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MORE BIRDS NEST IN HYBRID COTTONWOOD TREES

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ABSTRACT.—Natural hybrid zones can be centers of insect abundance and species richness. We investigated the possibility that this pattern may extend to other trophic levels. We found more bird nests in a cottonwood hybrid zone than in pure stands of *Populus fremontii* or *P. angustifolia*. Furthermore, within the hybrid zone, there were more nests in hybrid trees than in trees of either parental type. Differences in architecture between hybrids and the two parental species may account for these differences in nest distribution. Breeding bird surveys in each of the three zones showed no differences in overall abundance or diversity; however, there were significant differences among zones in the abundances of the most common species. Management of riparian areas should not overlook the importance of hybrid plants. *Received 25 May 1993, accepted 20 Nov. 1993.*

The role of habitat in structuring avian communities has been well studied. Complex habitats appear to support more species than simple ones; however, this complexity may be manifested in both the physical structure of the vegetation (physiognomy) and the plant taxonomic composition (floristics), and there is some debate as to which factor is more important (Rotenberry 1985). Studies that support the importance of physiognomy include MacArthur and MacArthur (1961), Willson (1974), and James and Wamer (1982), whereas Wiens (1969), Anderson and Shugart (1974), and Rice et al. (1984) emphasize the role of floristics. Here, we suggest that another factor, plant hybridization, may be an important component of habitat complexity, especially through its influence on nest site selection.

Riparian habitats support extremely high bird populations (Carothers et al. 1974, Szaro 1980, Knopf 1985). Over 50% of 166 species breeding in riparian areas of the Southwest are completely dependent on this habitat (Johnson et al. 1977). While several authors report that cottonwood stands contain the highest bird densities of riparian areas in western North America (Carothers et al. 1974, Johnson et al. 1977, Strong and Bock 1990), the potential role of hybrid trees has not been examined.

Hybridization in *Populus* is widespread and well documented (Eckenwalder 1984). We studied hybrids between Fremont (*P. fremontii*) and narrowleaf (*P. angustifolia*) cottonwood along the Weber River in northern Utah. Hybrids can be F_1's, which are intermediate between the two parental species, or backcrosses to *P. angustifolia* (Keim et al. 1989), producing a continuum of tree types. Fremont and narrowleaf cottonwood have quite different architectures and F_1 type hybrids make up another

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FIG. 1. There are three distinct categories of tree architectures: pure Fremont cottonwood, F_1 hybrid type (includes F_1 hybrids and close backcrosses), and narrowleaf cottonwood type (includes pure narrowleaf and complex backcross hybrids).

distinct architectural class (Fig. 1). The hybrid zone contains all of these tree types and is structurally more complex than the pure zones.

Hybrid zones can also be centers of insect species richness and abundance (Whitham et al. 1991), potentially increasing the resource base for insectivorous birds. For example, in the Weber River system, a dominant insect herbivore of cottonwood, the gall aphid *Pemphigus betae,* is often eaten by birds and is concentrated in the hybrid zone (Whitham 1989).

We investigated the possibility that birds respond to increased architectural complexity and insect abundances in the hybrid zone. We first examined patterns of nest distribution in pure stands of each cottonwood species and in the hybrid zone. Second, we looked at nest distributions among Fremont, narrowleaf, and F_1 type hybrid trees within the hybrid zone. Finally, we conducted breeding bird surveys to determine whether or not there are differences in avian communities among the three zones.

METHODS

Cottonwoods are the dominant tree throughout the drainage of the Weber River. Fremont cottonwood grows at elevations of approximately 1300–1500 m, and narrowleaf cottonwood grows at elevations of approximately 1400–2300 m. Where their ranges overlap, there is a 13 km long zone where extensive hybridization occurs. Complex backcross trees closely resembling pure narrowleaf cottonwood occur in the narrowleaf zone, but for the purposes of this study the hybrid zone was defined as the zone of overlap.

