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FACILITATION OF SAP-FEEDING BIRDS BY THE WHITE-FRONTED WOODPECKER IN THE MONTE DESERT, ARGENTINA¹

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Abstract. In the Monte desert of South America, the overall supply of water and food for birds decreases in the dry, cold season (June through September). During this period the White-fronted Woodpecker (*Melanerpes cactorum*) drills holes in the trunks and branches of *Prosopis flexuosa* and feeds on the exuded sap. Other bird species, diverse in ecological attributes and taxonomic affinities, take advantage of this resource which otherwise would be rarely available. Sap is a major constituent of the diet of the White-fronted Woodpecker and 11 other bird species, and sap feeding comprises between 16% to 83% of foraging observations made during June and July. Aggression by White-fronted Woodpeckers significantly reduced the time smaller bird species spent feeding on sap, indicating that White-fronted Woodpeckers actively compete for this resource. Other bird species profit from having access to a resource rich in water and sugar.

Key words: *Argentina, competition, facilitation, Melanerpes cactorum, Monte desert, sap feeding, White-fronted Woodpecker.*

Resumen. En el desierto del Monte de Sudamérica, la oferta de agua y alimento para las aves disminuye durante la estación seca de invierno (junio a septiembre). Durante este período, el Carpintero de los Cardones (*Melanerpes cactorum*) taladra los troncos y ramas de *Prosopis flexuosa* y se alimenta de la savia que

fluye de las perforaciones. Otras especies de aves, de diferentes grupos ecológicos y taxonómicos, aprovechan este recurso, que de otro modo raramente está disponible. La savia es un componente importante de la dieta del Carpintero de los Cardones y de otras 11 especies de aves; durante los meses de junio y julio constituye del 16% al 83% de las observaciones de forrajeo. La agresión por los Carpinteros de los Cardones reduce significativamente el tiempo de alimentación en las perforaciones con savia de las especies más pequeñas. En la explotación de este recurso se revela una compleja combinación de interacciones positivas y negativas entre las aves. Las interacciones agonísticas sugieren que el Carpintero de los Cardones compite activamente por este recurso, mientras que las otras especies de aves se favorecen al acceder a un recurso rico en agua y en azúcares.

In Europe and North America, several species of woodpeckers feed on the sap flowing from drilled holes (Foster and Tate 1966, MacRoberts and MacRoberts 1976, Short 1982). This behavior is perhaps best exemplified by the Yellow-bellied Sapsucker (*Sphyrapicus varius*). The sap from holes drilled by this species attracts, and is used by, other taxa including insects, birds, and mammals (Foster and Tate 1966, Wiens 1989, Holmes 1990). Use of this food resource may be particularly important to hummingbirds, because they require food of high energy content (Miller and Nero 1983).

In South America, two species of woodpeckers of the genus *Melanerpes* use sap as a food resource: the

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Acorn Woodpecker (*M. formicivorus*) of the lower montane wet forest in Colombia (Kattan and Murcia 1985, Kattan 1988) and the White-fronted Woodpecker (*M. cactorum*) (Genise et al. 1993). In the thorn-scrub woodland of the semiarid Chaco in Argentina, the White-fronted Woodpecker feeds on sap only during the austral winter; other avian species and insects are attracted to the drilled holes (Genise et al. 1993). Here I document sap consumption by White-fronted Woodpeckers in woodlands occupying the driest portion of their range, interactions with other bird species that use this resource, and seasonal variation in the exploitation of sap. If sap is a valuable resource during the dry season when both water and food are scarce, then inter- and intraspecific agonistic interactions are expected.

METHODS

The study was conducted from November 1996 through November 1997 in the Flora and Fauna Reserve of Telteca (32°21'S, 68°03'W), Mendoza Province, Argentina. This reserve is located within the Monte Phytogeographical Province (Cabrera and Willink 1980), a narrow arid and semi-arid latitudinal strip in western Argentina, at the foot of the Andes. Telteca is a desert area with marked climatic seasonality, rainy summers, and cold dry winters. Mean annual rainfall is 161 mm (data from Meteorological Program of the Regional Center for Scientific and Technological Investigations, Mendoza). The landscape is characterized by a system of dunes and scrublands dominated by *Larrea divaricata* (jarilla), *Trichomania usillo* (usillo), and *Bulnesia retama* (retamo). Open woodlands of *Prosopis flexuosa* (algarrobo dulce) grow in the low-lying areas between dunes, with a shrub layer dominated by *B. retama*, *Capparis atamisquea* (atamisqui), and *Lycium tenuispinosum* (Haullín).

