WINTER ECOLOGY OF MIGRANT AND RESIDENT LEWIS' WOODPECKERS IN SOUTHEASTERN COLORADO

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The ecology of species widely distributed in heterogeneous habitat may be expected to vary throughout their distribution. Such species are necessarily generalists that must use different food items, face various intensities of competition and predation, and perhaps even encounter relatively large climatic variation in separate portions of their range. Their behavior, and perhaps morphology, will vary accordingly.

The opportunistic Lewis' Woodpecker (*Asyndesmus lewis*), widely distributed over the western half of the United States, is an example of one such generalist. Although highly modifed for flycatching, with wide gape (Spring 1965) and short, wide wings (Bock 1970), *Asyndesmus* is sufficiently adaptable to feed almost entirely upon vegetative matter during certain months (Bock 1970; this study). Bock (1970) has recently published a study of *Asyndesmus* in California where it winters sympatrically with the similar Acorn Woodpecker (*Melanerpes formicivorus*). The two species remain in contact in spite of intense competition because of either a shifting ecological advantage that favors first one and then the other, or the opportunistic habitat selection of *Asyndesmus* which limits contact to areas with large mast crops. Colorado is outside of the range of the Acorn Woodpecker, and Colorado-wintering *Asyndesmus* are not sympatric with any closely related species, so winter competition in Colorado should differ from that in California both in species of competitors and intensity of competition.

Although almost totally migratory in Montana, Idaho, eastern Oregon, and eastern Washington (Bock 1970), and almost totally resident in the Salt Lake region of Utah (Snow, unpubl. data, quoted in Bock 1970), *Asyndesmus* is only partially resident on the eastern plains of Colorado. With the onset of cold weather about half of these birds, which commonly breed in clumps of cottonwood (*Populus sargentii*) surrounding ranches, migrate west to the foothills of the Rocky Mountains and amass stores of acorns from Gambel's oaks (*Quercus gambelii*). The others remain resident and store corn kernels (see below), often in the same cottonwoods in which they nested. To compare the winter ecology of migrant and resident birds, I studied intensively one pair of Lewis' Woodpeckers wintering on the plains and a second pair wintering in the foothills (see fig. 10 for location of the areas), from October 1969 to April 1970. Observations totaled 10,281 bird-minutes, approximately distributed equally between the two pairs. Additional observations were made at two other locations in the foothills during that winter, and sporadically at all locations in the following 2 years. This paper describes Lewis' Woodpecker migration, feeding ecology, competition, and predation in the areas described below and terminates with a discussion of the recent range extension by *Asyndesmus* onto the eastern plains of Colorado.

STUDY AREAS

The plains study area is located one mile SE of Olney Springs, Colorado, at King's Center (R. 58 W., T. 22 S., sec. 33, Crowley County), elevation 4350 ft, on the site of a hay mill that has been inactive for many years (figs. 1, 2, 10). A pair of *Asyndesmus* has wintered and bred for the past 3 years in a clump of nine mature cottonwoods. Corn fields and open range surround the study area, and there are no other trees close to those around the mill. No other *Asyndesmus* wintered or bred within a mile of this site.

In 1969–70, migrant Lewis' Woodpeckers wintered in the foothills along Hardscrabble Creek from about 5 miles NE of Wetmore, Colorado (elevation 5800 ft), to about 3 miles SW of the town (elevation 6200 ft). Narrow-leafed cottonwoods (*Populus angustifolia*) and willows (*Salix* spp.) were dominant elements of the riparian vegetation; the cottonwoods providing food storage sites for all but two *Asyndesmus*. Those two birds stored in a power pole and a dead Gambel's oak. A belt of Gambel's oaks covered the edges of the river valley on both sides throughout the wintering grounds. At the northeastern extreme, the upland surrounding the creek was grassland used for cattle ranching, but southwest of Wetmore the agricultural lands gave way to rugged limestone ridges covered with Gambel's oaks, ponderosa pine (*Pinus ponderosa*), and juniper (*Juniperus americana*). This oak-pine-juniper complex gradually was replaced by a dense Douglas fir (*Pseudotsuga*

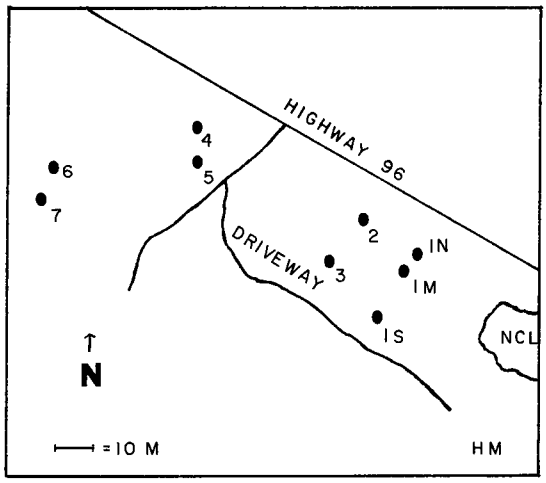

FIGURE 1. Lewis' Woodpecker study area at King's Center. Numbered circles represent mature cottonwoods; corn kernels were stored in 1N, 1M, 1S, 2,4; NCL is a clump of immature locusts; HM is an unused hay mill.

mensiesii) forest above 7000 ft, but south-facing slopes retained vestiges of the oak complex up to at least 8000 ft elevation.

The pair of *Asyndesmus* selected for intensive study wintered on land belonging to Mrs. E. Branstine (designated Branstine's below) at the eastern edge of Wetmore, Colorado (R. 69 W., T. 21 S., sec. 10, Custer County; fig. 10). The storage cottonwood (designated Lw, figs. 3, 4) was 70 m from the nearest unoccupied cottonwood, on the edge of a beaver pond. A garden of several acres, east of the storage tree, contained four clumps of Gambel's oaks (fig. 3). The nearest conspecific wintered 84 m from tree Lw in a power pole (designated Pl, fig. 3).