This research was conducted in the 13 km hybrid zone and in the adjacent (closest 5–8 km upstream and downstream) narrowleaf and Fremont zones. Thus, we were able to make comparisons among zones while also controlling for possible site differences not related to cottonwood trees. For example, several studies report different bird communities associated with different elevations (Knopf 1985, Strong and Bock 1990, Finch 1991). However, our lowest site (Fremont zone) was 1295 m, and our highest site (narrowleaf zone) was 1487 m, a difference of less than 200 m. Further, the only obvious habitat differences among zones are the different cottonwood tree phenotypes.

In early April 1991, before bud break, we surveyed trees for previous years' nests. The first survey compared nest densities among the three zones. At five sites in each zone, we examined the first 100 mature (>20 cm dbh) cottonwoods we encountered by walking along the river from west to east. We recorded numbers and species (if possible) of nests. The sites were matched for tree density as well as tree size. We looked at only living trees, so numbers of cavity nests were low.

The second survey compared nest densities on three groups of trees (Fremont architecture, narrowleaf architecture, and F_1 type hybrid architecture—see Fig. 1) within the hybrid zone. Backcross hybrids are common in the hybrid zone and their architecture closely resembles narrowleaf cottonwood. We surveyed 100 trees of each type for a total of 300 trees. Differences in nest densities were compared using χ^2 tests.

We conducted breeding bird censuses during late May and early June 1991. Birds were censused by direct count on fixed-width belt transects 200 m long and 100 m wide. We chose this length transect because it approximates the maximum length of relatively undisturbed mature cottonwood habitat along much of the Weber River. We censused five transects in each of the three zones. To determine if there were differences in the bird communities of Fremont, narrowleaf, and hybrid zone cottonwoods, we ran a MANOVA using the abundances of five common species: Black-billed Magpie (*Pica pica*), Northern Oriole (*Icterus galbula*), American Robin (*Turdus migratorius*), Yellow Warbler (*Dendroica petechia*), and Warbling Vireo (*Vireo gilvus*). We then used discriminant analysis to see if the distributions of these species would separate the transects into the three different zones.

RESULTS

There were almost three times as many bird nests in the hybrid zone as in either the Fremont or the narrowleaf zone ($\chi^2 = 53.09$, $P < 0.001$, Fig. 2A). The majority of these nests belonged to magpies and orioles, but we also found robin nests, several types of smaller cup nests, raptor nests, and some nest cavities.

Within the hybrid zone, we found twice the number of nests in cottonwood trees with the F_1 hybrid architecture as in either parental type ($\chi^2 = 13.58$, $P < 0.005$, Fig. 2B). The architecture of these hybrids is intermediate between that of the two species (Fig. 1). They may be more attractive as nest sites because they have both the relatively open crown of Fremont cottonwood and some of the fine branching of narrowleaf cottonwood.

Based on the abundances of the five common riparian species, there were significant differences in the bird communities of the hybrid zone, the Fremont zone, and the narrowleaf zone (Wilks' $\lambda = 0.063$, $P < 0.01$). The abundances of three of the five species were significantly different

