USE OF WATER-FILLED RED-COCKADED WOODPECKER CAVITIES BY OTHER ORGANISMS

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Abstract: We monitored 619 red-cockaded woodpecker cavities bimonthly from March 1997 through September 2001 in the Apalachicola National Forest in northern Florida. Of the cavities monitored, 79 (12.7%) contained water on at least one visit. Approximately 14% of water-filled cavities were in dead trees. Water presence in cavities was highly variable: some cavities contained water for several years, some only during wet seasons, and others for less than 2 months. Between periods when the cavity contained water, many cavities remained empty. Of vertebrates that used cavities subsequent to inundations, red-bellied woodpeckers, flying squirrels, and red-cockaded woodpeckers were the most frequent users. Rat snakes, red-bellied woodpeckers, tree frogs, scorpions, and a roach used cavities that contained water. At least 15 species of vertebrates and invertebrates were found to use cavities after water had evaporated from them. Within the water contained in cavities were found at least 24 species of protozoa, mites, nematodes, at least 3 species of rotifers, and at least 5 species of dipteran larvae. Cavities varied substantially in abundance of all invertebrate species. Protozoa were present in most cavities with water, whereas larvae were more variable. Size of cavity entrance, height above ground, and length of inundation did not appear to be predictors of the invertebrate community. Red-cockaded woodpecker cavities that serve as phytotelmata (aquatic container habitats) have received little previous attention, but here we show that water-filled cavities may provide a resource for invertebrates, especially during dry periods in

longleaf pine forests. Vertebrates appear to be opportunistic in their use of cavities that tend to contain water.

Key words: phytotelmata, water-filled cavities, invertebrates, mosquito, Florida, red-cockaded woodpecker, red-bellied woodpecker, eastern bluebird, great crested flycatcher, southern flying squirrel, gray rat snake, corn snake, squirrel tree frog

The red-cockaded woodpecker (*Picoides borealis*) excavates cavities for roosting and nesting in living pine trees of the southeastern United States. Because of the difficulty in excavating cavities in living trees, this species prefers to excavate pine trees that are infected with red heart fungus (*Phellinus pini*) (Conner and Locke 1982, Hooper 1988, Hooper et al. 1991, Rudolph et al. 1995). A red-cockaded woodpecker typically excavates several cavities during its lifetime, and the time needed to excavate an individual cavity can vary from months to years (Conner and Rudolph 1995). As cavities age, red-cockaded woodpeckers abandon them to excavate newer cavities in other trees. Reasons for leaving a particular cavity can include usurpation by another species, damage due to fire, death of the tree, inundation of the cavity with water, unsuitability of the cavity or the tree (e.g., reduced resin flow, diameter of cavity entrance), and disturbance. Over time, cavities accumulate in the defended area of a family group of red-cockaded woodpeckers, and eventually the cavity trees die but may still harbor cavities for a number of years. This aggregation of cavity trees (hereafter termed "cluster") is eventually used by a variety of species ranging from birds to mammals, amphibians, reptiles, and invertebrates (Table 1).

Occupants of both new and old cavities created by red-cockaded woodpeckers are known as the community assemblage, and these occupants interact in various ways. Many compete for cavities because cavities are thought to be limiting in the habitats in which red-cockaded woodpeckers are found. Occupants differ according to time of year: during summer, species richness and occupancy are greatest because many migratory cavity-nesting species are present (e.g., eastern bluebird, *Sialia sialis*). Occupancy is also influenced by seasonal pulses in cavity

users. For example, red-cockaded woodpecker fledglings may roost in cavities within their natal

territories (the areas defended by their parents) within a month of fledging. Similarly, other resident

species fledge young that may require roost sites within the cluster (e.g., red-bellied woodpeckers,

Melanerpes carolinus). Our observations over several years reveal that some cavities fill with water

at various frequencies.

Phytotelmata are aquatic habitats in or on plants (Kitching 2000), including tree holes and

the leaves of pitcher plants and bromeliads. Rich communities of organisms have been described in

these systems, and most commonly include bacteria, protozoa, rotifers, and dipteran larvae

(Kitching 2000, Ellison et al. 2003). The inhabitants of water-filled tree cavities excavated by

woodpeckers have been ignored by both those who study phytotelmata and those who study

woodpecker-cavity occupants. Therefore, an understanding of this community will begin with a

description of its inhabitants and with association of richness and abundance patterns with other

community components.

