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WESTERN HARVESTER ANTS’ FORAGING SUCCESS AND NEST DENSITIES IN RELATION TO GRAZING INTENSITY

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ABSTRACT—Western harvester ants, *Pogonomyrmex occidentalis*, are seed eaters that occur in short- and mid-grass prairies. Harvester ants are efficient seed predators but they may also be seed dispersers. We examined what ants collect to address that question. We also studied how different cattle grazing intensities affected harvester ant nest densities. Items collected by western harvester ant foragers returning to their nests were categorized as non-seeds, seeds, and nothing. Harvester ants collected large amounts of non-seeds (48%), followed by seeds (33%) and nothing (19%). Western harvester ants tolerate some environmental stress caused by grazing because nest densities were highest in moderately grazed grasslands. Interestingly, other aboveground arthropods in Colorado grasslands are reported to decrease in response to grazing, especially moderate to heavy grazing regimes. Harvester ants prefer to collect seeds but do not collect them exclusively.

Key Words: granivorous ants, foraging efficiency, grazing, nest density, western harvester ants, *Pogonomyrmex occidentalis*

Introduction

Granivorous (seed-eating) ants, such as western harvester ants (*Pogonomyrmex occidentalis*: Hymenoptera, Formicidae), are a conspicuous element of prairie communities and have been since before European settlement. Maximilian of Wied (1843) recorded, “There were a great many ant hills” along the Missouri River west of present-day Yankton, SD, in 1833. Edwin James (1823) was with Steven Long’s expedition on the South Platte River in 1820, not far from one of our study locations, the Central Plains Experimental Range in Nunn, CO). He wrote, “A striking feature...
is formed by innumerable ant-heaps, rising from 12 to 18 inches above the surface. They occur with some uniformity, at intervals of about 20 feet. They consist so entirely of small grains of flesh-coloured feldspar, that they have all of them an uniformly circular entrance on the eastward side.” This description cannot be improved upon today, except the “ant-heaps,” nest mounds of the harvester ants, now appear to be farther apart, often 50 feet or more, than James estimated.

During many months of the year in warm, arid countries, insect protein available to ants is either very scarce or competition for food among ants and other animals is fierce. Thus, a number of ant species have become vegetarians. Herbaceous plant seeds provide an accessible and nutritious food for harvester or granivorous ants (Wheeler 1910). Since western harvester ants are granivores, they actively forage for seeds. This activity can have a significant effect on plant community structure and individual plant species density (Wight and Nichols 1966; Pulliam and Brand 1975; Mares and Rosenzweig 1978; Inouye et al. 1980; Hobbs 1985; Milchunas et al. 1989; Coffin and Lauenroth 1990).

Harvester ants, such as the western harvester, may affect plant distribution in at least two ways. First, they often act as seed dispersers for plants by actively relocating the seeds in the environment (Wight and Nichols 1966; Pulliam and Brand 1975; Mares and Rosenzweig 1978; Inouye et al. 1980; Hobbs 1985; Milchunas et al. 1989; Coffin and Lauenroth 1990). We have observed that dispersal also may occur through the accidental dropping of seeds away from the parent plants during foraging bouts. Second, harvester ants preferentially collect seeds of some plant species over those of others. Such preferential selection may alter the abundance of these plant species and cause the most preferred species to become less abundant over time (Rogers 1974; Rogers and Lavigne 1974; DeVita 1979; Nowak et al. 1990).

In Colorado grasslands, 91% of the seeds collected by western harvester ants were from two native seed species, pepperweed (*Lepidium densiflorum*) and Indian rice grass (*Oryzopsis hymenoides*), and the ants collected 11.1% of all available seeds from these species (Crist and Wiens 1994). Crist and MacMahon (1992) found that in certain years western harvester ants might collect up to 100% of the seeds from these preferred species.

