Territory sizes were determined with the aid of a compensating polar planimeter.

The activities of the banded birds were divided into the following categories and timed with a stop watch: territorial activities including singing, calling, chasing other birds, and fighting; searching for and consuming food such as juniper or mistletoe berries, insects, snow and water; quiet perching, whisper singing and grooming; and flight (not including chasing). The duration of short periods of flight were estimated. In 1973-74, we gathered data on 283 activity bouts (27,081 bird-sec) which we categorized into territorial establishment (6,742 bird-sec) and territorial maintenance (20,339 bird-sec) phases on the basis of behavioral changes observed in the field. In 1974-75, we gathered data on 280 bouts (8,991 bird-sec), but the two phases could not be separated. A bout was defined as a period of one continuous type of activity clearly separated from other activities by a distinct behavioral change. The first bout of any sequence of bouts was not included in the time studies, nor were instances where only one bout was observed. The amount and type of food consumed were also noted. As nearly as possible, observation sessions were divided equally among the banded birds

and throughout the day. Observations were continued for the entire winter period and were ended when territories broke down in the spring. Data from all observations in each winter were combined for analysis.

Preliminary observations indicated that Townsend's Solitaires relied on juniper berries for food so we estimated the number of available berries. Two parallel transect lines were established about 100 m apart. At 50 m intervals, the nearest juniper tree with berries was selected and a branch whose tip was below 3 m high was picked at random for sampling. The natural foliage of the outer 0.5 m of the branch was measured to the nearest dm² and the berries therein counted. The branch tip was inconspicuously marked for future identification. Berries on these branch tips were recounted every month to determine how many had been lost. The total volume sampled was 185 dm³ on 17 trees in 1973-74. In 1974-75, the berries contained in 250 dm³ foliage samples on 10 trees were counted. On the basis of these data, the quantity of berries per m³ of berry-laden foliage was estimated.

In 1973-74, we located every berry-covered tree in each territory. Each tree was designated as either cylindrical, conical, or spherical and then the volume of the outer 0.5 m shell of foliage was calculated. Observations showed that most of the berries were contained in this outer shell. We then computed the volume of berry-laden foliage in each 1973-74 territory and per hectare. The quantity of berries on each territory was estimated by combining these data with the number of berries per m³ of berry-laden foliage obtained from the transect lines.

In the spring of 1974, we maintained a solitaire on juniper berries in an outdoor cage for 8 days (\bar{x} day length about 10 h, \bar{x} temperature 2.8°C) to determine the daily amount of berries needed to maintain existence metabolism. The bird was provided with ample water. The cage was large enough to permit hopping but not flight. This experiment was repeated in the fall of 1974 using one solitaire for 6 days and another for 14 days (\bar{x} day length about 10 h, \bar{x} temperature 2.7°C). The average caloric contents of a whole juniper berry ($n = 100$) and a juniper seed ($n = 150$) were determined by oxygen bomb calorimetry. The stomach contents of 13 Townsend's Solitaires obtained within 2 km of the study area were examined.

RESULTS

TERRITORIES AND TERRITORIAL BEHAVIOR

Territorial Individuals. Both immediately before and after banding, all banded Townsend's Solitaires sang, restricted their activities to rather indistinct yet recognizable geographic areas, searched for other singing birds in the immediate vicinity, and chased or attempted to chase other solitaires from their areas. These behaviors are characteristic of territoriality. Those banded birds that remained in the study area succeeded in establishing territories in every sense of Brown and Orians' (1970) definition. Five banded birds were unable to establish territories on the study area although they attempted to do so.

All three banded territorial Townsend's

TABLE 1. Territory sizes and available food of Townsend's Solitaires in different winters.

| Territory | Size (ha) | Millions of juniper berries | Food ratio ^a |
|-----------|------------------|-----------------------------|-------------------------|
| 1973-74 | $\bar{x} = 0.70$ | | |
| A | 0.61 | 13.1 | 311 |
| B | 0.65 | 24.7 | 588 |
| C | 0.74 | 14.0 | 333 |
| D | 0.82 | 25.0 | 595 |
| 1974-75 | $\bar{x} = 3.85$ | | |
| E | 2.48 | 2.4 | 29 |
| F | 3.74 | 3.7 | 44 |
| G | 5.34 | 5.3 | 63 |

^a Number of berries on trees in territory at start of winter/minimum number of berries consumed per bird per winter.

Solitaires and all six unbanded but presumably territorial birds that we examined were males. In 1973-74, four of the unbanded territorial birds were sub-adults (less than 1 year old), three of the four banded territorial birds were sub-adults, and two of the banded birds that disappeared were sub-adults. In 1974-75, all four banded birds were adults. None of the banded birds that successfully established a territory died during the study.

In addition to territorial Townsend's Solitaires, there were also nonterritorial floaters. These birds presumably wandered throughout the countryside using resources within other birds' territories. Their behavior can only be described as sneaky; they remained well below treetop level, never making a sound. The floaters were always chased from a territory when discovered by the territory owner. Generally, floaters occurred singly, but flocks of up to four birds were seen occasionally. It was not possible to estimate the size of the floater population, its mortality rate, nor the amount of food it consumed. The five floaters collected in 1973-74 included an adult male, a sub-adult male, and three adult females.

Territories. In 1973-74, each of the four banded birds established and maintained a small exclusive territory (fig. 1, table 1). Each territory contained a tall ponderosa pine. Once territories were firmly established, each solitaire restricted his activity to his own territory until April 1974. Boundaries of these territories were well defined narrow lines.