The objectives of our study were to document the frequency with which red-cockaded

woodpecker cavities fill with water, to determine how this inundation affects cavity occupancy, and

to quantify species richness and abundance of invertebrates in tree cavities as a function of water

permanence, temporal variation, and predator exclusion.

STUDY AREA

We monitored red-cockaded woodpecker clusters in the Apalachicola National Forest

(ANF) of northwestern Florida from March 1997 through September 2001. The ANF supports 2

populations of red-cockaded woodpeckers. The western half of the forest (the Apalachicola Ranger

District, ARD) harbors approximately 500 red-cockaded woodpecker groups (the largest population

in the United States), and the population appears stable. In contrast, the population in the eastern

half of the forest (the Wakulla Ranger District, WRD) has experienced a 23% decline in less than

10 years (Hess et al. 2003).

METHODS

On the WRD, we monitored 22 clusters containing a total of 220 cavities from March 1997 through September 2001 and 12 other clusters, containing a total of 124 cavities, from May 1999 through September 2001. On the ARD, we monitored 42 clusters containing a total of 275 cavities from June 1999 through August 2001. The clusters were randomly selected as part of another study and were monitored bimonthly throughout the year (i.e., each cavity was observed on 6 occasions during the year). Any cavities that were originally excavated by a red-cockaded woodpecker were included in our sample, regardless of the age or condition (i.e. alive or dead) of the cavity or tree. Cavity occupancy was determined at night because most species use the cavities then. Exceptions are nocturnal species like eastern screech-owls (*Otus asio*) and southern flying squirrels (*Glaucomys volans*), which use cavities in the daytime but can frequently be observed there at night. We determined occupancy by shining a flashlight at the cavity entrance and observing the occupant with binoculars as it looked out. If no occupant was observed by this method, we used a remote inspection device (RID).The RID was an infrared camera mounted on a 15-m telescoping fiberglass pole with a black-and-white video monitor at the base of the pole (Furhman Diversified, Seabrook, TX). Disturbance to occupants was minimized because the device produced no light visible to organisms unable to see the infrared spectrum.

To investigate aquatic inhabitants of water-filled cavities, we randomly sampled a subset of cavities on the WRD that were known to contain water at least once during the study. We took water samples from 24 water-filled cavities on 2–5 occasions from November 2001 through July 2002 to determine the differences between cavities that were permanently filled and those that were only intermittently filled, the effect of time (i.e., differences between successive samplings of the same cavity), the effect of season (i.e., differences between samples taken at different times of year), and the effect of exclusion of top-level predators (mosquitoes) from aquatic habitats. We excluded predators by screening cavity entrances with bridal-veil material.

We conducted sampling by gently stirring the water inside cavities and removing 40 ml from each one for laboratory analysis. In cases where less than 40 ml of water was present, we added enough distilled water to allow extraction of 40 ml. When the entrance hole was large enough, we extracted water samples with a large plastic pipette (a turkey baster). Otherwise, we used a siphon. We took three 1-ml subsamples without visible mosquito larvae from each 40-ml sample, so as to remove the protozoans in them from further predation. All equipment was cleaned with alcohol between samples, and all samples were kept on ice until they reached the laboratory. Samples were filtered, and larvae were identified and counted. Mites, rotifers, and protozoa from 1-ml subsamples were measured with a Sedgewick-Rafter cell.

We conducted a one-way analysis of variance (ANOVA) to test the effects of water permanence, time, season, and predator exclusion on larvae, protozoan species richness, total protozoan abundance, and the abundance of common protozoan species, rotifers, mites, and nematodes. We performed Pearson correlations to determine whether cavity characteristics such as diameter, height above ground, and tree condition were related to protozoan species richness and abundance, rotifer abundance, or dipteran larval abundance.

Linear regression was used to measure the relationship between monthly precipitation and the proportion of cavities with water in them.

RESULTS

We found 57 (16.6%) of 344 cavities on the WRD and 22 (8.0%) of 275 on the ARD to contain water on at least one occasion. However, during the period when the ARD was being sampled (i.e. June 1999 through September 2001), only 37 (10.8%) of 344 cavities on the WRD contained water on at least one occasion. The proportion of cavities containing water during any one survey ranged from 0.01 to 0.15 on the WRD and from 0.02 to 0.05 on the ARD. The length of time during which cavities retained water was highly variable: some contained water for several years, some only during wet seasons, and others for less than 2 months.