The effects of grazing on vegetation and soils, and to a lesser extent on vertebrates other than cattle, have been well documented. However, the effects of grazing on harvester ants, which can be a large component of the ecosystem, have not been studied extensively. In this study our aim was to discover how grazing affected harvester ant nest density and their foraging behavior in shortgrass prairies.
Western harvester ants often occur in both grazed and ungrazed grasslands, which suggests that the ants can tolerate some amount of disturbance caused by grazing. However, the extent to which different grazing intensities affect western harvester ants' foraging abilities and nest densities remains unknown. Heavy grazing may cause different plant species to dominate the plant community, especially exotic annuals that were shown to be undesirable to the ants (Usnick 1996). The observations available from Colorado and other areas suggest that western harvester ant foragers are not 100% effective in retrieving seeds on their foraging bouts (De Vita 1979; Crist and MacMahon 1991, 1992). However, the percentage of unsuccessful ants and how this percentage relates to grazing intensity has not been examined.

Our primary objectives for this study were: (1) to determine how successful western harvester ants were in foraging in grazed and ungrazed grasslands; (2) to determine the type and frequency of items brought back to the nests by western harvester ants in Colorado; and (3) to evaluate the effects of grazing intensity on the abundance of western harvester ant nests. Harvester ants, such as the western harvester, potentially can affect significantly the structure and composition of the prairie, which subsequently could affect the quality of grazing lands for cattle.

Materials and Methods

Study Sites

We conducted our study in two locations in Colorado: Central Plains Experimental Range, 60 km northeast of Fort Collins, in Weld County, and Falcon, 30 km east of Colorado Springs, in El Paso County. The dominant plant species at both sites were grasses (Bouteloua gracilis, Buchloe dactyloides, Aristida longiseta, and Sporobolus cryptandrus) and sagebrush (Artemisia frigida) (Hart 2001). The cactus Opuntia polyacantha and the herb Sphaeralcea coccinea were extremely abundant at Central Plains Experimental Range, but not at Falcon. Basal cover of the vegetation was generally low (25%-35%) (Milchunas et al. 1989). The grazing regimes in the two sites were similar.

Grazing intensities were defined by the number of heifers per 130 ha (320 acres). At Central Plains Experimental Range, lightly grazed prairies carried 15 heifers, moderately grazed pastures carried 20 heifers, and heavily grazed pastures carried 25 heifers or more on 320 acres (129.6 ha) for 5-6
summer months. Ungrazed prairies were those that had not been grazed for a minimum of four years at Falcon and 59 years at Central Plains Experimental Range. We considered grazing intensities as a function of cattle grazing only. Both sites have other herbivores, such as rodents and antelope, but these were assumed to be uniform across all treatments.

**Forager Efficiency**

To examine the ants’ foraging efficiency, at each of the two sites, a pair of moderately grazed and ungrazed grasslands (as described above) was chosen. At Central Plains Experimental Range, the grazed site was across a fence from the ungrazed site. At Falcon, the grazed site was located approximately 3 km from the ungrazed grassland. To determine what items the harvester ant foragers collected, we counted foragers and recorded their collected materials as they returned to the nest, for one half hour at each nest. Foragers were considered returning to the nest when they reached the edge of the nest clearance. Only active foragers returning from a foraging bout were counted. Harvester ants maintaining or defending the nest were not counted. Collections of returning foragers were categorized according to what they carried: (1) non-seeds (gravel, insect parts, bird feces, and plant parts), (2) seeds (seeds and fruits), and (3) nothing (when ants reached the mound carrying nothing). The majority of items collected by the ants were visible and easy to place into one of the three categories. If not, the ant was collected and their collected item was examined and counted in the appropriate category. At each of the two grazed and two ungrazed sites, we randomly chose one ant nest for each testing period.

The nests were paired by apparent age and size. Observations were made at one nest in the grazed location and one nest in the ungrazed location on any given day. When possible, more than one pair of nests was tested per day. Since the two sites were a four-hour drive apart, only one site was evaluated per day. At least one observation was made each month during the harvester ants’ foraging season, beginning in June. Although the ants may be active before June, initially they spend a large amount of time maintaining the nest instead of actively foraging. Data were collected primarily between 10:00 and 10:30 a.m., which was during the ants’ active foraging periods. We collected data at the same time during each testing period, which allowed us to eliminate large variances in temperature during the day as a factor in the statistical analysis. We gathered data on 19 dates in 1998.
Density of Harvester Ant Nests

To examine the harvester ant nest densities, twelve pastures, seven at Central Plains Experimental Range and five at Falcon, were chosen in the four different grazing intensities (lightly, moderately, heavily, and ungrazed pastures) at each location. There were fewer pastures available for study in Falcon because of limited access and variation in grazing regimes. At both sites, moderately grazed pastures were the most abundant. At Falcon, lightly grazed grasslands were not available.