In 1974-75, the three territories averaged 5.5 times larger than in 1973-74. Again, each territory contained a tall ponderosa pine. In places, the territories of the banded birds overlapped each other and those of adjoining unbanded birds. The overlapping areas were defended throughout the winter by each of the involved territory owners. However, no

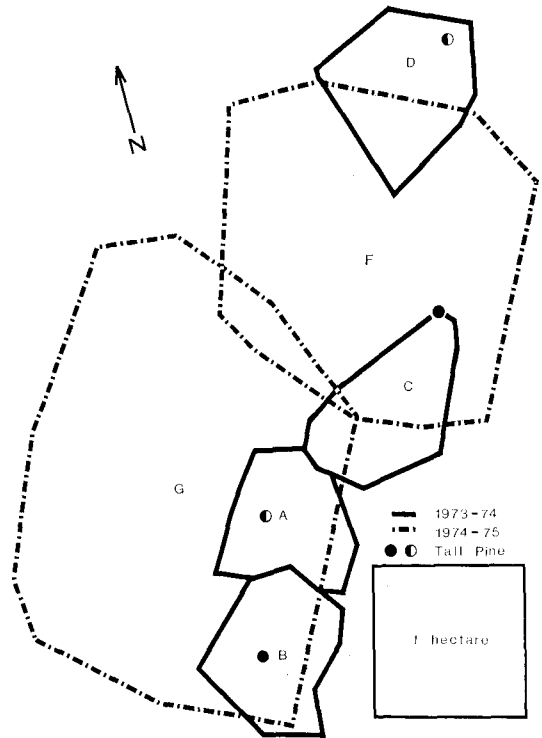


FIGURE 1. Territories of banded Townsend's Solitaires from both winters. Darkened circles indicate tall ponderosa pines utilized as primary song and lookout posts in both winters. Semidarkened circles are tall pines used only in 1973-74. Letters correspond to territories in table 1.

individual was ever clearly dominant, so ownership of these areas fluctuated from day to day. Territorial boundaries were broader and less distinct than in 1973-74.

The largest territory (territory G in fig. 1, table 1) was originally established during October 1974 by a bird color-banded Orange-Orange. The tall ponderosa in this territory was the same tree used by Yellow-Blue (territory B in fig. 1, table 1) the previous year. On 20 October 1974, Yellow-Blue returned and in three days regained his former territory by forcing Orange-Orange into another unoccupied area. Yellow-Blue's assault consisted of considerable singing and chasing. Yellow-Blue abandoned this territory about 23 November and established a new territory (territory E, table 1) about 350 m from the old one. Orange-Orange then quietly reoccupied his former territory over a 10-day period, once again centering his activities in the same tall ponderosa. However, he did not relinquish any of the interim territory, thereby ending up with the largest territory of the study.

Intraspecific Territoriality. Townsend's Solitaires arrived on the study area in early October both winters and began setting up

territories immediately. In 1973-74, the establishment phase lasted until about 1 December, ending shortly after the first snowfall of the season. Territories were maintained until early April when banded solitaires started leaving their own territories and trespassing into those of their neighbors. In some instances the solitaires were absent from their territories for many hours. At first, territories were defended from trespassers but defended areas soon dwindled to individual distances of 10 to 20 m radius. By 24 April, although the banded Townsend's Solitaires still spent much of their time within the old territorial boundaries, they ignored other solitaires unless their individual distances were violated.

In 1974-75, the banded birds began leaving their territories about 1 March 1975. Because ample food was still present, this probably resulted from the unseasonably warm days in January and February. We took this as an indication that territorial behavior was waning so the banded birds were collected and sexed, and the study terminated.

The Townsend's Solitaires' advertisement song is melodious and variable, similar to that of the Black-headed Grosbeak (*Pheucticus melanocephalus*). Individual variation exists, making it possible to recognize some of the banded birds solely on the basis of song. Songs rarely are sung from anywhere other than the tops of trees or in the tall ponderosa pines. The few exceptions occur when birds involved in close confrontations descend into the trees and sing at each other. Because we observed no evidence of breeding or mate attracting activity, it appears that the only function of singing in winter is territorial advertisement and defense.

Call notes are high pitched *tew* notes given either singly or in series at a constant loud volume. They usually are given in response to call notes or songs from adjacent territorial birds although they are also elicited by the sight of another Townsend's Solitaire and occasionally are given spontaneously. Call notes are not infrequently given from below treetop levels, but most commonly they are given from treetops. They apparently function as low intensity advertisement signals.

Chases and fights developed when call notes, songs, and winnowing (see below) failed to frighten an intruder from the territory. Although chases were sometimes initiated without warning, fights always were preceded by one or more of the agonistic vocalizations. Chases generally ended at territory boundaries, but occasionally a floater was chased well into an adjoining territory

whose owner then chased both birds. This disturbance frequently alerted other neighboring territory owners to the presence of the floater who would then be chased from one territory to another until out of sight. Vigorous fights, consisting of grappling with feet, pecking, and flailing with wings occurred infrequently as the culmination of confrontations between territory owners. Generally during fights, one or both birds repeatedly sang a short, three-five note song which sounded like a phrase from the Townsend's Solitaires' longer advertisement song. No obvious injuries occurred as a result of fighting.

Boundary patrols appear to function in territorial advertisement and in reaffirmation of the boundary. In 1973-74, patrols were rare, but in 1974-75 they occurred frequently probably because of the poor views of the territorial boundaries from the tall ponderosa pines. During boundary patrols, the Townsend's Solitaires fly from one of the taller trees to another along the boundary where they perch quietly, sing, or give call notes. The same trees are generally used as lookout and song posts on all boundary patrols. Short periods of feeding often interrupt the patrols.

In addition to the territorial behavior described above, territorial Townsend's Solitaires often produced a winnowing sound which, although probably not intended to frighten intruders, was sufficient to scare some birds off the territory. Winnowing in solitaires evidently results from the passage of air between the flight feathers on each downward wing beat. It is heard just prior to touchdown when a territorial Townsend's Solitaire approaches another solitaire in or near its territory. It apparently is the result of flight characteristics associated with a hesitant approach toward a presumably frightening object. Such approaches are much slower than typical silent approaches toward familiar objects. Thus, contrary to winnowing in *Hylocichla* spp. (Dilger 1956), winnowing in Townsend's Solitaires may be characteristic of an escape drive rather than an attack drive. However, intruders have evidently learned to associate the sound with a territorial individual and generally flee the territory when it is heard.