Two additional observation sites were vegetatively similar to that already described, but the density of wintering *Asyndesmus* was quite different. At a site 1 mile SW of Wetmore, eight birds wintered in a stand of riparian cottonwoods 76 m long, with three of them defending stores in the same tree. At Morlan's Ranch on the extreme northeastern edge of the study area, one *Asyndesmus* wintered in an oak clump, 200 m from its nearest conspecific. Neither *Asyndesmus* nor Gambel's oaks were present downstream from this location.

METHODS

I used standard field techniques in this study, i.e., observing behavior with a Swift spotting scope of 20, 40, or 60 power and a pair of Swift 8.5 × 44 binoculars, and recording results in a field notebook. Observations were made either from a parked car or from the shelter of available buildings, always at least 40 m from a given storage tree. Feeding be-

FIGURE 2. King's Center photographed from the NE at a location corresponding to the upper right-hand corner of fig. 1.

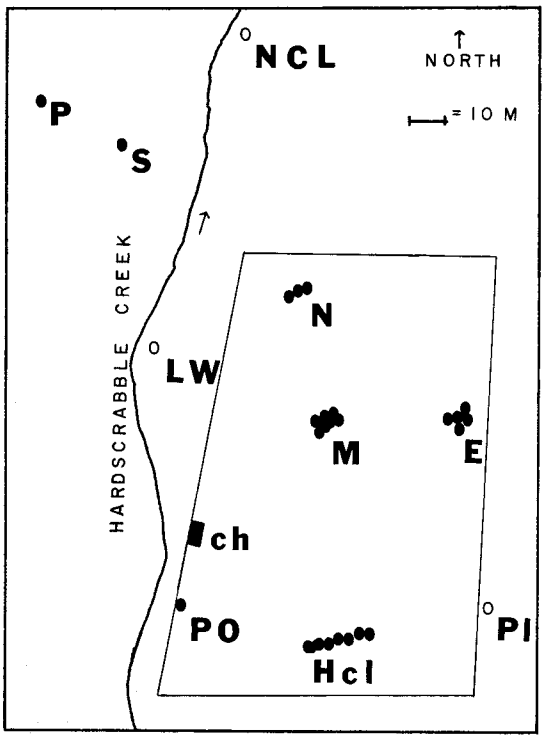

FIGURE 3. Foothills study area at Branstine's. Open circles represent storage sites of *Asyndesmus* during the winter of 1969–70; solid circles represent unused mature cottonwoods. A fence (light solid line) delimits a garden containing four clumps of Gambel's oaks (solid clusters); ch is the chicken house from which the pair was observed.

haviors were recorded continuously to the nearest 0.5 min as gleaning, flycatching, storing, or working stores, based upon criteria explained in table 2. Hawking flights and other specific behavioral segments were timed to the nearest 0.1 min with an Elgin stop watch. For aggressive encounters, the species of intruder, time of encounter, and behavior of the defending Lewis' Woodpecker were recorded; the location of the encounter was plotted on a field map of the study area. Weather conditions were noted at hourly intervals during the day. Since continuously timed observations do not logically lend themselves to statistical treatment, statistical tests were limited.

FALL MIGRATION

The migratory patterns of Lewis' Woodpeckers are highly variable. Bock (1970) listed the following reasons for this variability: (1) the distance from nesting sites to the wintering grounds may vary from 0–100 miles or more; (2) some *Asyndesmus* are nomadic during the late summer, and spend several weeks wandering in the mountains at up to 10,000 ft elevation after leaving the breeding ground and before arriving at the wintering ground; (3) *Asyndesmus* opportunistically select wintering and breeding grounds, concentrating where insects are abundant in the spring and where mast is abundant in the fall. Furthermore, migrants do not necessarily use the same wintering ground in successive years; none has returned to the Hardscrabble drainage in either of the two winters since my study.

Asyndesmus populations that breed on the plains of Colorado are only partly migratory (Bailey and Niedrach 1967). In June 1970, the locations of 34 pairs of Lewis' Woodpeckers which bred in Crowley County, Colorado, were plotted on topographical maps as part of a study of their sympatry with the Red-headed Woodpecker (*Melanerpes erythrocephalus*) (Bock et al. 1971). I censused the area twice, on 27 and 29 November 1970, when 15 pairs were found amassing corn stores at their nesting sites. No *Asyndesmus* was found at sites other than those noted in the June census. Eight of 18 pairs that nested less than 100 m from cornfields remained resident, compared with 7 of 16 pairs that nested more than 100 m from cornfields. This suggests that even though *Asyndesmus* requires storable resources to winter in an area, something other than proximity to cornfields determined which birds migrated. Intraspecific aggression might be involved, though this seems unlikely in view of the variation in densities seen in the foothills. If *Asyndesmus* pair before leaving their wintering grounds, there may be a genetic explanation such as Howell (1953) found in *Spyrapicus*. This problem demands further study.

In 1969, migrant Lewis' Woodpeckers arrived at Wetmore in early October. I walked through the Hardscrabble Creek drainage each weekend in September, seeing no *Asyndesmus* there until 30 September when two were seen perched on a dead cottonwood across the road from Branstine's. There was no evidence that the birds had selected this as a storage tree, and no *Asyndesmus* stored there in 1969. These might have been transients on the advanced edge of the migration. On 4 October, I observed about 300 Lewis' Woodpeckers in small loose flocks moving up the valley from northeast to southwest. Most had not selected storage sites at that time, but some had done so and were beginning to amass and defend stores. The greatest concentration of migrants was at Branstine's, with the upper limit about 200 m W of Wetmore, and the eastern extreme at Morlan's Ranch. The upper limit advanced 3 miles by the next morning to the highest elevation that *Asyndesmus* wintered in 1969.

FIGURE 4. Photograph of Branstine's study area, taken at Hcl (fig. 3) facing northwest. LW is on the extreme left, NCL is the distant cottonwood in the center, oak clump M is on the extreme right.

The behavior of these migrants differed from that described by Adams (1941) and Smith (1941). Instead of flying in a straight line like the birds they observed, these migrants circled the area in small flocks of up to 20 individuals, sometimes landing en masse on a cottonwood or power pole, only to fly off minutes later and circle again. Yet there was a net movement toward the lower concentration of birds upstream, and it was as if the birds were diffusing to equilibrium, with movement in all directions, but a net movement upstream. By 11 October, all but about 50 of the birds were gone; these 50 had established territories and were accumulating stores.