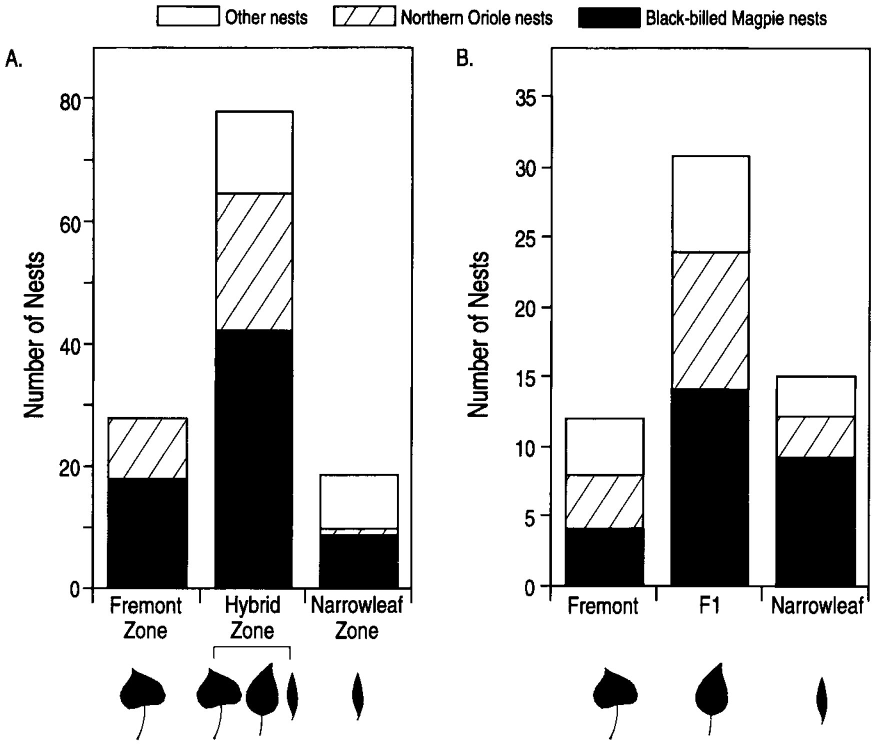

FIG. 2. A) Differences in nest distribution among the pure Fremont zone, the hybrid zone, and the pure narrowleaf zone (all nests: $\chi^2 = 53.09$, $P < 0.001$; magpie nests: $\chi^2 = 26.52$, $P < 0.001$; oriole nests: $\chi^2 = 22.16$, $P < 0.001$; N = 500 trees). B) Differences in nest distribution among tree types within the hybrid zone (all nests: $\chi^2 = 13.58$, $P < 0.005$; magpie nests: $\chi^2 = 6.1$, $P < 0.05$; oriole nests: $\chi^2 = 5.35$, $0.05 < P < 0.10$; N = 100 trees).

(Table 1). Magpies and orioles were clearly more abundant in the hybrid zone than in the narrowleaf zone, and orioles were slightly more common in the hybrid zone than in the Fremont zone. Also, discriminant analysis using bird species and abundance correctly classified 14 of the 15 transects as being either in the hybrid, Fremont, or narrowleaf zones.

DISCUSSION

Nest sites.—Genetically-different cottonwoods have very different architectures (Fig. 1), and our data suggest that birds respond to this physiognomic complexity by choosing to build nests in F_1 hybrids. We found more nests in the hybrid zone and more nests in F_1 hybrid trees within the hybrid zone. Because of their numerous lateral branches and associ-

TABLE 1
BREEDING BIRD CENSUS DATA AND RESULTS OF UNIVARIATE ANOVA'S FOR THE FIVE MOST COMMON SPECIES[a]

Zone		Black-billed Magpie	Northern Oriole	American Robin	Yellow Warbler	Warbling Vireo
Fremont	$\bar{x}$	5.4	2.0	6.6	3.2	0.55
	SE	0.51	0.71	1.53	1.16	0.24
Hybrid	$\bar{x}$	4.8	2.8	4.0	6.4	1.0
	SE	0.86	0.86	0.55	1.53	0.55
Narrowleaf	$\bar{x}$	0.6	0.4	5.0	13.6	3.2
	SE	0.4	0.24	1.18	1.50	0.80
ANOVA	*F*	17.69	3.45	1.27	14.28	5.88
	P	<0.001	0.066	0.316	0.001	0.017

[a] (MANOVA: Wilk's $\lambda = 0.063$; $P < 0.01$).

ated crotches, these hybrid trees may be better nest sites for some species of birds.

Other studies have emphasized the importance of nest site selection in driving avian abundance and species diversity. Martin and Roper (1988) proposed that Hermit Thrushes (*Catharus guttatus*) select habitats that contain many potential nest sites in order to reduce nest predation, and Martin (1988) argued that nest predation is important in organizing bird communities. Recently Steele (1993) tested the role of nest site selection versus foraging site selection and concluded that nest site requirements are probably more important.