Interspecific Territoriality. In 1973-74, only two interactions of a possibly interspecific territorial nature were observed. In one instance, a banded Townsend's Solitaire chased a Gray-headed Junco (*Junco caniceps*) out of its tall pine, but the chase ended after about 15 m. In the other instance, a banded bird gave a horizontal stretch display toward a flock of

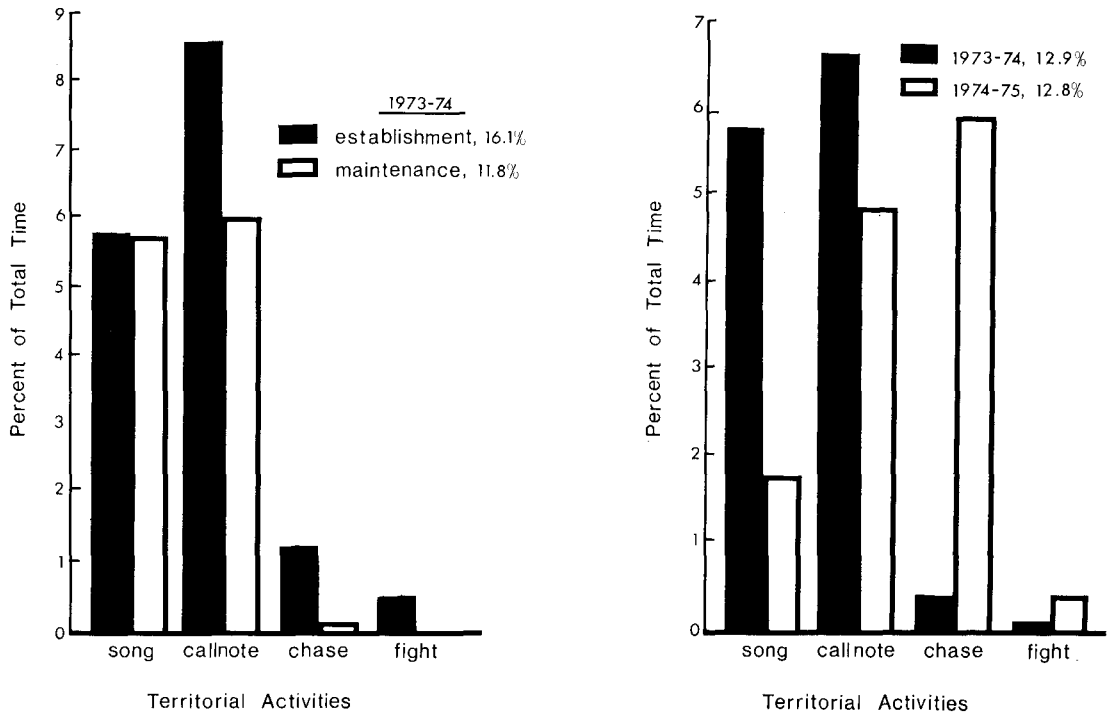


FIGURE 2. Percentages of Townsend's Solitaires' winter time devoted to various types of territorial behavior. Left graph compares establishment and maintenance phases in 1973-74. Right graph compares total times for the two winter periods. Percentages for each period are summed in the legends.

Western Bluebirds (*Sialia mexicana*). The head and neck were extended horizontally, feathers were sleeked, the bill was gaped, a *waaa* call resembling the scold of a Steller's Jay (*Cyanocitta stelleri*) was given, and the wings and tail were partially extended and quivered. The flock was not chased. No Townsend's Solitaire was seen in the flock although a similar flock containing a solitaire was seen two days later.

In 1974-75, however, definite interspecific territoriality occurred. In 62.5% of the observed chases, Townsend's Solitaires chased Gray-headed Juncos, Western Bluebirds, and in one instance, a Pygmy Nuthatch (*Sitta pygmaea*). One banded Townsend's Solitaire often chased small flocks of Gray-headed Juncos and Western Bluebirds for as long as 2 min. During these chases, he forced the flocks into the air and then prevented them from relanding within the territory. The *waaa* call often accompanied these chases. In 1973-74, only about 0.14% of territorial activity time was devoted to interspecific encounters, whereas, in 1974-75, 43.5% of this time was so spent.

Interspecific territoriality was apparently directed toward juniper berry consumers. Western Bluebirds ate many juniper berries; Gray-headed Juncos were never observed eat-

ing berries but could have been viewed as competitors by solitaires once both species were foraging on the ground. The Pygmy Nuthatch was chased when both a solitaire and the nuthatch were hawking insects from the former's tall ponderosa.

Despite the fact that interspecific territoriality was more pronounced in 1974-75, juniper berry consumers were apparently less plentiful than in 1973-74. In 1973-74, flocks of Evening Grosbeaks (*Hesperiphona vespertina*) numbering 100 or more individuals, and flocks of American Robins (*Turdus migratorius*) containing about 200 individuals were common, as were Sage Thrashers (*Oreoscoptes montanus*) seen singly or in pairs. In 1974-75, no Sage Thrashers were seen, Evening Grosbeaks were not seen after mid-November, and American Robins were observed infrequently singly or in small flocks of not more than 12 birds. The numbers of Gray-headed Juncos and Western Bluebirds were about the same each winter.

Territorial Time Budgeting. During establishment in 1973-74, proportionately more time was spent in territorial activities than during territorial maintenance. The difference resulted from less time spent chasing, calling, and fighting during maintenance (fig. 2). Also, less time was devoted to perching activi-

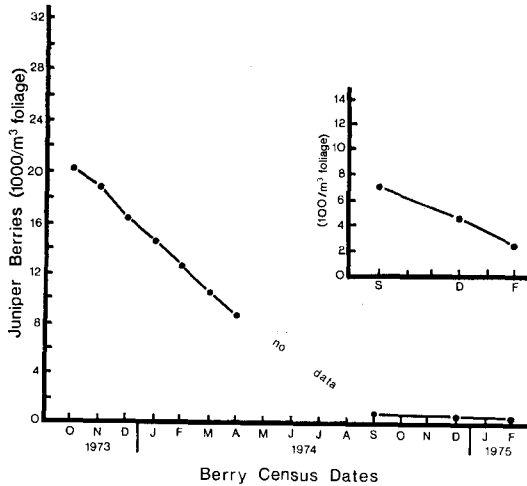


FIGURE 3. Mean monthly quantities of one-seed juniper berries per m³ of berry-laden foliage. Smaller graph is an enlargement of the data for the last six months of the study.

ties (which may have a territorial function) during maintenance. It appears that once territories were firmly established, the birds changed from territorial to foraging activities (see figs. 4, 5).