In June and July 1997, I made three to nine (mean \pm SD = 7.4 ± 2.5) 5-min focal observations of all birds visiting 11 *P. flexuosa* trees that were being used by eight White-fronted Woodpecker flocks. I also recorded the number of individuals of each species that fed on sap, and the time they spent at the sap tree. From November 1996 through October 1997, I made periodic random observations of the foraging behavior of birds showing sap-feeding habits. Whenever possible, I collected information on feeding behavior. To ensure sample independence, I recorded a single feeding event for each individual and, when flocks were involved, only one individual per species (Hejl et al. 1990, Recher and Gebski 1990). I did not knowingly include the same individual twice in any one day. In order to diminish overestimation of the most conspicuous foraging activities, I only considered the feeding behavior 10 sec after a focal bird had been sighted (Wiens 1989).

The number of sap holes in each tree was estimated by counting the number of trunks and branches, over 10 mm in diameter, showing drilled holes with actual sap-flow.

I used 35-mm mesh mist-nets, 12.4 m long, to assess bird relative abundance. Nets were placed near shrubs and trees in the low-lying areas between dunes. Mist-nets were operated between April and August of 1997, for a total trapping effort of 1,142 net hours. Two sets

of 13 nets were operated periodically, each of them distributed on an area of about 7 ha.

RESULTS

During the dry season, White-fronted Woodpeckers drill holes through the bark and into the phloem of *Prosopis flexuosa* trunks (Fig. 1). Either individually or in flocks of up to six birds, White-fronted Woodpeckers periodically visited the drillings to feed on the exuded sap. Each group of woodpeckers simultaneously maintained numerous trees with active holes. On a few occasions, I observed holes with flowing sap in trunks of *Bulnesia retama*, whereas the two other tree species present in the area, *Geoffroea decorticans* (chañar) and *Ephedra boelckei* (parrón), were not used by woodpeckers. During the focus sampling period (June–July), woodpeckers drilled holes only in trunks and branches of *P. flexuosa*. I observed only one sap hole in a trunk of *B. retama* in the month of June. However, subsequent observations suggest that, as the dry season progressed, woodpeckers modified their foraging strategy. By early September, they continued to use *P. flexuosa*, but *B. retama* and *Larrea divaricata* shrubs also were frequently drilled, and occasionally *Capparis atamisquea*. By September, only 33% of the observations of sap feeding by all bird species was of *P. flexuosa*, and 30% each of *B. retama* and *L. divaricata*.

The number of holes in trees and the frequency of feeding events of the White-fronted Woodpecker were positively correlated ($r_s = 0.65$, $n = 11$, $P = 0.03$). Other bird species clearly took advantage of sap flow (Table 1), only accessible at recently drilled woodpecker holes. It is not surprising that the frequency of visits by the other birds also was higher at the most intensely drilled trees ($r_s = 0.78$, $n = 11$, $P = 0.005$), regardless of the presence or absence of woodpeckers.

Sap consumption by birds was inversely correlated with rainfall (Fig. 1). During June and July, for bird species using this resource, at least 16% of my foraging records was comprised of sap from drilled holes (Fig. 2). For each species, I compared the frequency of feeding at focal sap trees with the species' relative abundance estimated with mist-nets (Table 1). Sap consumption was not proportional to bird species abundance in the Telteca Reserve (Fig. 3). At least five of these species appeared to actively select this resource, including the White-fronted Woodpecker and Tufted Tit-Spintail (*Leptasthenura platensis*), whereas other abundant species such as the Common Diuca-Finch (*Diuca diuca*) and Picui Ground-Dove (*Columbina picui*) were not observed to use it at all (Fig. 3).

White-fronted Woodpeckers defend their feeding holes by driving away smaller bird species attempting to use them. On 58.2% of the 122 occasions in which I observed smaller birds (weight < 11 g) like the Tufted Tit-Spintail, the Ringed Warbling-Finch (*Poospiza torquata*), and the Greater Wagtail-Tyrant (*Stigmatura budytoides*) visiting sap trees with woodpeckers present, the smaller heterospecifics were chased away by the woodpeckers. However, on only 6.3% of the observed instances ($n = 32$) did wood-