Although the survey undoubtedly included nests of different ages, there is no reason to believe that nests would persist longer in the hybrid zone. How long nests stay in trees should be in large part a function of wind velocity. High winds are prevalent during much of the year throughout Weber Canyon, and the hybrid zone is located in one of the most exposed areas. Also, as cottonwoods are the dominant vegetation throughout this drainage, it is unlikely that we missed many nests located in other species of trees.

Foraging sites.—While our data indicate that nest site choice influences bird distributions in the hybrid zone, it is possible that some species are also responding to an abundant food resource. Rotenberry (1985) suggests that the most important source of variation among plants that birds are likely to respond to is the provision of food.

The cottonwood gall aphid, *Pemphigus betae,* is concentrated in the hybrid zone (Whitham 1989). Each gall contains up to 300 aphids, and a single tree has up to 50,000 galls (Whitham 1983). The galls mature in

June, so they become available at an important time for breeding birds. Rates of avian predation on these galls may be 25% or higher (Whitham 1987). We have observed Black-capped Chickadees (*Parus atricapillus*) opening galls and feeding on aphids (Whitham 1987). Other documented cases of birds preying on aphid galls include: Gila woodpecker (*Melanerpes uropygialis*; Speich and Radke [1975]), Tree Sparrow (*Passer montanus*; Sunose [1980]), and Great Tit (*Parus major*; Burnstein and Wool [1992]). Probably all of the species that we used for statistical analyses are capable of slicing open galls.

Conservation of hybrid plants.—Recent conservation policy has emphasized discouraging hybridization between species (O'Brien and Mayr 1991). This policy is based on studies of animal hybrids, where hybridization is thought to cause "genetic disintegration." However, hybridization in plants is important: an estimated 70% of angiosperms originated as interspecific or intergeneric hybrids (Stace 1987). And, as our data suggest, plant hybrid zones may provide unique habitat for different animal species.

The conservation of riparian areas, and specifically the importance of riparian habitats to birds, are issues that have recently received considerable attention (reviewed by Knopf et al. 1988). We propose that the value of riparian areas is augmented by the hybrid status of the riparian vegetation. Hybridization is common in both cottonwoods (Eckenwalder 1984) and willows (*Salix* sp.) (Brunsfeld et al. 1991), another native riparian plant. While hybrid zones occur in most drainage systems, they may be restricted to small areas (e.g., the cottonwood hybrid zone in Weber Canyon occupies only 13 km of the ca 500 km drainage of the Weber River). By providing better nesting habitat than either Fremont or narrowleaf cottonwood, this hybrid zone may influence avian community structure. For these reasons, we urge not only the conservation of riparian areas but the conservation of hybrid zones as well.

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LITERATURE CITED

Anderson, S. H. and H. H. Shugart, Jr. 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology 55:828–837.

Brunsfeld, S. J., D. E. Soltis, and P. S. Soltis. 1991. Patterns of genetic variation in *Salix* section Longifoliae (Salicaceae). Am. J. Bot. 78:855–869.

BURNSTEIN, M. AND D. WOOL. 1992. Great Tits exploit aphid galls as a source of food. Ornis Scand. 23:107–109.

CAROTHERS, S. W., R. R. JOHNSON, AND S. W. AITCHISON. 1974. Population and social organization of southwestern riparian birds. Am. Zool. 14:97–108.

ECKENWALDER, J. E. 1984. Natural intersectional hybridization between North American species of *Populus* (Salicaceae) in sections Aigeiros and Tacamahaca. II. Taxonomy. Can. J. Bot. 62:325–335.

FINCH, D. M. 1991. Positive associations among riparian bird species correspond to elevational changes in plant communities. Can. J. Zool. 69:951–963.

JAMES, F. C. AND N. D. WAMER. 1982. Relationships between temperate forest bird communities and vegetation structure. Ecology 63:159–171.