The total amount of time spent in territorial activities for both winter periods was about the same although apportioned differently. In 1974-75, less time was devoted to intraspecific defensive singing and calling whereas more time was spent chasing (all species) and fighting (solitaires) than in 1973-74 (fig. 2).

FOOD AVAILABILITY AND FORAGING BEHAVIOR

In the summer of 1973, a huge crop of berries was produced on about one-third of the *Juniperus monosperma* trees. Although called "berries," these fruits are actually modified conifer cones with fleshy, fused cone scales usually containing one seed. No additional berries were produced the following summer; thus, the 1973 crop provided most of the Townsend's Solitaires' food for both winters of the study. In October 1973, each m³ of berry-laden foliage contained about 20,000 berries. The number of berries declined steadily throughout the study (fig. 3).

Throughout the 1973-74 winter period, the bluish berries, averaging 7 mm in diameter, were clustered in huge masses on the branch tips. They were plump, juicy, and soft. Although some fell to the ground each month, they were never as concentrated there as on the trees. In 1974-75, the remaining tree-borne berries were shriveled, leathery, dry, and widely scattered throughout the foliage.

TABLE 2. Metabolic coefficients, daily existence energy requirements, and daily energy consumption of captive Townsend's Solitaires.

| | Wt. (g) | Consumption/day | | Existence Metab. (kcal) ^c | Metab. Coeff. |
|-----------|---------|------------------------------|-------------------|--------------------------------------|---------------|
| | | Juniper Berries ^a | kcal ^b | | |
| Bird 1 | 32.1 | 221.5 | 69.8 | 24.6 | 35.3% |
| Bird 2 | 30.1 | 192.8 | 60.8 | 23.8 | 39.2% |
| Bird 3 | 31.0 | 199.1 | 62.8 | 24.2 | 38.5% |
| \bar{x} | 31.1 | 204.5 | 64.5 | 24.2 | 37.6% |

^a Averaged over 8, 6, and 10 days.

^b Based on an average of 315.31 calories/berry flesh.

^c Computed using Pimm's (1976) equation, 10 h photoperiod, and 2.8°C mean ambient temperature.

Large quantities of berries had fallen to the ground under some of the trees.

The captive solitaires consumed an average of 204 berries per day (table 2). The caloric content of an average juniper berry's flesh (seeds are passed through solitaires intact) was calculated to be 315.31 calories. Therefore, the birds' average gross energy intake was 64.5 kcal/day while maintaining existence metabolism under a 10-h photoperiod at 2.8°C. Using Pimm's (1976) equation, we estimated that the caged solitaires needed 24.2 kcal/day for existence metabolism; hence, their metabolic coefficient (energy for existence metabolism/gross energy intake) was about 37.6%.

Existence energy measures the energy requirements of birds whose activities are restricted by a cage. Thus, the energy needs of free-living birds should be higher because they are more active. The magnitude of the increase depends upon the types and durations of the activities. Nevertheless, existence energy can be used to estimate the energy requirements of free-living birds (Kendeigh 1970). Because wintering Townsend's Solitaires spend so much time perching (see Perching and Aerial Activities), we believe that the existence energy estimate for the captive birds closely approximates the minimum energy needs of free-living solitaires where the mean winter photoperiod was 9 h, mean temperatures were between -4° and 1°C, and the mean body weight was 31.7 g ($n = 12$; $R = 29-36$ g).

The amount of food available to each territory owner, with respect to his minimum energy needs, was estimated. Based on the average daily berry consumption of the caged birds (204 berries), each territorial solitaire had to eat at least 42,000 berries in 1973-74 to maintain existence energy. We calculated that berry consumption rates doubled the next winter so 1974-75 solitaires should have consumed about 84,000 berries. Actual consump-

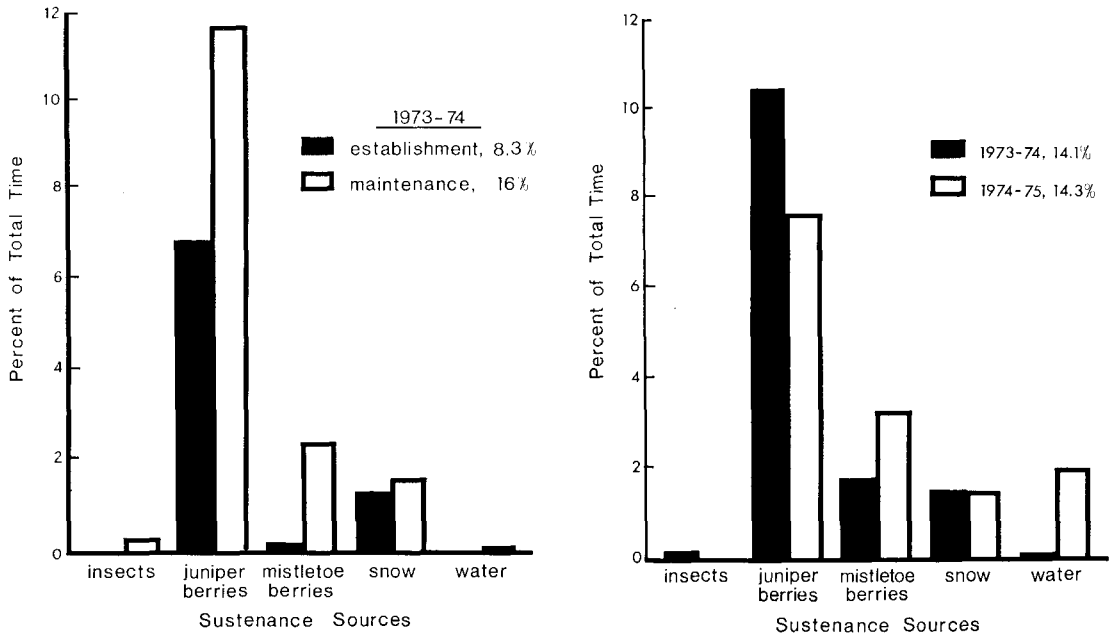


FIGURE 4. Percentages of Townsend's Solitaires' winter time devoted to locating and consuming various foods. Left and right graphs compare the same periods as the corresponding graphs in figure 2.

tion was undoubtedly higher in both winters. Each territory had enough tree-borne berries at the start of the winter periods to supply these needs although the ratios of available food to needed food were smaller in 1974-75 than in 1973-74 (table 1). The territory with the smallest ratio (table 1: E) was occupied by the bird that was most active in interspecific territoriality. In 1974-75, many additional berries were available on the ground beneath some of the trees, but these were ignored by the solitaires until after territories were established.