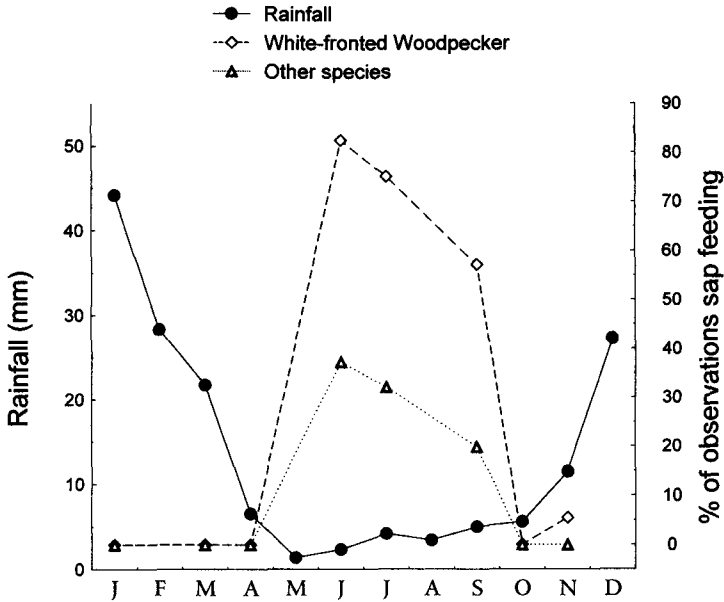


FIGURE 1. Mean monthly rainfall at Encón (30 km northeast of Telteca), and relative occurrence of sap feeding (371 foraging-independent observations from May to September, and 150 from October through March) by White-fronted Woodpecker and other birds (11 species, see Table 1). Correlation between sap consumption and mean monthly rainfall: White-fronted Woodpecker: $r_s = -0.81$, $n = 8$, $P = 0.014$; other species: $r_s = -0.87$, $n = 8$, $P = 0.005$.

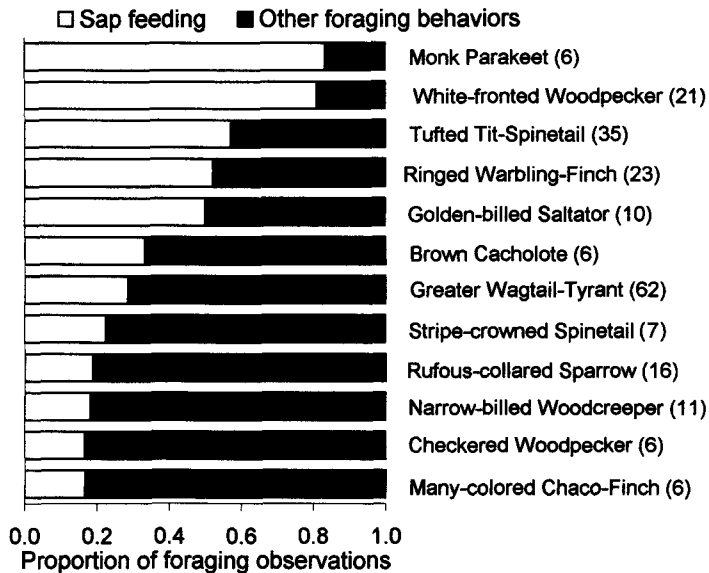


FIGURE 2. Relative importance of sap feeding at *Prosopis flexuosa* trees in June and July by birds of the Monte desert, Argentina. Number of foraging-independent observations in parentheses ($n = 209$).

TABLE 1. Birds feeding on sap recorded at the Telteca Reserve. Columns indicate: relative abundance of each species based on total mist-net captures (April through August, $n = 242$), total number of individuals per species ($n = 323$) recorded sap-feeding at White-fronted Woodpecker's holes in 5-min focal observations, and mean foraging time spent at trees with sap holes.