To quantify behavioral changes that might occur while the birds were setting up their winter territories, I timed observations on one bird at the upper extreme (Tough Teat Dairy), one at the lower extreme (Morlan's), and the pair at Branstine's in the middle of the wintering grounds. Since on 4 October the bird at Tough Teat Dairy was not present, the pair at Branstine's had not established a territory, and the bird at Morlan's was established and encountering few transients, I feel certain that this series represented (1) a transient with no stores, (2) a recently established pair, and (3) a bird that had been established for several days, respectively, on 5 October. Observations were made on 5 October, beginning at the Tough Teat Dairy at 12:03, at Morlan's at 13:00, and at Branstine's at 15:47. The results are summarized in table 1. While the data are limited, there appears to be a correlation between storing and aggressive behavior.

Adams (1941) and Smith (1941) were probably observing migrants on the way to the wintering grounds since the dates given are within the time period that Bock (1970) listed for "leaving the breeding ground," are 2 weeks early for "arrival on the wintering grounds," and their birds were not in normal winter habitat when observed. If so, mine are the first published observations of Lewis' Woodpeckers arriving at their wintering grounds and setting up mast stores.

From the data of Adams (1941), Smith

TABLE 1. Changes in behavior upon establishing winter territories in migratory *Asyndesmus lewis*.

Location	Per cent feeding behavior					
	Flycatching	Gleaning	Storing	Work. St.[a]	Enc./hr[b]	BM[c]
Morlan's	39.0	0.0	54.2	6.0	2	83
Branstine's	0.0	0.0	100.0	0.0	4	178
Tough Teat	62.8	37.2	0.0	0.0	0	45

[a] Working stores.
[b] Aggressive encounters per 60 bird-minutes of observation.
[c] Number of bird-minutes observation at a specified location.

(1941), and this study, the following picture of *Asyndesmus* migration emerges: (1) migrants travel to and arrive at the wintering grounds more or less as a group; (2) upon arrival, the large flock (Smith counted 1018 migrants passing over him in 30 min) disperses into smaller groups that explore the area until individuals establish territories; (3) when all of the suitable territories are claimed, the remaining transients leave or perish. The spacing of birds on the wintering grounds is probably determined by some combination of food or storage-site availability and competition, as Bock suggested (1970).

Apparently, the behavior of *Asyndesmus* changes when they establish territories. Before doing so, they feed mainly on insects obtained by flycatching or gleaning, and they are not the aggressors in any encounters; upon acquiring a territory they set about amassing stores as rapidly as possible, and aggressive encounters are frequent (table 1). When the territorial boundaries are more firmly established and the transients have moved on, the residents are freed to leave their stores to feed on insects or to rearrange the stores (see feeding section below). Smith's observation (1941) that the migrants traveled silently supports the above, because if aggressive encounters were occurring, one would expect to hear chatter-calling (Bock 1970; Bock et al. 1971).

WINTER FEEDING ECOLOGY

Bock (1970) described the feeding behavior of wintering Lewis' Woodpeckers, and my terminology follows his, except that I split his "working acorn stores" into storing and working stores. This split seemed necessary since these activities involved different behavior patterns and competitors, and *Asyndesmus* usually did not defend unstored acorns. Continuous observations of behavior were made for 4004 bird-minutes at Branstine's, and 6277 bird-minutes at King's Center. Behavior patterns based upon the criteria in table 2 were identified and recorded. The importance of these behaviors for obtaining food are discussed below.

The per cent of time that *Asyndesmus* spent performing the various behaviors differed between the foothills and plains study areas and changed throughout the winter (fig. 5). Working stores made up a greater percentage of total feeding behavior at Branstine's, while flycatching and storing were much more important (percentage-wise) at King's Center.

TABLE 2. Description of Lewis' Woodpecker wintering behavior patterns based upon Bock (1970) and this study.

Behavior	Behavioral objective	Characteristics used to identify behavior
Flycatching or hawking	Capture air-borne insects	Erratic, short duration flights from an elevated perch; variable periods of scanning, characterized by an alert posture and rapid head movement.
Gleaning	Capture surface insects	Vertical and peripheral movement over tree surface, probing, light tapping, visual observation of tree surface, no drilling.
Storing	Obtain, prepare, store mast items	Plucking of acorns or corn kernels; removal of acorn shells; positioning of acorn meats or intact corn kernels in bark crevices; tapping into place.
Working stores	Feeding upon and movement of stored items	Similar to gleaning, but done in areas known to contain stores; items identifiable as corn or acorn meats; movement from lower to higher in the tree.
Perching	Maintenance	Inactivity, feathers fluffed, preening, etc.

Gleaning was observed only at King's Center. Storing behavior generally decreased as the winter progressed in both locations, but it decreased more markedly at Branstine's. Working stores was most important during the mid-winter months at Branstine's, decreasing as flycatching became more important in the spring.

The stores were used more at Branstine's than at King's Center, probably because harsh weather conditions prevented greater use of insects as a food source in the foothills. Thirty-one per cent of my observations at Branstine's were made on days when the temperature never rose above freezing and the ground was completely covered with snow. The pair spent 99.0% of its feeding time working stores on such days, as opposed to 58.0% when conditions were less harsh. At King's Center, there were no days when the ground was completely covered with snow, and few days when it did not warm up to more than 0°C. *Asyndesmus* would discontinue other behaviors to flycatch if insects became active at either location. I conclude that the stores serve primarily as a reserve food supply and that insects are preferred when available.