None of the 13 stomachs examined contained anything other than juniper berries. Nevertheless, Townsend's Solitaires ate mistletoe berries (*Phoradendron* sp.) in the field. In 1973-74 these berries made up less than 3% of the diet, and in 1974-75 they equaled 7.2% of the diet based upon field estimates of the number of each type of berry consumed and the average dry weight of each type of berry collected from where the solitaires were feeding. Insect-eating was noted only twice during the study.

The solitaires spent less time foraging for juniper berries during territorial establishment and throughout 1974-75 than they did during maintenance or 1973-74 (fig. 4). Nevertheless, when daily berry consumption rates were compared, we found that the birds ate 2 times more berries in 1974-75 than in 1973-74 and 1.2 times more berries during establishment

than during maintenance. They accomplished this through shorter feeding bouts and faster feeding rates (table 3). Although Kendeigh et al. (1969) reported that birds feed most actively in the early morning, the solitaires' feeding activity increased toward midday as territorial activity declined.

Water consumption was higher in 1974-75 than in 1973-74, apparently to compensate for the dryness of the juniper berries (fig. 4). Consumption of moist mistletoe berries was 7.9 times greater in 1974-75, possibly as a supplementary water source. Desert-dwelling House Finches (*Carpodacus mexicanus*) are thought to receive much of their water from mistletoe berries (Walsberg 1975).

Throughout 1973-74 and early in 1974-75, 90% of the time solitaires spent foraging for

TABLE 3. Juniper berry feeding factors of free-living Townsend's Solitaires in different winter periods.

| Factor ^a | Estab. 1973-74 | Maint. 1973-74 | Total 1973-74 | Total 1974-75 | Signif. of diff. |
|---------------------|------------------|------------------|---------------|---------------|------------------|
| A | 13.2 | 28.9 | | | $P < 0.002$ |
| A | | | 24.7 | 8.5 | $P < 0.002$ |
| B | 51.1 | 94.9 | | | $P < 0.01$ |
| B | | | 83.3 | 24.5 | $P < 0.002$ |
| C | 4.2 ^b | 3.6 ^b | | | NS |
| C | | | 3.6 | 2.7 | $P < 0.05$ |

^a A: \bar{x} no. of foraging sec./berry consumed; B: \bar{x} no. sec./feeding bout; C: \bar{x} no. berries consumed/bout.
^b Adjusted means from analysis of covariance. Unadjusted means: Establishment = 3.5, Maintenance = 3.6.

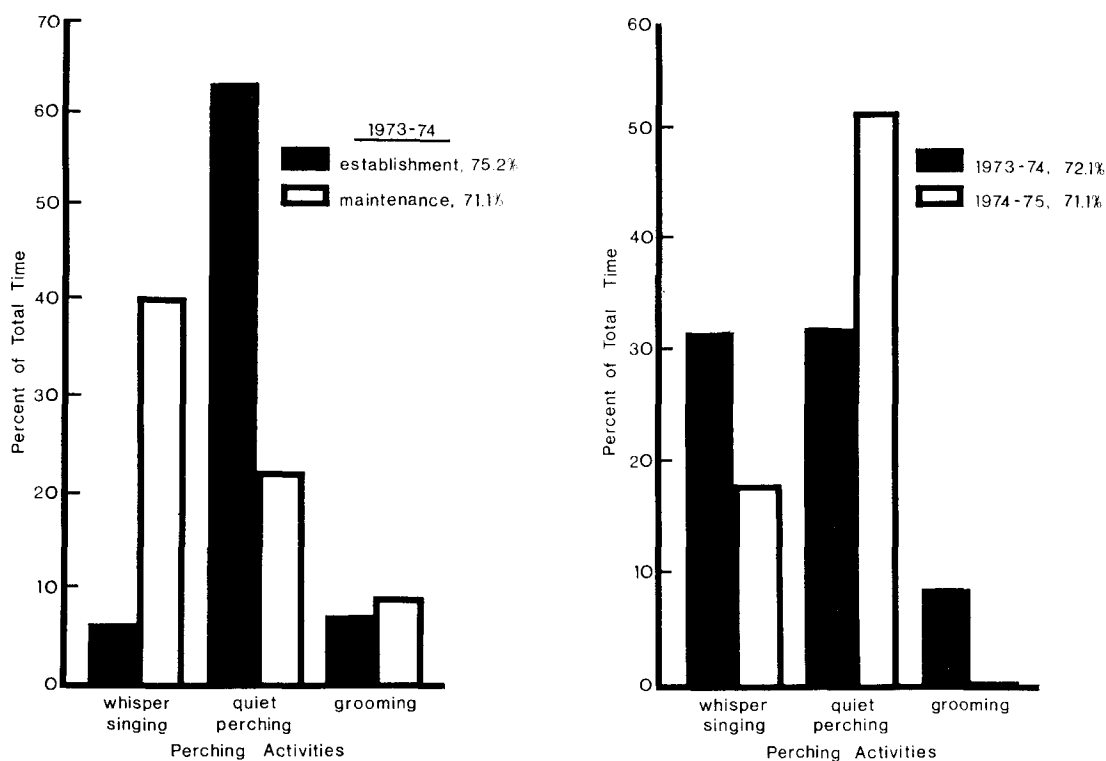


FIGURE 5. Percentages of Townsend's Solitaires' winter time devoted to different types of perching behavior. Left and right graphs compare the same periods as the corresponding graphs in figure 2.

juniper berries was spent in trees. After 15 December 1974, the Townsend's Solitaires began feeding more intensely on the ground, and by 26 January 1975, they spent more than 95% of the time they devoted to foraging for juniper berries on the ground. After the shift, foraging in the trees took place within 0.5 m of the ground whereas, prior to the shift all foraging in the trees took place above 1 m. We compared the mean number of foraging seconds/berry consumed, the mean number of seconds/berry feeding bout, and the mean number of berries consumed/bout, but we found no significant differences between foraging in the trees and on the ground.