Of the 9,326 cavity observations, water was present during 474 (5.1%). Most cavities that had previously contained water were found either to contain water or to be unoccupied on subsequent surveys (Table 1). Of the species that occupied cavities known to contain water previously, the most frequent on the WRD were red-bellied woodpeckers, followed by red-cockaded woodpeckers and flying squirrels. On the ARD the order was reversed; flying squirrels used these cavities more frequently than did red-cockaded woodpeckers and red-bellied woodpeckers. Overall, 15 species were observed using cavities that had formerly contained water. In addition, we confirmed 16 cases in which nonaquatic occupants were using cavities that still contained water: snakes (*Elaphe obsoleta* or *Elaphe guttata*) (6), red-bellied woodpeckers (4), squirrel tree frogs (*Hyla squirella*) (3), scorpions (Scorpionida: Buthidae) (2), and a roach (Blattaria: Blatellidae) (1).

Water samples collected from cavities harbored at least 24 species of protozoa, mites, nematodes, at least 3 species of rotifers (bdelloid), and at least 5 species of dipteran larvae (Table 2). Aquatic communities varied substantially in abundance of all invertebrate species. Protozoa were present in most cavities that contained water, whereas dipteran larvae were more variable. Tree cavities with permanent water did not differ significantly from those that dried periodically in any of the measured variables (Table 3), but a number of important trends were evident. Protozoan species richness and abundance were lower in permanent water bodies than in those that dried periodically. In contrast, the abundances of dipteran larvae, rotifers, and several common protozoan species were greater in permanent phytotelmata.

Protozoan species richness and abundance as well as dipteran larval abundance decreased over time in tree-cavity phytotelmata. Time had no significant effect on rotifer species. Season affected protozoan richness and abundance as well as larval abundance. Cavities that contained aquatic organisms in the autumn were sampled in the following spring but did not yield any organisms at that time. Exclusion of predators produced no significant effect, and none of the

dependent variables (aquatic invertebrate species identity or abundance) was correlated with cavity diameter, height above ground, or tree condition.

Monthly precipitation pattern (Figure 1) was a good predictor of water presence in cavities. The proportion of cavities containing water on the ARD increased significantly with monthly precipitation ($r^2 = 0.5486$, $P = 0.01$), whereas the proportion on the WRD did not exhibit as strong a relationship ($r^2 = 0.1471$, $P = 0.07$) (Figure 2).

DISCUSSION

Our data suggest that a substantial proportion of red-cockaded woodpecker cavities fill with water at some time during their life spans. Cavities that fill temporarily may eventually provide roosting or nesting sites for a variety of organisms while dry. Cavity size and local precipitation patterns are probably the best predictors of cavity filling (Figures 1, 2). The proportion of cavities containing water in our study is similar to that found in Texas for cavities greater than or equal to 7 cm in diameter (2.8–15.8%; Conner et al. 1997). Interestingly, we found that the two ranger districts were very similar in overall proportion of cavities filled with water on at least one occasion, but the proportion containing water during any one survey was far greater on the WRD. This result suggests that either more cavities are permanently water-filled on the WRD or that cavities on the WRD that are prone to water inundation are more frequently filled by precipitation. There are more cavity trees per cluster on the WRD (10.1 cavities per cluster) than on the ARD (6.5 cavities per cluster), probably because of different fire-management schedules. The ARD was burned much more regularly than the WRD (James et al. 1997), and more frequent burning may have increased loss of older, and possibly dead, cavity trees. The cavity entrance tends to become larger with age, particularly once the tree dies and increasing entrance diameter probably increases the likelihood of water entering the cavity. Enlargement rates appear to be greater on the WRD.

We are the first to document organisms living in water-filled woodpecker cavities. Exclusion of adult mosquitoes from water-filled cavities had no effect on mosquito abundance

because *Ochlerotatus triseriatus* is known to lay eggs in tree holes before they fill (Novak and Shroyer 1978). Another surprising result was that permanently filled cavities did not differ from intermittently filled ones in any variable measured. We would have expected species to differ in their tolerance of desiccation. For example, Juliano et al. (2002) found mortality of mosquito eggs varied with length of drying periods. In addition, we found no relationship between larvae abundance and protozoan abundance or richness, perhaps because many of the bacterial, protozoan, and larval species remain dormant during dry periods and species composition is therefore unaffected. In contrast, many pond systems that experience periodic drying events differ in species assemblage from those that do not. For example, fish (a top predator) are not normally found in temporary ponds, and species assemblages in temporary ponds therefore differ markedly from those in permanent ponds (Wellborn et al. 1996). When we inundated a sample of cavity detritus in the laboratory, we observed 5 protozoan species and 1 rotifer species within 48 hours, so many organisms are present in "empty" cavities before they fill with water. Second, the lack of top-predator (dipteran-larva) effects may result from high resource levels in the cavities that may allow populations to overcome the negative effects of predators (Kneitel and Miller 2002).