	Body mass (g)	Mist-net captures	Sap feeding	Mean \pm SD time spent at sap trees (min)
White-fronted Woodpecker (<i>Melanerpes cactorum</i>)	34.6	10	118	6.1 \pm 6.5
Tufted Tit-Spinetail (<i>Leptasthenura platensis</i>)	9.4	18	61	2.3 \pm 2.3
Greater Wagtail-Tyrant (<i>Stigmatura budytoides</i>)	10.1	31	60	1.8 \pm 1.3
Monk Parakeet (<i>Myiopsitta monachus</i>)	94.0	3	32	11.7 \pm 9.3
Ringed Warbling-Finch (<i>Poospiza torquata</i>)	10.3	14	30	2.1 \pm 2.0
Golden-billed Saltator (<i>Saltator aurantirostris</i>)	47.0	6	9	3.3 \pm 2.9
Many-colored Chaco-Finch (<i>Saltatricula multicolor</i>)	22.9	16	4	4.0 \pm 2.6
Brown Cacholote (<i>Pseudoseisura lophotes</i>)	64.0	1	3	8.0 \pm 5.0
Rufous-collared Sparrow (<i>Zonotrichia capensis</i>)	18.2	38	3	—
Narrow-billed Woodcreeper (<i>Lepidocolaptes angustirostris</i>)	25.3	6	1	—
Checkered Woodpecker (<i>Picoides mixtus</i>)	28.2	3	1	—
Stripe-crowned Spinetail (<i>Cranioleuca pyrrhophia</i>)	11.0	4	1	—
Common Diuca-Finch (<i>Diuca diuca</i>)	25.6	35	0	—
Picui Ground-Dove (<i>Columbina picui</i>)	45.0	17	0	—
Short-billed Canastero (<i>Asthenes baeri</i>)	17.4	10	0	—
Chaco Earthcreeper (<i>Upucerthia certhioides</i>)	22.6	8	0	—
Gray-bellied Shrike-Tyrant (<i>Agriornis microptera</i>)	52.7	3	0	—
Least Shrike-Tyrant (<i>Agriornis murina</i>)	27.5	3	0	—
Crested Gallito (<i>Rhinocrypta lanceolata</i>)	55.0	3	0	—
House Wren (<i>Troglodytes aedon</i>)	9.5	3	0	—
Other species ($n = 7$)		9	0	—

peckers displace species weighing more than 40 g. Indeed, there was a clear inverse relation between mean body mass of each bird species and the frequency of aggressive encounters between them and individual *M. cactorum* ($r_s = -0.96$, $n = 7$, $P < 0.001$). The observation that smallest species spend less time on foraging sites (Table 1) ($r_s = 0.86$, $n = 8$, $P = 0.007$) is thus at least partly explained by the agonistic behavior of woodpeckers. Supporting this is the fact that, for all three of the smallest bird species combined, the average time spent at the drilled trees was significantly shorter when woodpeckers were present (Mann-Whitney U -test, $z = 5.05$, $n_1 = 106$, $n_2 = 90$, $P < 0.001$). Although with lower frequency, I also recorded aggressive behavior among other bird species, even against woodpeckers.

DISCUSSION

In the northern Monte desert, the supply of food resources strongly decreases during the dry season (Fig. 1; Blendinger, unpubl. data). Between May and September, the Telteca Reserve receives only approximately 10% of its total annual rainfall. The productivity of drylands is related to the quantity of precipitation (Dunning and Brown 1982, Wiens 1991). Accordingly, the drastically diminished availability of arthropods and fleshy fruits results in increased shortage of preformed water for birds and many other organisms. As the dry season progresses, birds increasingly resort to resources (rarely if ever consumed in summer) which are high in water content. Almost all of the bird species < 100 g occurring in the Telteca

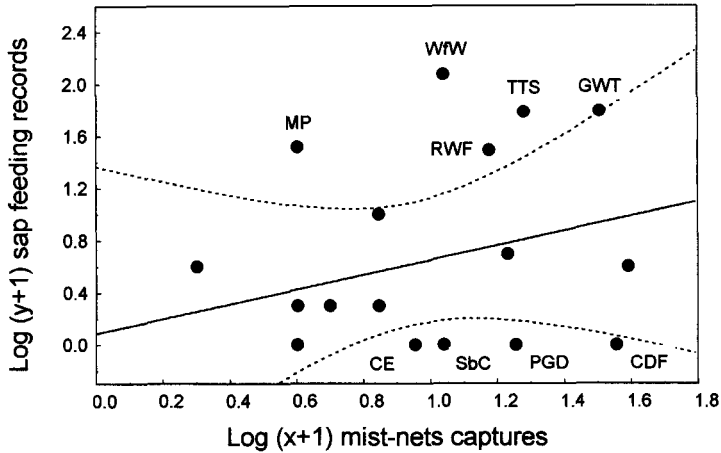


FIGURE 3. Relationship between abundance and frequency of sap feeding by bird species during the dry season (simple regression, $R^2 = 0.08$, $n = 20$, $P = 0.11$). Dotted lines give 99% confidence interval. CDF = Common Diuca-Finch, CE = Chaco Earthcreeper, GWT = Greater Wagtail-Tyrant, MP = Monk Parakeet, RWF = Ringed Warbling-Finch, Sbc = Short-billed Canastero, PGD = Picui Ground-Dove, TTS = Tufted Tit-spinetail, WW = White-fronted Woodpecker.

Reserve feed to some degree on the fruit of *Lycium* spp. (Solanaceae), the only fleshy fruit available in the dry season.