Harvester ant nests in each pasture were counted to determine nest density at each of the three grazing intensities (lightly, moderately, and heavily) and at ungrazed pastures. In each pasture, we measured out two to four 50 m x 50 m plots (0.25 ha) from an arbitrarily chosen central point. We walked 2-m-wide lines throughout the length of the plots and counted all of the harvester ant nests. Both sites and all grazing intensities combined totaled 12 plots (3 ha) for each. Mean number of nests are reported by site per 0.25 ha.

Statistical Analyses

In order to study forager efficiency, we took forager counts of different nests over time. We could not use time as a classification variable because the time of measurements varied among sites and grazing treatments. The time effect as a classification variable was confounded with site and the treatment * site interaction. Preliminary ANOVAs were done using measurements in time as a replicate, however, to look at variance contributed by site, treatment, site * interaction. The only site with enough data to look at effects over time was Central Plains Experimental Range. We used regression analysis to fit a linear model for the percentage of seeds collected as a function of time for each treatment.

For the analysis of nest density by grazing treatment, means (SE) were calculated and compared. A mean was calculated for each site by grazing treatments.

Results

Collection Patterns

We observed a total of 1,709 harvester ant foragers returning to their nests during the season. Out of those 1,709 foragers, 821, or 48% of the
TABLE 1

TOTAL NUMBER OF ITEMS COLLECTED BY THE ANTS OVER TIME IN GRAZED AND UNGRAZED GRASSLANDS

<table>
<thead>
<tr>
<th>Date</th>
<th>Grazing treatment</th>
<th>Non-seeds</th>
<th>Seeds</th>
<th>Nothing</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>9 June</td>
<td>Ungrazed</td>
<td>68</td>
<td>5</td>
<td>13</td>
<td>86</td>
</tr>
<tr>
<td>9 June</td>
<td>Grazed</td>
<td>51</td>
<td>7</td>
<td>10</td>
<td>68</td>
</tr>
<tr>
<td>24 June</td>
<td>Grazed</td>
<td>47</td>
<td>17</td>
<td>23</td>
<td>87</td>
</tr>
<tr>
<td>24 June</td>
<td>Ungrazed</td>
<td>45</td>
<td>16</td>
<td>21</td>
<td>82</td>
</tr>
<tr>
<td>1 July</td>
<td>Ungrazed</td>
<td>46</td>
<td>6</td>
<td>10</td>
<td>62</td>
</tr>
<tr>
<td>16 July</td>
<td>Ungrazed</td>
<td>16</td>
<td>1</td>
<td>8</td>
<td>25</td>
</tr>
<tr>
<td>28 July</td>
<td>Grazed</td>
<td>45</td>
<td>11</td>
<td>7</td>
<td>63</td>
</tr>
<tr>
<td>5 August</td>
<td>Ungrazed</td>
<td>55</td>
<td>12</td>
<td>8</td>
<td>75</td>
</tr>
<tr>
<td>5 August</td>
<td>Grazed</td>
<td>51</td>
<td>11</td>
<td>7</td>
<td>69</td>
</tr>
<tr>
<td>15 August</td>
<td>Grazed</td>
<td>75</td>
<td>16</td>
<td>16</td>
<td>107</td>
</tr>
<tr>
<td>15 August</td>
<td>Grazed</td>
<td>106</td>
<td>23</td>
<td>13</td>
<td>142</td>
</tr>
<tr>
<td>15 August</td>
<td>Ungrazed</td>
<td>54</td>
<td>27</td>
<td>32</td>
<td>113</td>
</tr>
<tr>
<td>23 September</td>
<td>Ungrazed</td>
<td>17</td>
<td>14</td>
<td>8</td>
<td>39</td>
</tr>
<tr>
<td>23 September</td>
<td>Grazed</td>
<td>34</td>
<td>12</td>
<td>18</td>
<td>64</td>
</tr>
<tr>
<td>25 September</td>
<td>Grazed</td>
<td>14</td>
<td>155</td>
<td>17</td>
<td>186</td>
</tr>
<tr>
<td>26 September</td>
<td>Grazed</td>
<td>9</td>
<td>80</td>
<td>11</td>
<td>100</td>
</tr>
<tr>
<td>7 October</td>
<td>Ungrazed</td>
<td>60</td>
<td>29</td>
<td>4</td>
<td>93</td>
</tr>
<tr>
<td>7 October</td>
<td>Grazed</td>
<td>42</td>
<td>30</td>
<td>9</td>
<td>81</td>
</tr>
<tr>
<td>9 October</td>
<td>Grazed</td>
<td>55</td>
<td>66</td>
<td>12</td>
<td>133</td>
</tr>
<tr>
<td>9 October</td>
<td>Ungrazed</td>
<td>43</td>
<td>49</td>
<td>20</td>
<td>112</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>933</td>
<td>587</td>
<td>267</td>
<td>1787</td>
</tr>
</tbody>
</table>