Work on communities associated with cavities in trees has largely emphasized vertebrates or parasites (see, e.g., Pung et al. 2000) associated with those vertebrates. We find that water-filled cavities also provide habitat for organisms not normally considered when woodpecker cavities are discussed. This rich community of dipteran larvae, protozoa, rotifers, and bacteria is similar to those of other water-filled habitats. Most research on phytotelmata has addressed pitcher plants, bromeliads, and tree holes (e.g., Aspbury and Juliano 1998, Kitching 2000, Kneitel and Miller 2002), and our study adds another example for a widespread community. Woodpecker cavities clearly provide habitat for aquatic communities, the further study of which would improve understanding of the dynamics of patchy communities (see, e.g., Caswell 1978, Mouquet and Loreau 2002). Another avenue of phytotelmata research is to explore how water chemistry and

nutrients affect population and community-level dynamics (Walker et al. 1991, Paradise 2000). In addition, the influence of woodpecker cavities on the population dynamics of mosquito larvae should be addressed, especially in light of the role that mosquitoes play as disease vectors.

MANAGEMENT IMPLICATIONS

Several cavities known to have contained water were eventually used by red-cockaded woodpeckers. One tree, in particular, was used for nesting for several years even though the cavity frequently contained water before and after nesting. Because cavities are limiting, such water-filled cavities may act as a buffer, serving when no better cavities are available. In our study area, a July–September peak in precipitation coincides with the period when fledgling woodpeckers are looking for cavities (i.e., a period of great demand for cavities). We observed organisms roosting in cavities that contained water, suggesting that cavities are in short supply.

Many aquatic organisms that rely on phytotelmata may be limited by potential breeding sites during periods of drought. Clearly, some red-cockaded woodpecker cavities provide breeding habitat to aquatic invertebrates in pine forests where water is frequently in short supply during certain times of year. Red-cockaded woodpecker cavities that contain water should not be viewed as inhospitable to organisms associated with cavities. In fact, such cavities may play an important role for both vertebrate and invertebrate cavity users.

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Table 1. Frequency of water content and occupation (excluding aquatic invertebrates) of red-cockaded woodpecker cavities that have previously contained water. The two ranger districts of the Apalachicola National Forest (Florida) differ in rank order of frequency of the three most common occupants.

Common name	Wakulla Ranger District $n = 829$	Apalachicola Ranger District $n = 180$
Water-filled	0.376	0.456
Empty	0.367	0.250
Red-bellied woodpecker	0.100	0.056
Red-cockaded woodpecker	0.051	0.089
Southern flying squirrel	0.040	0.106
Great crested flycatcher (*Myiarchus crinitus*)	0.022	0.011
Rat snake	0.018	0.011
Mud dauber (Hymenoptera: Sphecidae)	0.012	0.022
Eastern bluebird	0.008	0.022
Northern flicker (*Colaptes auratus*)	0.008	0.000
Eastern screech-owl	0.004	0.000
Squirrel tree frog	0.001	0.022
Scorpion	0.001	0.006
Roach	0.001	0.000
Beetle (Coleoptera)	0.001	0.000
Anole (*Anolis carolinensis*)	0.001	0.000
Wasp (Hymenoptera: Vespidae)	0.000	0.006

Table 2. Aquatic species found in water samples (*n* = 58) taken from red-cockaded woodpecker cavities in the Apalachicola National Forest, Florida.

Species	Mean abundance (individuals/ml)	Range
Protozoa		
Bodo	55.44	0-7200
Colpidium	0.33	0-20
Chrysomonad sp 1	216.02	0-2711
Chrysomonad sp 2	0.09	0-1
Cryptomonas sp 1	0.12	0-5
Colpoda	152.11	0-13500
Cryptomonas sp 2	7.19	0-594
Cyclidium	2.77	0-225
Euplotes	0.10	0-10
Paramecium	31.66	0-1034
Tetrahymena	0.08	0-7
Vorticella	1.43	0-40
Unknown 1	0.07	0-9
Unknown 2	2.16	0-291
Unknown 3	0.07	0-10
Unknown 4	0.05	0-4
Unknown 5	3.53	0-140
Unknown 6	85.37	0-3900
Unknown 7	3.53	0-146
Unknown 8	0.18	0-23
Unknown 9	0.36	0-32
Unknown 10	54.89	0-3450
Unknown 11	52.52	0-6900
Unknown 12	0.01	0-1
Invertebrates		
Mites	0.04	0-2
Nematode	0.10	0-10
Rotifers	27.66	0-460
Larvae		
Psychodid sp.	0.10	0-14
Ochlerotatus triseriatus	0.75	0-24
O. signifera	0.13	0-7
Unknown dipteran larvae	0.02	0-3
Syrphidid sp.	0.09	0-12