Phloem sap is both a source of water and a food item with high energy content (Foster and Tate 1966). Although White-fronted Woodpeckers drill holes throughout the year, sap consumption is much greater during the dry season. Other bird species do not appear to use this resource at all during the rainy season. These other bird species that feed at woodpecker drilled holes belong to diverse ecological and taxonomic groups. These include both birds that forage primarily on the ground and those that feed in trees and shrubs, and both insectivores and granivores (Marone 1992, Marone et al. 1997). The importance of sap as a food resource for these birds in the dry season becomes evident when comparing the frequency of sap consumption with the total number of feeding events. Such an approach reveals that sap is particularly important to White-fronted Woodpeckers and Monk Parakeets (*Myiopsitta monachus*).

Although some of the most abundant species in the Telteca Reserve do not eat sap, it is clearly an important resource for certain rarer species including Monk Parakeet and Golden-billed Saltator (*Saltator aurantiorostris*). In the semi-arid Chaco, only the Greater Wagtail-Tyrant showed a close association with woodpeckers' drillings (Genise et al. 1993), although this conclusion is probably largely a reflection of this species' abundance in the area. In the Telteca Reserve, I also found Greater Wagtail-Tyrant to be one of the most frequent visitors at White-fronted Woodpeckers' holes. However, in comparing the rate of sap eating with other foraging activities, it appears that other less abundant bird species may be more dependent upon sap than wagtail-tyrants.

Associations between the Yellow-bellied Sapsucker

or the Acorn Woodpecker and other avian species are typically regarded as commensal relationships (Miller and Nero 1983, Kattan and Murcia 1985, Wiens 1989). These woodpecker species do not defend their sap-supplying holes against intruders (but see Foster and Tate 1966, MacRoberts and MacRoberts 1976). In the case of interactions between White-fronted Woodpeckers and facultatively sap-feeding heterospecifics, the relationship is more complex. White-fronted Woodpeckers in Telteca do actively defend their sap-flowing drillings by displacing smaller birds that approach them.

Aggressive interactions among sap-eating birds suggest the existence of interference competition. According to Wiens (1989), when agonistic behavior is related to spatially-defined territories, aggression provides strong evidence of competition. White-fronted Woodpeckers live in sedentary groups, as revealed by frequent recaptures and sightings of marked birds on sampled sites. Furthermore, they defend their territories against conspecific intruders. Trees with sap-holes "belong" to specific groups within the different territories. To assert that interactions are competitive requires that sap be a limiting resource. Several observations suggest that this is true. But for a few exceptions, sap only is accessible to heterospecific birds at woodpeckers' drillings. Only some *Prosopis flexuosa* trees are used for the purpose of sap consumption, and intensity of this use varies among trees based upon the presence of wounds in branches and trunks. However, the use of such trees is temporally dynamic. Trees may be used in successive years, but not continuously (pers. observ.). For example, in the present study, the use of sap holes in five of six studied focal trees of *P. flexuosa* notably diminished or ceased over the course of one month's observations. In the semi-arid Chaco, Genise et al. (1993) found that only 23% of *Aspido-*

sperma quebracho-blanco (quebracho blanco), the tree species most used by woodpeckers, exhibited wounds. Furthermore, many of these trees were re-used in subsequent years (Genise et al. 1993). Finally, in the Telteca Reserve, larger wooded patches supported several groups of White-fronted Woodpeckers, and possibly the number of *P. flexuosa* trees available per group might be fewer than in smaller patches; in support of this contention I observed woodpeckers dwelling in larger patches to generally be more aggressive towards heterospecifics at sap holes compared to woodpeckers belonging to single groups occupying smaller patches.

Sap is a major food source for White-fronted Woodpeckers in arid and semi-arid environments in western Argentina, particularly during the dry season. Holes drilled by woodpeckers enable other species to use the sap, facilitating their access to a food item rich in water and sugar during the season when availability of such resources are limited. Given the importance of sap to the diet, this food item presumably plays a relevant role in both the individual survival and population persistence of various species in this desert environment.

Interactions among species are likely to have very different consequences for the birds involved. My observations reveal the existence of an intricate nexus of positive and negative interactions, that can be defined as a combination of facilitation and competition. Although the White-fronted Woodpecker displaces many birds from drillings, these heterospecific avian species still gain access to a food resource that would otherwise be unavailable to them. Alternatively, observed agonistic interactions, especially those between White-fronted Woodpeckers and individuals of smaller bird species, strongly suggest that woodpeckers compete for sap. This assertion is strengthened by observations indicating that sap is a limiting resource for birds. Further experimental studies should evaluate the effect of sap availability on the survivorship of individuals and persistence of populations of the various bird species which rely on this resource.

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