total, returned carrying non-seeds (primarily gravel), but they also carried insect and plant parts (Table 1). A total of 579 foragers, or 33%, returned to the nest carrying seeds, and 319 foragers, or 19%, returned carrying nothing. Over the season the number of harvester ants that returned carrying nothing averaged 15.95 per 0.25 ha (SE = 3.09; n = 19). The mean number of ants carrying non-seeds was 41.05 per 0.25 ha (SE = 3.67; n = 19). The number of harvester ants returning to the nest carrying seeds was 28.95 per 0.25 ha (SE = 8.10; n = 19). At Central Plains Experimental Range, the ants
collected more non-seed materials, 47% ± 12%, in each half-hour observation period than at Falcon, where the ants collected an average of 23% ± 15% non-seed materials.

Site and Grazing Treatment Differences

We used preliminary ANOVAS to examine measurements over time treated as replicates to look at variation by site, treatment, and site * treatment. There was a significant site effect (F = 6.29, P = 0.096) and site * treatment effect (F = 10.14, P = 0.014). Therefore, we used ANOVAS to look at each site separately. The only site with enough data to examine variation over time within the site was Central Plains Experimental Range. Regression analysis did not find a significant difference between the slopes for percentage of seeds collected by the harvester ants as a function of time by treatment (F = 10.58, P = 0.0043), using an F-test for homogeneity of slope.

Temporal Variation

The numbers of seeds collected by western harvester ants varied significantly over time (F = 21.14, P = 0.0013). Ants collected the largest amounts of seeds later in the field season, during August, September, and October (Fig. 1). On 25 September 1999, at a grazed nest in Falcon, the ants collected 155 seeds within one half-hour period (Table 1). These seeds were almost exclusively from a neighboring perennial native plant, Heterotheca villosa (Asteraceae), or golden hairy aster. However, when golden hairy aster was not available, the ants collected other species, including the most abundant native plant species at both sites, Bouteloua gracilis, or blue grama grass.

More foragers returned to the nest with nothing earlier in the season than during September and October (Fig. 1). The non-seed category varied significantly in the ants’ collections over time. Early in the field season (June, July), the ants collected more non-seeds, primarily gravel that was used for nest maintenance (Fig. 1). We observed that the amount of gravel collected by the ants was about 70% of the total non-seed collections.

Nest Densities

At both sites, the nests of western harvester ants were more abundant in moderately grazed than in heavily, lightly, or ungrazed grasslands (Table 2). Heavily and lightly grazed grasslands had the fewest number of harvester ant nests (Table 2).
Figure 1. Forager ants were classified into one of three categories based on what they returned to the mound carrying: non-seeds, seeds, and nothing. This graph represents the total number of forage items, at both grazed and ungrazed grasslands, collected by the ants per half-hour test period.
Western Harvester Ant Nest Densities

TABLE 2
MEAN (SE) WESTERN HARVESTER ANT DENSITIES AT EACH SITE
(PER 0.25 HA) WITH GRAZING INTENSITY

<table>
<thead>
<tr>
<th>Grazing intensity</th>
<th>CP ER</th>
<th>Falcon</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>High</td>
<td>2.8 (0.63)</td>
<td>4.0 (1.0)</td>
<td>3.2 (0.54)</td>
</tr>
<tr>
<td>Moderate</td>
<td>24.2 (0.48)</td>
<td>10.5 (0.50)</td>
<td>20.3 (2.96)</td>
</tr>
<tr>
<td>Light</td>
<td>0.8 (2.22)</td>
<td>—</td>
<td>0.8 (0.48)</td>
</tr>
<tr>
<td>None</td>
<td>19.0 (1.16)</td>
<td>6.5 (2.50)</td>
<td>14.0 (3.22)</td>
</tr>
</tbody>
</table>