Some of the berries the Townsend's Solitaires picked from the ground and trees were dropped. Although in most cases this appeared to occur accidentally while the birds attempted to swallow the relatively large (in relation to bill size) berries, some may have been rejected because they were too hard or dry. If solitaires rejected berries on a large scale, rejection most likely occurred visually prior to picking. Berries that had been damaged by insects differed in external appearance from undamaged ones and were more woody than fleshy.

PERCHING AND AERIAL ACTIVITIES

In both winter periods, more time was spent in perching activities than in all other activities combined (fig. 5). Perching activities are characterized by their lack of extensive motion. Quiet perching includes slight body and head movements related to maintaining watchfulness over the surrounding country and quite probably the territory in particular. Birds engaged in grooming or whisper singing appear to be less attentive to their surroundings than birds that perch quietly.

In the 1973-74 maintenance phase, banded Townsend's Solitaires spent less time quietly perching than during the establishment phase and more time grooming and whisper singing. Perching activities also occupied less time during the maintenance phase; the extra time apparently was used in foraging. In 1974-75, the distribution of time among the perching activities closely resembled that in the establishment phase of 1973-74, with most time devoted to quiet perching (fig. 5). This may indicate a high state of territorial vigilance in the establishment phase and throughout 1974-75. On a 24 h basis, perching accounted for about 27% of the day (table 4). If these activities occur at or near existence

TABLE 4. Daily time budget of territorial Townsend's Solitaires in winter.

| Activity | Percent of 24 h day | | | |
|--------------------------|---------------------|-------------|---------------|---------------|
| | Establishment | Maintenance | 1973-74 Total | 1974-75 Total |
| Territorial ^a | 5.7 | 4.1 | 4.6 | 2.4 |
| Aerial ^b | 0.8 | 0.3 | 0.4 | 3.0 |
| Foraging | 3.3 | 5.7 | 5.3 | 5.4 |
| Perching | 29.8 | 25.2 | 27.0 | 26.7 |
| Night | | | | |
| Roosting | 60.4 | 64.6 | 62.5 | 62.5 |
| Other | — | 0.1 | 0.1 | — |
| Total | 100.00 | 100.0 | 99.9 | 100.0 |

^a Excluding chases and aerial fights.

^b Including chases and aerial fights.

metabolic levels (as seems likely), then they are an energetically economical means of maintaining vigilance. During the establishment phase of 1973-74, 63.4% of the perching occurred in the tops of trees or in the tall ponderosa pines, but during the maintenance phase, this was reduced to 57.7%. In 1974-75, 71.2% of the perching took place in the treetops or tall pines compared to a winter average of 59.2% during 1973-74.

Flight, aerial chases, and aerial fighting probably were the most energy-demanding activities. Teal (1969) estimated the cost of flight in small birds at 10 times the resting metabolic rate. More time was devoted to these activities in 1974-75 than in 1973-74 (fig. 6). The establishment phase had more aerial activity than the maintenance phase. Thus, these activities were most prevalent during periods of intense territoriality and when territories were large. Because many of the differences between the 24 h time budgets resulted from increases in aerial activity (table 4), it appears that territorial establishment is energetically more costly than maintenance, and large territories are more costly than small ones. The energetic costs of activities such as foraging and singing have never been measured, but various authors (Orians 1961, Schartz and Zimmerman 1971) have estimated that these costs are near those of existence or resting metabolism.

UTILIZATION OF TREES

In 1973-74, 43% of the total time was spent in the tall ponderosa pines located in each territory (fig. 6). These trees, presumably because of the excellent views that they afforded, served as lookout posts and primary song posts in the small territories, thereby eliminating the need for boundary patrols. In 1974-75, the tall pines did not provide clear

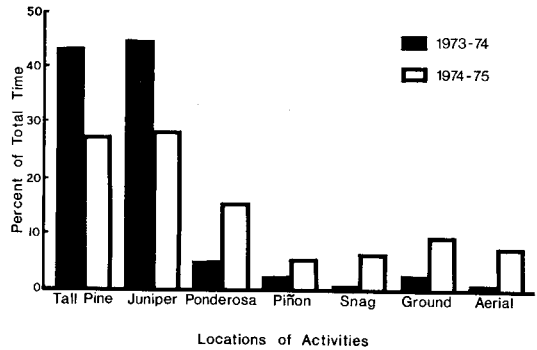


FIGURE 6. Percentages of Townsend's Solitaires' winter time spent in different trees or other locations within territories. Tall Pine refers to the tall ponderosas shown in figure 1.

views of the territories, and only 26.6% of the total time was spent in them. However, more time was spent boundary patrolling than in 1973-74. All time spent in the tall pines (82% of which was spent in perching activities) may involve territorial vigilance regardless of other activities in which the birds engaged.

In an unusual situation in 1973-74, one of the banded birds and an unbanded Townsend's Solitaire shared the same tall ponderosa pine for the entire wintering period. The territory boundary apparently bisected the tree, and each bird was always observed to be on his own side. The birds tended to ignore each other when both were in the tree although they never were observed singing simultaneously from the tree. At other locations along their common boundary, they defended their territories from each other in a typical fashion. Welch (1975) mentioned a somewhat similar situation for Savannah Sparrows (*Passerculus sandwichensis*).

The amounts of time spent by territorial Townsend's Solitaires in other locations differed from one winter period to the next. While on boundary patrols in 1974-75, solitaires frequently used medium-sized ponderosas, taller piñons, and dead snags that protruded above the average treetop level as song and lookout posts. In 1973-74 when boundary patrolling was minimal, these trees were largely ignored (fig. 6). The percent of time spent in juniper trees in 1974-75 was less than in 1973-74, but the percent of time spent on the ground was greater as a result of the changes in foraging locations.