Asyndesmus stored all winter at King's Center, but very little at Branstine's after November (fig. 5). After November, almost no acorns were available in the foothills, either because they were covered by snow or because they had been eaten or stored by other organisms. Corn was available all winter at King's Center. Bock (1970) commented that in California *Asyndesmus* stored as long as there were storable items available, even though not all of the stores were used during the winter. Storing increased in spring at both Colorado locations (fig. 5) because a few acorns were made available when the snow melted at Branstine's, and because a pair of Sparrow Hawks (*Falco sparverius*) took over the storage tree at King's Center for a nesting site in late February. The evicted Lewis' Woodpeckers amassed new stores in tree 4 (fig. 1), part of which were corn kernels removed from the stores in tree 1M when the Sparrow Hawks were not present.

The importance of gleaning at King's Center may have been an artifact of my definition of gleaning, but it probably was caused by the spacing of birds at the two locations. Since the birds at King's Center were the only *Asyndesmus* within at least a mile, they could glean in any of the trees near the hay mill. At Branstine's, conspecifics defended stores in the nearby cottonwoods, making those trees

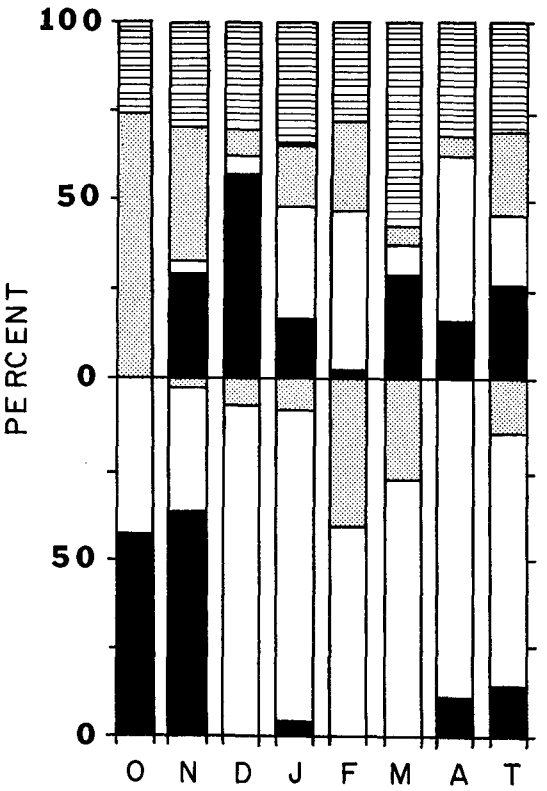

FIGURE 5. Distribution of *Asyndesmus* feeding time in flycatching (stipple), gleaning (hashed lines), working stores (white), and storing (solid black); at King's Center (above) and Branstine's (below). Data are for 4004 and 6277 bird-minutes of observation at Branstine's and King's Center during the winter of 1969–70.

unavailable for gleaning. The pair at King's Center frequently left their stores unattended for a half-hour or more while gleaning in the locust stand or around the hay mill (fig. 1), and flickers (*Colaptes cafer* × *C. auratus* intergrades) sometimes worked over the stores at such times unmolested. The birds at Branstine's never left their stores unattended for more than a few minutes. Competition and spacing, then, did not permit gleaning at Branstine's because no gleaning areas were available nearby, and the birds could not "afford" to leave the stores unattended while gleaning some distance away.

Amassing and defending mast stores seems to be common behavior in melanerpine woodpeckers. Red-headed (Kilham 1958a,b) and Acorn (Ritter 1921; Macroberts 1970) Woodpeckers also store mast during the winter, but the three species differ in specific details of their storing behavior. Acorn Woodpeckers communally store and defend acorns, which are placed intact into individual holes excavated by the woodpeckers to fit one acorn