1 Central Plains Experimental Range
— Dash indicates not available

Discussion

Western harvester ants are effective seed harvesters (Rogers 1974; DeVita 1979; Crist and MacMahon 1991, 1992). However, foraging harvester ants often collect objects other than seeds. Over the field season, we found that 33% of foraging ants successfully located and transported seeds. More western harvester ants were successful in their collection of seeds later in the field season, when most of the C₄ plants had set seeds and there were newly available seeds for the ants to collect. In our study, seed collection by the ants reached a peak in late September, when the harvester ants collected a total of 155 seeds in one half-hour period (Fig. 1). DeVita (1979) also found that foragers of another harvester ant species, *Pogonomyrmex californicus*, returned to the nest with an increasing number of seeds over the field season. The majority of the seeds collected in our study were golden hairy aster (*Heterotheca villosa*), the preferred seed species of this harvester ant (Usnick 1996). Although golden hairy aster was available for only a short period during the summer, the ants' preference for these seeds did not change (Usnick 1996). However, when golden hairy aster was not available, the ants collected other species. These plant species included the most abundant native plant species at both sites, blue grama grass (*Bouteloua gracilis*) (Usnick 1996). This pattern of seed collection was especially apparent at Central Plains Experimental Range, where golden hairy aster was rare. Rogers (1974) also found that western harvester ants collect a large number of blue grama seeds.
Rogers (1974) found that non-seeds comprised 34% of the foraged items. However, the percentage of non-seed items returned by the ants in his study was lower than ours (48%). In our study, we observed that a large percentage of the non-seed category, up to 70%, was composed of gravel, mostly reddish feldspar. The ants’ collection of gravel was especially apparent during June and July, when the ants did most of their nest maintenance after the winter and spring precipitation. This gravel is used to enhance the nests’ solar radiation by increasing the angle of the sun on the ant mound (Cole 1994). However, late in the field season, the harvester ants collected a large number of non-seed items that were not gravel. For example, at Central Plains Experimental Range, the ants clipped *Chenopodium album* (Chenopodiaceae) flowers in October. The collection of plant parts could have been a response to low seed numbers. Thus, our study verifies Rogers’s (1974) observations that harvester ants retrieve not only seeds but other items such as plant or insect parts. Western harvester ants most likely use the plant and insect parts as food during times when seeds are not readily available, such as during the winter or early spring. Although these ants will collect insects, they have the morphological characteristics, such as saw-like mandibles and large heads, that are suited for granivory (Wheeler 1910). In addition, harvester ants are primarily scavengers and they rarely kill insects, except in cases of nest defense (Wheeler 1910).

A relatively large percentage (19%) of western harvester ants returned to the nest carrying nothing. Crist and MacMahon (1991) also examined the percentage of unsuccessful foragers. They found that 14 out of a total of 48 foragers (34%) were unsuccessful in their seed collections, which was higher than we found (19%). Although the methods of the two studies and sample sizes differ significantly, both studies clearly show that western harvester ant foragers are not always successful in their foraging attempts. We observed that one possible reason for returning with nothing was that these ants had dropped their collected item on their return to the ant nest. If the dropped item were a seed, the ants would be functioning as seed dispersers. However, some of the ants who dropped their initially collected item may have obtained a second item and then were counted in either the seed or non-seed category. Also, some ant species, such as honey pot ants, may appear to return to the nest carrying nothing after a foraging bout because they store nectar or other liquids inside their body. However, harvester ants do not ingest nectar or other liquids (Wheeler 1910). Therefore, the number of ants that functioned as dispersers remains unknown.