JOHNSON, R. R., L. T. HAIGHT, AND J. M. SIMPSON. 1977. Endangered species vs. endangered habitats: a concept. Pp. 68–79 *in* Importance, preservation and management of riparian habitat: a symposium (R. R. Johnson and D. A. Jones Jr., tech. coords.). U.S.D.A. For. Serv. Gen. Tech. Rep. RM-43.

KEIM, P., K. N. PAIGE, T. G. WHITHAM, AND K. G. LARK. 1989. Genetic analysis of an interspecific hybrid swarm of *Populus*: occurrence of unidirectional introgression. Genetics 123:557–565.

KNOPF, F. L. 1985. Significance of riparian vegetation to breeding birds across an altitudinal cline. Pp. 105–111 *in* Riparian ecosystems and their management: reconciling conflicting uses (R. R. Johnson, C. D. Ziebell, D. R. Patten, P. F. Ffolliot, and R. H. Hamre, tech. coords.). U.S.D.A. For. Serv. Gen. Tech. Rep. RM-120.

———, R. R. JOHNSON, T. RICH, F. B. SAMSON, AND R. C. SZARO. 1988. Conservation of riparian ecosystems in the United States. Wilson Bull. 100:272–284.

MACARTHUR, R. W. AND J. W. MACARTHUR. 1961. On bird species diversity. Ecology 42: 594–598.

MARTIN, T. E. 1988. Processes organizing open-nesting bird assemblages: competition or nest predation? Evol. Ecology 2:37–50.

——— AND J. J. ROPER. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90:51–57.

O'BRIEN, S. J. AND E. MAYR. 1991. Bureaucratic mischief: recognizing endangered species and subspecies. Science 251:1187–1188.

RICE, J, B. W. ANDERSON, AND R. D. OHMART. 1984. Comparison of the importance of different habitat attributes to avian community organization. J. Wildl. Manage. 48:895–911.

ROTENBERRY, J. T. 1985. The role of habitat in community composition: physiognomy or floristics? Oecologia 67:213–217.

SPEICH, S. AND W. J. RADKE. 1975. Opportunistic feeding of the Gila Woodpecker. Wilson Bull. 87:275–276.

STACE, C. A. 1987. Hybridization and the plant species. Pp. 115–127 *in* Differentiation patterns in higher plants (K. M. Urbanska, ed.). Academic Press, New York, New York.

STEELE, B. B. 1993. Selection of foraging and nesting sites by Black-throated Blue Warblers: their relative influence on habitat choice. Condor 95:568–579.

STRONG, T. R. AND C. E. BOCK. 1990. Bird species distribution patterns in riparian habitats in southeastern Arizona. Condor 92:866–885.

SUNOSE, T. 1980. Predation by Tree Sparrow (*Passer montanus* L.) on gall making aphids. Kontyu 48:362–369.

SZARO, R. C. 1980. Factors influencing bird populations in southwestern riparian forests. Pp. 403–418 *in* Workshop proceedings: management of western forests and grasslands for nongame birds (R. M. DeGraff, tech. coord.). U.S.D.A. For. Serv. Gen. Tech. Rep. INT-86.

WHITHAM, T. G. 1983. Host manipulation of parasites: within plant variation as a defense against rapidly evolving pests. Pp. 15–41 *in* Variable plants and herbivores in natural and managed systems (R. F. Denno and M. S. McClure, eds.). Academic Press, New York, New York.

———. 1987. Evolution of territoriality by herbivores in response to host plant defenses. Amer. Zool. 27:359–369.

———. 1989. Plant hybrid zones as sinks for pests. Science 244:1490–1493.

———, P. A. MORROW, AND B. M. POTTS. 1991. Conservation of hybrid plants. Science 254:779–780.

WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. 8:1–93.

WILLSON, M. F. 1974. Avian community organization and habitat structure. Ecology 55: 1017–1029.