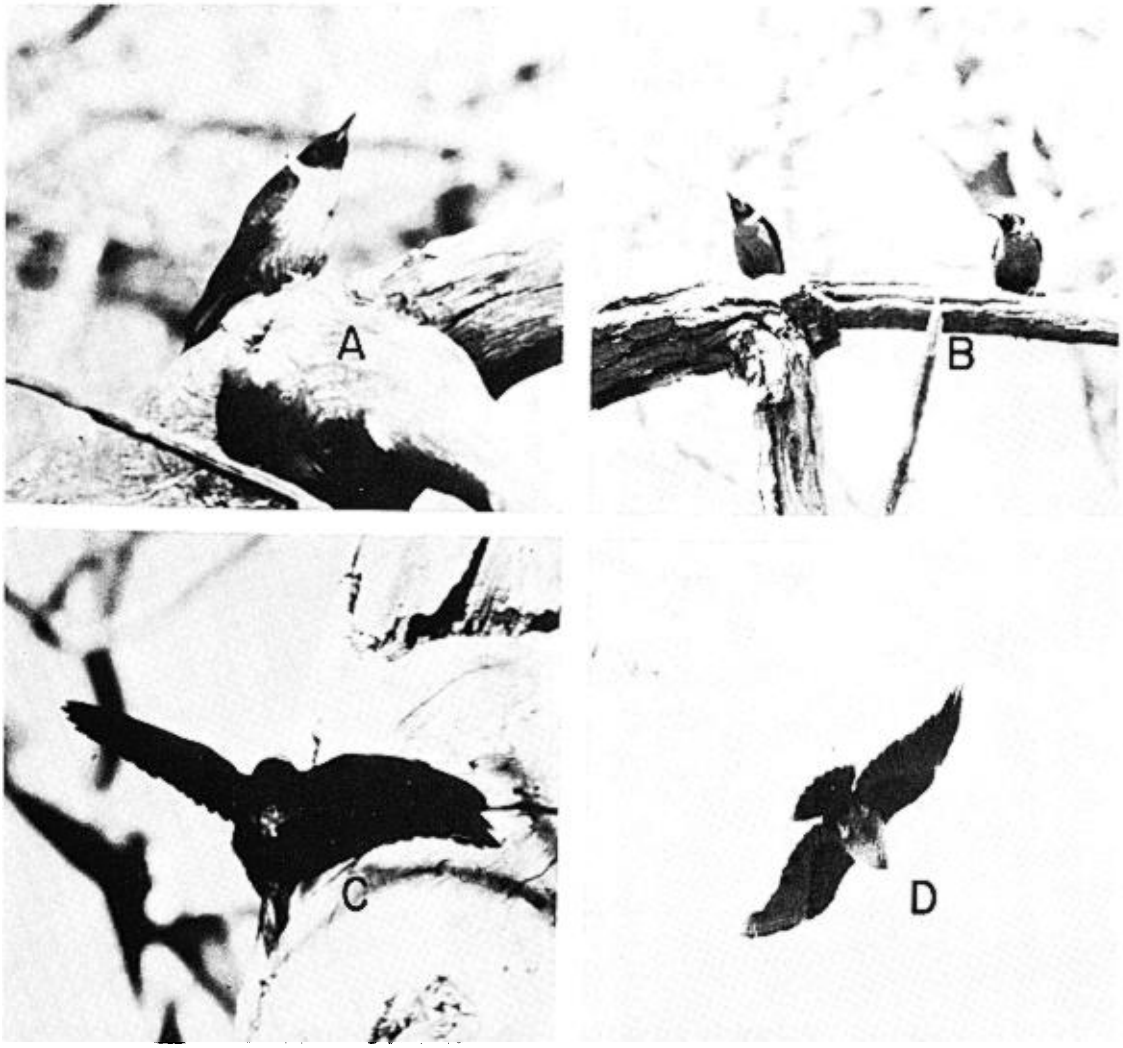

FIGURE 6. Aggressive displays of the Lewis' Woodpecker: A. Bill-up display given to a Black-billed Magpie; B. Bill-up display to the bird's mate; C. Wings-out display to a conspecific intruder; D. Circle-flight to a conspecific intruder.

each (Ritter 1921; Bock 1970; Macroberts 1970). The Red-headed Woodpecker may store large quantities of intact acorns in cavities within the trunk of a tree or may store acorn meats in the cracks of bark, covering them with wedges of wet bark after a rain (Kilham 1958a,b). This covering is adaptive, since Red-headed Woodpeckers disperse shelled acorn meats throughout their winter territory. Both *Asyndesmus* and the Acorn Woodpecker defend concentrated mast stores. Red-headed Woodpeckers eat corn kernels when available, and may store them (Kilham 1958a,b), but this has not been described for Acorn Woodpeckers.

COMPETITION

Orians and Willson (1964) explained that while most of the evidence for interspecific competition is indirect, there is one source of direct evidence: the physical conflict that occurs when two individuals contend for some component of the environment. Bock (1970) further reasoned that if direct conflict over a food source is evidence of competition for that commodity, then the frequency and intensity of aggressive encounters should be a quantitative measure of the intensity of that competition. Macroberts (1970) disagreed with the above, suggesting that not all of the birds displaced by his Acorn Woodpeckers were actual competitors, since the birds in his study supplanted any intruder that landed in their storage tree, irrespective of proximity to the stores. This did not seem to be the case in my study because of the differential aggressiveness (described below) with which *Asyndesmus* defended their mast stores. There-

fore, I feel that the encounters observed during my study occurred because of competition for the stores, and the quantification of competition to follow is based on the assumptions of Orians and Willson (1964) and Bock (1970).

When an intruder landed near or approached defended stores, the resident *Asyndesmus* would respond in one of five ways: (1) it would ignore the intruder; (2) the resident would respond with a bill-up display, frequently accompanied by one or more squeak notes; (3) it would respond with a wings-out display; (4) it would respond with a circle-flight display (both elements of the display usually accompanied by chatter calls); or (5) it would displace the intruder aggressively by flying at it, usually chattering loudly and evicting it. Which response occurred in a given situation was determined partly by factors extrinsic to the defending *Asyndesmus*, such as proximity to the stores, species, sex (if conspecific), and partly by the intrinsic aggressiveness of the defender. In the following paragraphs, "aggressive encounter" or "displacement" refers to bouts in which aggressive behavior by a defending Lewis' Woodpecker evicted an intruder from a storage tree or its immediate vicinity.

The bill-up display was given to con- and heterospecific intruders and was sometimes given when the mate returned to the stores from outside the store tree. The bill was pointed at the intruder (fig. 6–A), and the back flattened so that the tail, back, neck, and head were essentially a straight line terminating in the bill. The bill seemed to be the character emphasized in this display. A bill-up display was identical when given to the mate except that the body was oriented away from the stimulus (fig. 6–B). Usually, when this display was given, it was the only indication that an intrusion was noticed by the resident *Asyndesmus*, but it could be followed by more intense aggressive behavior, especially if the intruder moved toward the stores. In several encounters against Black-billed Magpies (*Pica pica*) and Common Crows (*Corvus brachyrhynchos*), an *Asyndesmus* gave a bill-up display as it moved toward the intruder, and (in the case of the magpie) the intruder was supplanted without the resident taking flight. Short (1971) described similar displays for four species of his genus *Picoides*, and I have seen Red-headed Woodpeckers display similarly when defending nest holes from conspecifics. Apparently, the bill-up display is common within the Picidae. *Asyndesmus* gave it in conflict situations (attack vs. the pair-bond with the mate; attack vs. escape with large corvids; attack vs. ignore when an intruder was not close enough to "warrant" attack).

The circle-flight (fig. 6–D) and wings-out display (fig. 6–C) are both primarily intraspecific displays involving wing elevation and display of the rosy breast feathers. These feathers are probably species-recognition characters (Bock 1970). Either display could be given to the mate when it returned to the stores from outside the storage tree. (See Bock for a more complete description of these displays.)

An intrapair circle-flight begins with the displaying bird actually diving at the mate as though to supplant it, but circling out at the last moment into a glide with wings held abnormally high. The display ends with the displayer either landing on the stores or next to the mate. In the latter event, the mate assumes a mating-invitational posture, with wings slightly spread and tail elevated. The displaying bird mounts and copulates, and sometimes they reverse positions and copulate again. Short (1971) suggested that pseudo-copulation may reduce intrapair aggression in *Picoides*. Ligon (1970) stated that copulation during the nonbreeding season was triggered by unsettling conditions, and may have strengthened the pair-bond in the Red-cockaded Woodpecker (*Dendrocopos borealis*). Pseudo-copulation (or the mating-invitational posture) apparently enabled mate recognition or reduced intrapair aggression in *Asyndesmus*.