Grazing did not appear to significantly affect the type of items the ants returned to the nest. Similarly, Rogers (1974) also found no significant
difference in the rate of forage items returned by the ants in a lightly versus heavily grazed pasture. North America’s shortgrass-steppe plant community is among the least responsive to grazing in the world (Milchunas and Lauenroth 1993). Grazing decreases the aboveground plant biomass and increases the amount of bare ground (Milchunas et al. 1989, 1998). Moderate changes in grazing regimes apparently does not interfere with the ants’ ability to become established and survive.

Moderate grazing appeared to be beneficial for ant nest density, as well as for the long-term composition and structure of the plant community (Hart 2001). Harvester ants appear to be unusual in their tolerance of moderate grazing, because other aboveground arthropods at Central Plains Experimental Range decreased when grazing intensity increased from a moderate to heavy regime (Milchunas et al. 1998). The harvester ants’ abundance in moderately grazed grasslands may be explained by the availability of food. Biomass of golden hairy aster and blue grama, the ants’ preferred seed species (Usnick 1996), was intermediate at Central Plains Experimental Range (Hart 2001) when compared to other grazing regimes.

Similar to Milchunas et al. (1998), we found that the harvester ant nest density decreased in heavily grazed grasslands. Heavily grazed grasslands had the lowest densities of western harvester ant nests possibly because the soil was more compacted by larger numbers of cattle (Hart 2001). In addition, large numbers of cattle may increase the likelihood that the ants’ nests will be trampled, thus increasing nest maintenance costs. Heavy grazing also leads to larger numbers of exotic plant species, especially annuals such as Bromus japonicus, which the ants do not collect frequently (Usnick 1996).

The relatively high numbers of nests in the ungrazed grasslands at both sites is difficult to explain, especially in relation to the lack of nests in the lightly grazed grasslands. Hart and Ashby (1998) found the least amount of bare ground in ungrazed sites, but the difference between ungrazed and lightly grazed grasslands was small. High numbers of harvester ant nests may be related indirectly to another factor, that of rodent densities. Brown et al. (1979) found reciprocal density compensation between rodents and ants, implying competitive interactions between the two granivore taxa. Granivorous rodents and ants have overlapping requirements for seed resources, which are limited at times. So, seeds represent a potentially contested resource when these seed eaters co-occur (Brown et al. 1979). However, no data exist on competitive interactions between rodents and harvester ants in our grasslands sites.
In conclusion, our findings indicate grazing intensity affects western harvester ant nest density and that western harvester ants forage for both seeds and other items. These ants do successfully tolerate a certain amount of stress caused by grazing because the ant nest densities were highest in the moderately grazed grasslands. However, they do not do thrive in heavily or lightly grazed grasslands. Western harvester ants are highly visible and potentially important seed dispersers in western prairies. Our findings suggest that western harvester ants can be managed effectively by understanding their impact on the plant community and their interaction with grazers.

References


Religion on the Great Plains
March 27-29, 2003

27th Annual Interdisciplinary Symposium sponsored by the Center for Great Plains Studies, University of Nebraska-Lincoln Cornhusker Hotel & Burnham Yates Conference Center 333 South 13th Street, Lincoln, Nebraska

Keynote Speakers:

Martin Marty
Fairfax M. Cone Distinguished Service Professor Emeritus of History of Modern Christianity, University of Chicago Divinity School

Henrietta Mann
Professor and Endowed Chair in Native American Studies, Montana State University

Ferenc Szasz
Professor of History, University of New Mexico

“This symposium aims to explore, from all disciplinary points of view, the development and decline of religions, their institutional forms and varieties of expression, and their responses to the physical and social conditions of the Great Plains,” said Robert Haller, University of Nebraska-Lincoln professor of English and co-chair of the conference.

Co-chair Hugh Whitt, professor of sociology at the University of Nebraska-Lincoln, said, “We wish to have familiar topics discussed in a new light and forgotten topics restored to their rightful place in our understanding of how religions have come to the Plains.”

The conference will explore whether sparse population, ethnic variety, differing political forms, and the grassland agriculture of the Plains supported and sustained a religious life with identifiable qualities and histories.

For registration information: Center for Great Plains Studies, University of Nebraska-Lincoln, 1155 Q Street, PO Box 880214, Lincoln, NE 68588-0214. Phone: 402/472-3082; Email: cgps@unl.edu; Website: http://www.unl.edu/plains/events/2003symp.html