During the establishment phase of 1973-74, about 22% of the Townsend's Solitaires' time was spent on the tops of trees, not including the tall ponderosa pines. Once territories were established, however, only 7% of the time was

spent on the treetops, and for the entire winter period, time spent on the treetops averaged 10.8%. By contrast, in 1974-75, 36.6% of the time was spent on treetops. Solitaires rarely perched on top of the tall ponderosas, but instead, perched 1 or 2 m below the top in a place which gave good views of the territory.

DISCUSSION

It has often been postulated that one important function of territoriality is to secure a food supply for the territory owner, although, with few exceptions (Stenger 1958, Holmes 1970, Zahavi 1971), substantiating data have been difficult to gather (Hinde 1956). The data presented here show clearly that protection of the food source is the function of winter territoriality in Townsend's Solitaires. Their territories are strictly feeding territories, used neither for mate attraction nor for any other breeding activities. They are abandoned in the spring when the birds migrate to breeding grounds in quite different habitats.

In 1973-74, when food was abundant and of high quality, many male Townsend's Solitaires including both adults and sub-adults, were able to establish small exclusive territories, but in 1974-75, when food was less abundant and poorer in quality, fewer birds established territories and the territories of successful individuals were larger than in the previous winter. Based upon scant evidence, it appears that sub-adult males were excluded from establishing territories by competition from more experienced and/or aggressive adult birds in 1974-75. In both winters, some banded birds, apparently less aggressive or less experienced, were unable to establish territories on the study area. These individuals may have succeeded in establishing territories in less suitable habitats or among less aggressive neighbors elsewhere, or they may have existed as floaters near the study area. Females apparently do not establish territories in the piñon-juniper-ponderosa pine ecotone but persist as nonterritorial floaters along with some males.

It is noteworthy that each territory, regardless of its size, contained much more food than its owner required. None of the territories was devoid of food when abandoned at the end of the winter periods. Clearly, wintering Townsend's Solitaires are maximizing territory size with regard to their food supply rather than optimizing it, i.e., defending an area just large enough to yield a minimally sufficient amount of energy to meet the ter-

ritory owner's needs (Wilson 1975). This probably results from natural selection favoring the solitaires with large territories containing excessive food supplies (providing much more food than they require to meet energetic needs). These can serve as insurance against overexploitation of the food by other species and nonterritorial solitaires, and as insurance against natural "disasters" such as heavy snows which may destroy or make inaccessible part of the food supply. (Both winters of this study were relatively mild compared to other recent winters around Flagstaff.) Wintering solitaires could easily assess the total food supply available to them at the very beginning of the winter periods thus facilitating territorial establishment on the basis of food availability. The birds could not assess the magnitude of food use or of disasters in advance of winter. If winter territories are to provide only the amount of food needed during an "average" winter, then periodic and unpredictable catastrophes (deep snow, ice storms, etc.) could effectively destroy the birds or cause them to leave their territories. Under these harsh conditions, a territorial system based on an "average" winter is not a viable selective option. In contrast, selection for an apparently (but not really) extravagant territorial system would insure better survival under the rare circumstances of extreme environmental conditions.

Townsend's Solitaires whose territories contain excessive food should survive the winter in better condition than nonterritorial floaters or birds whose territories contain insufficient food supplies and, therefore, should be in better condition for migration and breeding. Smith (1968) showed that tree squirrels whose territories contained excess food survived winter better than individuals whose territories contained just enough food to provide for their needs. Jenkins et al. (1963) found that nonterritorial Red Grouse (*Lagopus lagopus*) suffered higher winter mortality than territorial birds as a result of greater predation, starvation, and disease.

Verner (in litt.) suggests that maximization of territory size functions to reduce the number of breeding members of a species, thereby increasing the relative fitness of more aggressive individuals. He suggests further that defense of space, per se, has become the primary selective agent maintaining territoriality. However, large territories probably result indirectly from selection for the defense of excesses of some other requisite such as food. In wintering Townsend's Solitaires, it appears

that the amount of food on the territory is biologically more important than the size of the territory itself. It seems logical that regardless of the nature of the defended resource, maximization of the territory for that resource should result in the spatially large territories and also in behaviorally induced interference competition for the resource, thereby forcing some individuals to accept resource-poor territories or to become floaters. Townsend's Solitaires relegated to such situations presumably survive the winter less well than those on territories providing excessive quantities of food. The reproductive potential of those that do survive may, indeed, be lower than that of resource-rich territory owners. This, however, is an incidental effect of a territorial system the main function of which is to enhance survival through the winter by providing ample food for the territory owner, not a direct effect of a concerted effort to reduce the fitness of other potential breeders within the population. Winter territory also may provide experience useful in establishing breeding territories, especially for immature birds.

Territory sizes of wintering Townsend's Solitaires are probably reached through a complex interaction of time and energy considerations (economic defendability of Brown 1964), aggressive tendencies of neighbors, and an individually variable settling response stimulated by some quality of the habitat. Hildén (1965) described habitat selection in terms of proximate and ultimate factors. Juniper berries are undoubtedly an ultimate factor in the Townsend's Solitaires' territorial system but may also act as a proximate factor that releases the settling response. The masses of tree-borne berries may serve qualitatively as a means of assessing the richness of the food supply. When berries are scarce, few birds are stimulated to settle, and those that do, perceive the "need" for large territories to provide ample food. Maximum territory size is limited by competitive interactions with neighboring birds and/or by the size at which it is no longer energetically economical to defend a territory. Plentiful berries stimulate many more birds to settle; less space is perceived as necessary to provide ample food and, indeed, increased competition for territories may make large territories indefensible. In either situation, territories are probably the maximum size possible given the existing set of environmental conditions. When food is abundant, territory size may approach the minimum acceptable by Townsend's Solitaires.