Two vocalizations frequently accompanied displacements or displays. The chatter call usually accompanied wings-out displays and circle-flights, and was sometimes given as a defending bird flew to supplant an intruder. It often was sufficient warning to displace intruders without an attack from the defending bird. The squeak note is a single, subdued note of a chatter call (Bock et al. 1971). Bock (1970) called it a warning note, but in my study it was given either simultaneously with, or under similar conditions as, the bill-up display. It was not usually sufficient to evict an intruder by itself. [See Bock (1970) or Bock et al. (1971) for further descriptions of these vocalizations.]

The bill-up, wings-out, and circle-flight displays appear to be points on a continuum of increasingly aggressive responses between the end points of "ignore" and "attack," much like the attack-flight continuum of Balph and

TABLE 3. Frequency of aggressive encounters between *Asyndesmus lewis* and intruders at the stores at Branstine's and King's Center.[a]

Species	Branstine's			King's Center		
	N	Enc./hr	% total	N	Enc./hr	% total
Lewis' Woodpecker (*Asyndesmus lewis*)	36	0.54	37.9	1	0.009	3.6
Flicker intergrade (*Colaptes cafer* × *auratus*)	9	0.13	9.5	21	0.20	75.0
Black-billed Magpie (*Pica pica*)	15	0.22	15.8	3	0.03	10.7
Starling (*Sturnus vulgaris*)	9	0.13	9.5	0	0.00	0.0
Steller's Jay (*Cyanocitta stelleri*)	11	0.16	11.6	0	0.00	0.0
Blue Jay (*Cyanocitta cristata*)	3	0.04	3.2	0	0.00	0.0
Oregon Junco (*Junco oreganus*)	2	0.03	1.1	0	0.00	0.0
Belted Kingfisher (*Megaceryle alcyon*)	1	0.01	1.1	0	0.00	0.0
Common Crow (*Corvus brachyrhynchos*)	6	0.09	6.3	0	0.00	0.0
House Sparrow (*Passer domesticus*)	0	0.00	0.0	3	0.03	10.7
Unidentified small passerines	3	0.04	3.2	0	0.00	0.0
Total	95	1.41	100.2	28	0.26	100.0

[a] Based upon 4004 bird-minutes at Branstine's and 6277 at King's Center.

Stokes (1963). This continuum exists only for intraspecific encounters, since the wings-out and circle-flight displays are primarily intraspecific displays. The circle-flight is essentially an aerial wings-out display, and a wings-out display is essentially a bill-up display with elevated wings and movement toward the intruder. Since energy expended, probability that the display will supplant the intruder, and intensity of accompanying vocalizations all increase with advancing position on the continuum, their relative positions on the continuum may be used to compare the aggressiveness of the two displays.

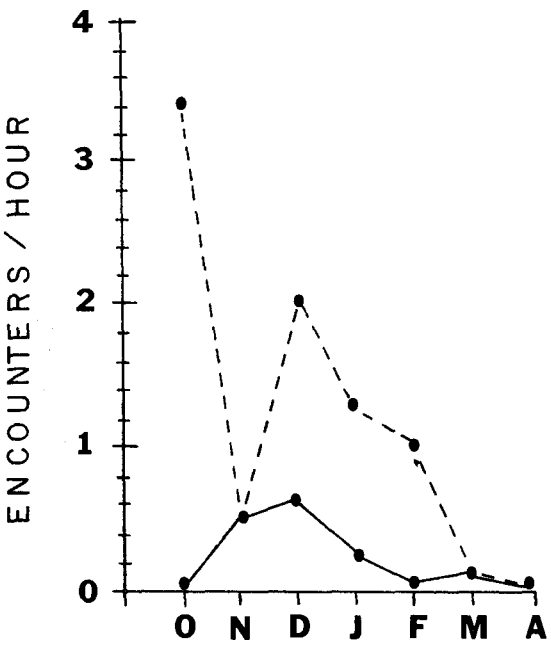

FIGURE 7. Frequency of aggressive encounters between *Asyndesmus* and intruders at the stores at Branstine's (solid line) and King's Center (dashed line), compared by months from October 1969 to April 1970, based on 4004 bird-minutes of observation at Branstine's and 6274 at King's Center.

Aggressive encounters in defense of the stores occurred more frequently at Branstine's, and there were more species of intruders there than at King's Center (table 3). At Branstine's, intraspecific encounters outnumbered interspecific encounters with any one species, but interspecific encounters outnumbered intraspecific encounters overall. Only one intraspecific encounter occurred all winter at King's Center, and flickers were the most commonly encountered heterospecific. An encounter-frequency curve (fig. 7) shows two peaks (October and December) at Branstine's, but only one December peak at King's Center. The frequency of encounters declined for the rest of the winter at both locations.

The frequency of aggressive encounters at Branstine's increased when the ground was covered with snow, and temperatures were below 0°C (designated "snowy" days; table 4) over days when the ground was at least partly bare and/or temperatures were above freezing (designated "nonsnowy" days; table 4). Blue Jays (*Cyanocitta cristata*), Steller's Jays (*Cyanocitta stelleri*), and flickers were displaced more frequently under the "snowy" conditions, intraspecific encounters were more important under "nonsnowy" conditions (table 4). On "snowy" days all intruders were evicted from the storage tree, flickers were frequently supplanted from the small cottonwoods in the creek bottom up to 40 m from tree LW and a neighboring *Asyndesmus* was supplanted from tree P (fig. 3), 70 m from LW. The creek bottom and P (a large, dead cottonwood) were defended at no other time during my study. Passerines were usu-

TABLE 4. The frequency of aggressive encounters between *Asyndesmus lewis* and intruders at the stores at Branstine's, compared between snowy and nonsnowy days.[a]