Table 3. Effects of four variables on invertebrate occupants of water-filled red-cockaded woodpecker cavities (ANOVA).

| Variable	*F*	*P*	Trend
1.Permanence of water in holes			
Protozoan richness	1.080	0.303	lower in permanently filled holes
Protozoan abundance	1.840	0.181	lower in permanently filled holes
Mosquito larval abundance	2.770	0.102	higher in permanently filled holes
Rotifer abundance	1.020	0.317	higher in permanently filled holes
Colpoda abundance	0.456	0.502	higher in permanently filled holes
Bodo abundance	0.445	0.507	higher in permanently filled holes
2. Time			
Protozoan richness	4.310	0.002	decrease over time
Protozoan abundance	5.740	<0.001	decrease over time
Mosquito larval abundance	4.646	0.001	decrease over time
Rotifer abundance	0.967	0.446	slight decrease over time
3. Season			
Protozoan richness	227.0	<0.001	higher in autumn than spring
Protozoan abundance	37.05	<0.001	higher in autumn than spring
Mosquito larval abundance	6.440	0.028	higher in autumn than spring
Rotifer abundance	2.900	0.115	higher in autumn than spring
4. Exclusion of adult mosquitos			
Protozoan richness	0.906	0.345	
Protozoan abundance	2.160	0.148	
Mosquito larval abundance	0.310	0.580	
Rotifer abundance	0.459	0.501	
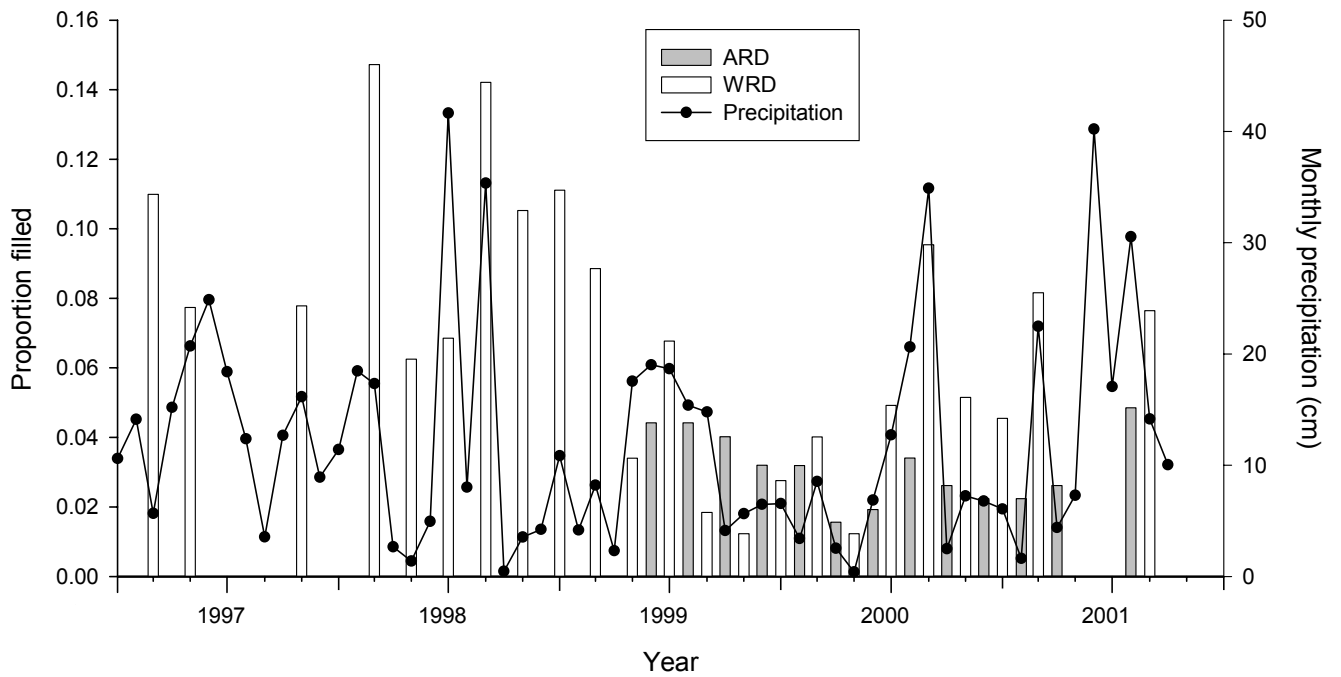
Figure 1. Proportion of red-cockaded woodpecker cavities filled with water relative to monthly precipitation levels (January, 1997 through October, 2001) on the Apalachicola Ranger District (ARD) and Wakulla Ranger District (WRD) of the Apalachicola National Forest, Florida.
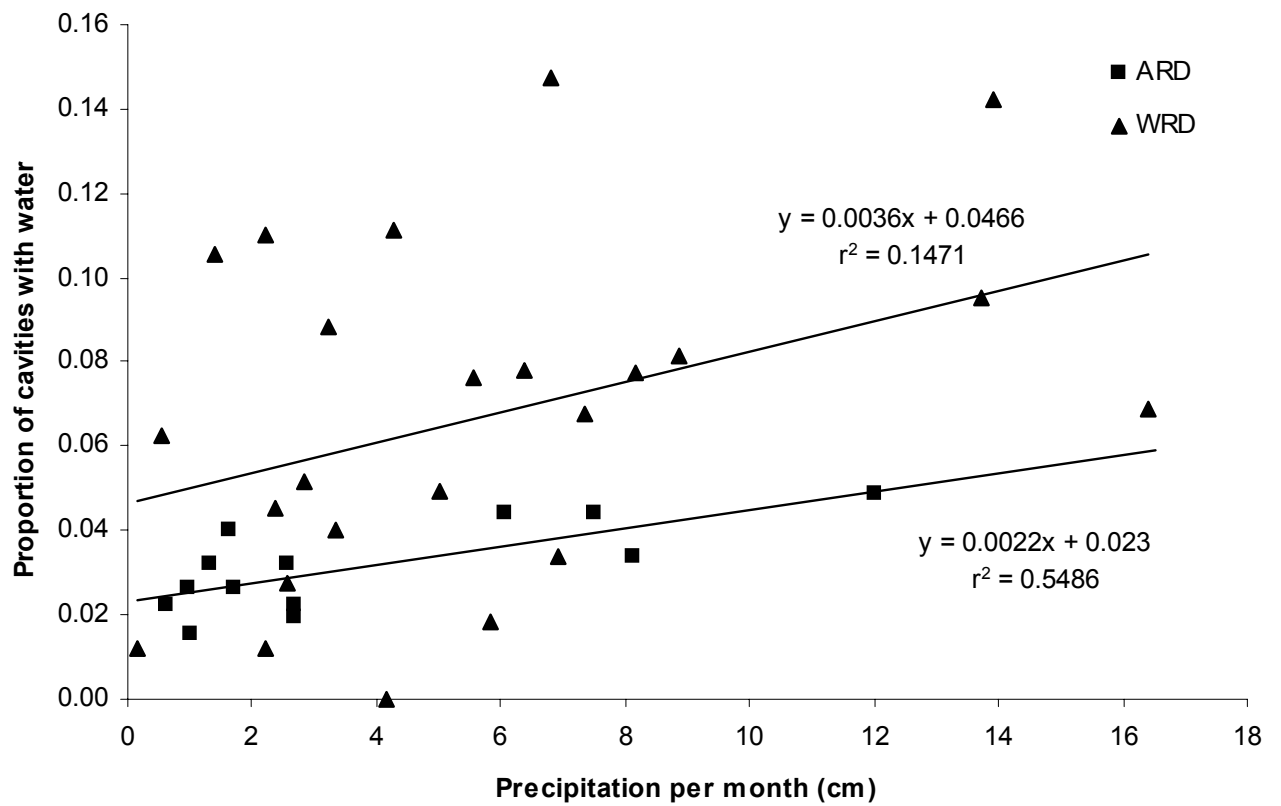
Figure 2. Proportion of red-cockaded woodpecker cavities filled with water as a function of monthly precipitation for the Apalachicola Ranger District (ARD) and Wakulla Ranger District (WRD) of the Apalachicola National Forest, Florida.