The solitaires' territorial system is centered around the tall ponderosa pines located in each territory. The use of these trees as primary lookout and song posts reduces the need for energetically costly boundary patrolling by enabling territory owners to detect intruders easily and quickly. Because solitaires perch within the foliage of the tall pines rather than in exposed locations on the tops (as they do on other trees when patrolling), their use of tall pines may also reduce exposure to predators and to the elements while enabling them to maintain watch over their territories. The presence of tall pines may make the ecotone an optimum habitat for territorial individuals. Piñon-juniper woodlands lacking tall pines were searched for solitaires during the fall of 1973 and, although they contained vast numbers of juniper berries, they were not occupied by solitaires as rapidly as the ecotone. In the absence of tall pines, solitaires may prefer steep-sided canyons where territories can be observed from high prominences. The presence of Townsend's Solitaires in such canyons during the winter has been noted frequently (Bent 1949). The importance of the tall ponderosa to the territorial system apparently decreases as territories become larger and more difficult to monitor from one location.

The abundance of food in 1973-74 made interspecific territorial defense unnecessary even though the densities of all juniper berry consumers were noticeably higher than in 1974-75. Indeed, the abundance of juniper berries may have attracted many more birds to the area than would have wintered there otherwise. Interspecific territorial defense against virtually hundreds of birds would have been impossible. In 1974-75, although food was not scarce, it was apparently inconspicuous enough to cause many birds of all berry-consuming species to pass over the area and to stimulate interspecific territoriality in Townsend's Solitaires.

Perching occupies much of the territorial solitaires' time budget and, because it requires little energy expenditure above that needed for existence metabolism, it is probably a means of conserving energy. Because so much perching occurs in tall ponderosas and on tree-tops, it is also an energetically economical way to maintain watch over the territories. As a result of perching, territorial solitaires are able to spend about 21 of every 24 h at or near existence metabolism levels during the winter. Although quantitative data are unavailable, field observations indicate that floaters, by comparison, spend less time perching and more time flying as a result of being

chased from territory to territory. Because flight requires so much energy, floaters would be expected to need much more energy than territorial birds.

During the establishment phase of 1973-74 and throughout 1974-75, foraging bouts were shorter than during corresponding winter periods. Presumably, this occurred during establishment because migrants, floaters, and territorial neighbors increased the frequency of trespass, thus requiring more vigilance than during maintenance. Larger territories, harder to defend than small ones, also required more vigilance. Long periods of time spent foraging, because of the location of the food within the foliage or on the ground, would increase the chances of another solitaire entering the territory undetected. By shortening the duration of feeding bouts and increasing the number of berries consumed per bout, the solitaires were able to check their territories more often, yet were able to eat more food than in corresponding periods.

Feeding bouts were shortened by reducing the amount of time spent inspecting juniper berries prior to picking and eating them. If inspections were important for discerning and rejecting bad berries (those that had suffered insect predation and consequently developed woody flesh), then a frenetic feeding rate may have been less efficient than a more leisurely one as a result of increasing the amount of poor quality, indigestible food that was eaten. The metabolic coefficient of solitaires feeding on juniper berries is about 37.6%, much less than the 70-80% coefficients of granivorous birds (Kendeigh 1969), the 68.5% coefficient of insectivorous male Dickcissels (*Spiza americana*, Scharz and Zimmerman 1971) and the 49% coefficient of Phainopeplas (*Phainopepla nitens*) feeding on mistletoe berries (Walsberg 1975). With such a low metabolic coefficient, a reduction in high quality food intake could lead to a detrimental energy balance. This may account for the fact that more food was eaten during periods with frenetic feeding rates even though time budgets and, hence, energy budgets for all periods were similar.

The shift from foraging in the trees to foraging on the ground that occurred in 1974-75 presumably took place because the juniper berries were more accessible on the ground throughout 1974-75. Its timing was not correlated with any other noticeable behavioral change; thus the solitaires simply may not have realized previously that food was more abundant on the ground. Although no significant differences existed in any aspects of

foraging in the two locations, three factors must be considered in evaluating the advantages of one site over another: (1) the amount of time spent foraging per unit of food eaten, (2) the amount of energy expended per unit of food eaten, and (3) the distribution and abundance of the food. Other factors such as predation also influence choice of feeding-site but probably were not as important here because we saw no indications of greater predation pressure at the time of the foraging shift. In those trees that had berries in 1974-75, the berries were sparsely but evenly distributed throughout the outer foliage whereas on the ground under those trees, berries were evenly, but more densely distributed. To maintain the same feeding rate in both places (as solitaires did), a bird would have to cover the distance between berries on the tree in a shorter time than on the ground thereby expending more energy for each berry that was consumed. Given the same feeding rate, the amount of energy expended to gather each unit of food should increase as the distance between the units increases. Thus, it became energetically more economical to feed on the ground once the berries were more concentrated there than in the trees. Solitaires foraging in the trees in 1974-75 could not, with few exceptions, obtain more than two berries without moving at least 25 cm, but birds foraging on the ground could easily eat 4 or 5 berries without changing locations.

SUMMARY

Winter territoriality of male Townsend's Solitaires was studied in a piñon-juniper-ponderosa pine ecotone near Flagstaff, Arizona. Winter territories were not related to any reproductive activities, but to food availability; they served to secure a food supply. Up to 97% of the Townsend's Solitaires' winter diet consisted of berries from the one-seed juniper (*Juniperus monosperma*). In the winter of 1973-74 when berries were plentiful, territories were small and delimited by well-defined narrow boundaries. Territories were larger and overlapped in the winter of 1974-75 when berries were more scarce; boundaries were less distinct. In each winter, every territory had ample food for its owner.

In 1973-74, territorial establishment and maintenance phases were clearly distinguishable because of behavioral changes. The establishment phase was characterized by intense territorial activity and lasted from early October until about 1 December. Territories

were maintained until early April. In 1974-75 territorial and foraging behavior differed from the previous year because of changes in the quality and quantity of the juniper berries. Interspecific territoriality occurred.

Townsend's Solitaires appear to be maximizing their territory size with regard to food. While this behavior may ultimately reduce the survival of nonterritorial birds, it enhances the survival of territory owners by insuring that adequate amounts of food are available should unpredictable environmental conditions occur during the winter. Territory size may be determined by the availability of berries and the aggressiveness of neighboring birds, among other factors. Juniper berries may act as both a proximate and ultimate factor in winter habitat selection by solitaires.

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