Species	Snowy days			Nonsnowy days		
	N	Enc./hr	% total	N	Enc./hr	% total
Lewis' Woodpecker	14	0.66	33.3	22	0.48	41.5
Flicker intergrade	7	0.33	16.7	2	0.04	3.8
Black-billed Magpie	4	0.19	9.5	11	0.24	20.8
Starling	2	0.09	4.8	7	0.15	13.2
Steller's Jay	10	0.47	23.8	1	0.02	1.9
Blue Jay	3	0.14	7.1	0	0.00	0.0
Oregon Junco	2	0.09	4.8	0	0.00	0.0
Belted Kingfisher	0	0.00	0.0	1	0.02	1.9
Common Crow	0	0.00	0.0	6	0.13	11.3
Unidentified small passerines	0	0.00	0.0	3	0.07	5.7
Total	42	1.97	100.0	53	1.17	100.1

[a] The observations on snowy days total 1278.5 bird-minutes, those for nonsnowy days total 2759.5. Enc./hr = encounters per hour.

ally not evicted from tree LW, and often flickers and conspecifics were not supplanted from the top of LW on "nonsnowy" days. There were no days at King's Center when the ground was completely covered with snow, and few days when the temperature did not rise above 0°C, so a similar comparison of aggressiveness was impossible there.

A potentially good measure of intrinsic aggressiveness was the intensity with which a defending *Asyndesmus* responded to the return of its mate to the stores from outside of the storage tree. Since species and sex of the intruder and proximity of the intruder to the stores was constant in intrapair encounters, differences in the responses would be due to changes in intrinsic aggressiveness of the defender. The defender never actually displaced its mate from the stores, but could respond with any of the four other responses on the "ignore-attack continuum" described above. I quantified the aggressiveness of the defender in intrapair encounters by assigning intensity factors of 0–3 to such bouts, based upon the criteria outlined in table 5, and compared the distribution of intensity factors between "snowy" and "non-snowy" days (fig. 8). The Lewis' Woodpeckers were significantly more aggressive on "snowy" days (fig. 8), and the aggressiveness of intrapair encounters appears to correlate with the degree of their reliance upon the stored mast (fig. 9).

If the frequency and intensity of aggressive encounters that occurred between *Asyndesmus* and intruders at the storage site are indicative of the degree of competition for these stores, then competition was more intense at Branstine's than at King's Center (table 3, fig. 7); competition was most intense when stores first were established in the foothills

TABLE 5. Behavioral characteristics used to define intensity factors of intrapair aggression, based upon the response of a Lewis' Woodpecker on its stores to the return of its mate. Larger intensity factors are thought to indicate higher aggression levels within the pair.

Intensity factor	Behavior of defending Lewis' Woodpecker
0	No response.
1	Bill-up display, squeak notes.
2	Wings-out display, chatter call, no movement toward mate.
3	Circle-flight, aggressive chatter, frequently accompanied by pseudo-copulation.

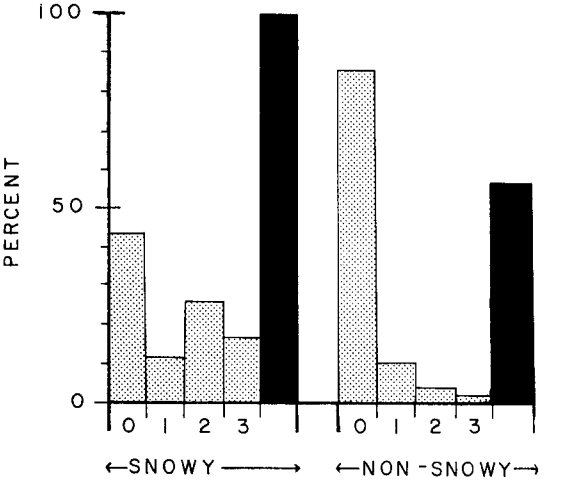

FIGURE 8. Distribution of intensity factors of Lewis' Woodpecker intrapair encounters (stipple), and per cent of feeding time working stores (solid black) on "snowy" and "nonsnowy" days at Branstine's. The mean intensity was 1.17 for "snowy" days (N = 48), and 0.22 for "nonsnowy" days (N = 247). This difference is significant: Chi square = 45.0, d.f. = 3, $P < 0.001$.

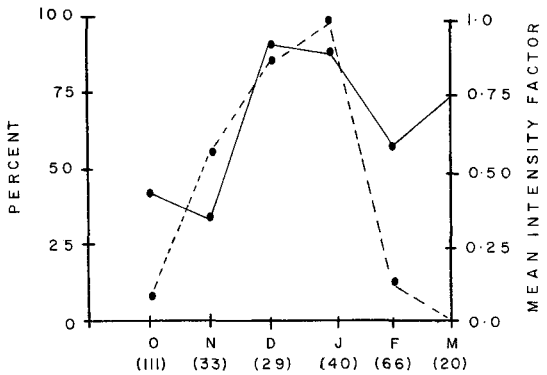

FIGURE 9. Correlation of mean intensity factor (dashed line) and the per cent of time Lewis' Woodpeckers spent working stores (solid line) at Branstine's during the period October 1969 to March 1970. Numbers in parentheses are the number of intrapair encounters upon which that month's mean was based.

(fig. 7); and competition in the foothills was dynamic, becoming more intense on days when the ground was covered with snow and temperatures were low (table 4). By defining competition as two individuals attempting to gain control of a commodity when there is not enough of that commodity for both, the variability in competition can be explained. At King's Center, the birds continued to amass stores all winter (fig. 5), suggesting that the food supply was not exhausted or in short supply. Thus there was little competition for the corn stores, since other birds could obtain corn kernels from the same locations as the pair obtained its stores. At Branstine's, acorns apparently were abundant for only a short time in the fall (fig. 5). There was not enough of this commodity for all; thus there was competition.

Competition at Branstine's was most intense when stores were first established (fig. 7). This probably reflects competition for storage sites as well as competition for the stores, since less than a sixth of the migrants established stores in the Hardscrabble Creek drainage (see migration section above). However, the frequency of aggressive encounters rose in November (fig. 7), the month in which storing began at King's Center, emphasizing again the correlation between amassing of stores and aggressive encounters.

There was a December peak at both places that corresponded with the period of most inclement weather. Competition was most intense on "snowy" days in the foothills because snow obscured foods on the ground, such as weed seeds and remaining acorns, and the low temperatures made insects inactive. The opportunistic Lewis' Woodpeckers spent 99.0% of their feeding time at their stores on such days, suggesting that other foods were not available (see also the feeding section of this paper). If not available to *Asyndesmus*, these foods probably would also be obscured from flickers and jays, and these birds would be forced to compete with *Asyndesmus* for the available food: the Lewis' Woodpeckers' stores. The apparent increase in competition resulted in an increased frequency of aggressive encounters, probably due in part to increased attempts to rob the stores, and to increased tenacity on the part of the robbers; but it was due also to increased aggressiveness on the part of the defending *Asyndesmus*. The same explanation would apply for the December peak in aggressive-encounter frequency at King's Center (fig. 7), though to a lesser degree since there was never sufficient snow to cover the ground. The inactivation of insects by cold weather apparently caused some increased competition with flickers for the stores. Bock (1970) found a similar, though not so pronounced, increase in the frequency of aggressive encounters during January in California, but attributed the increase in encounter frequency to increased numbers of competitors during mid-winter rather than to increased aggressiveness on the part of *Asyndesmus*. He used interspecific intensity factors to quantify aggressiveness, while I used intrapair measures. Also the weather conditions were apparently not as harsh in California, and changes in aggressiveness would be less apparent.

Apparently, selection has favored those *Asyndesmus* that supplanted any bird or mammal that came close to the stores, but defended a larger area against woodpeckers. A likely identifying characteristic of an intruding woodpecker is the vertical perching posture on the side of a tree. Birds that can perch vertically are a greater potential threat to the stores than are those that cannot, because an acorn meat stored anywhere in the tree could be taken by the former, while only those meats stored on horizontal surfaces could be taken easily by the latter. Differential defense of stores conserves energy since the greatest effort is spent against the most important competitors. No energy is spent on less important competitors unless they come close enough to the stores to be a threat, and more energy is spent defending stores on "snowy" days than when competition is potentially less intense. Differential defense of stores is certainly adaptive in view of the great

TABLE 6. Response of Lewis' Woodpeckers to avian predators at King's Center.

Predator	Predator's behavior	*Asyndesmus* behavior	N
Sparrow Hawk (*Falco sparverius*)	Lands in storage tree	Ducked under branch	3
Sparrow Hawk	Lands in storage tree	Flies to denser tree	2
Sparrow Hawk	Lands in storage tree	No response	3
Sparrow Hawk	Circles above tree	Alarm cry, flight	4
Sparrow Hawk	Flies through tree	Freezes in place	4
Sparrow Hawk	Lands in storage tree	Freezes in place	3
Red-tailed Hawk (*Buteo jamaicensis*)	Circles above tree	Crawls under limb	1
Marsh Hawk (*Circus cyaneus*)	Flies nearby, low	Flies up, circles	1
Marsh Hawk	Circles above tree	Crawls under limb	1

variety of competitors and weather conditions that *Asyndesmus* faces throughout its extensive winter range.

PREDATION

Very little is known about predation upon *Asyndesmus*; the only reference I could find was one reporting that feathers from one Lewis' Woodpecker were found in a regurgitation pellet from a Red-tailed Hawk (*Buteo jamaicensis*), along with the remains of eight Acorn Woodpeckers, three Red-shafted Flickers, and assorted other birds and mammals (Fitch et al. 1946). I observed 28 predator-prey interactions between five species of avian predators and *Asyndesmus*; these are summarized in tables 6 and 7. The attack by the Cooper's Hawk (*Accipiter cooperii*) and the first three attacks by the Sharp-shinned Hawk (*Accipiter striatus*) at Branstine's were definitely attempted predations. None was successful.

Lewis' Woodpeckers reacted in four ways to the presence of an avian predator: they "froze" in place; crawled to the underside of a branch; sought denser cover; or flew into the air and out-maneuvered the predator. The first three behaviors could occur any time that the birds detected an avian predator, the last occurred only when the birds were startled at close range. The Cooper's Hawk was within less than a meter of the Lewis' Woodpecker when the latter took flight after giving a loud cry of "fright," a call that was heard only one other time; and the Lewis' Woodpecker easily out-maneuvered the hawk which left after only one attempt. Three predation attempts by a Sharp-shinned Hawk were thwarted in the same fashion. Apparently, the keen eyesight and great maneuverability that are so adaptive for flycatching also aid the Lewis' Woodpecker in escaping predation.

WINTER RANGE EXTENSION OF THE LEWIS' WOODPECKER

This study suggested that it was adaptive for adult Lewis' Woodpeckers that bred on the plains to remain resident. Competition was less intense on the plains, due to the presence of fewer species of competitors, greater spacing between conspecifics, and more storable mast per individual. As a result, less energy was spent defending stores. More types of food were available on the plains during the winter since the milder weather permitted greater insect activity, and food supplies on the ground were not obscured by snow. Resident *Asyndesmus* spent no energy on migration or the establishment of a new winter territory, and they retained nesting sites for the next breeding season. Accipiter predators in the foothills probably took woodpeckers more effectively than did the buteos of the plains. *Asyndesmus* must have been more vulnerable to predation during migration than when established on breeding or wintering grounds. If it was maladaptive for adult plains-breeding *Asyndesmus* to migrate, perhaps the reason that some did was related to the species' recent range extension onto the eastern plains of Colorado.

Apparently, at the beginning of the 20th century (fig. 10), Lewis' Woodpeckers seldom bred or wintered farther east in Colorado than

TABLE 7. Response of Lewis' Woodpeckers to avian predators at Branstine's.

Predator	Predator's behavior	*Asyndesmus* behavior	N
Cooper's Hawk (*Accipiter cooperii*)	Attempted predation	Alarm, circles tree	1
Sparrow Hawk (*Falco sparverius*)	Flies by, 80 m away	Flight, circles tree	1
Sharp-shinned Hawk (*Accipiter striatus*)	Attempted predation	Circles tree	3
Sharp-shinned Hawk	Flies over tree	No reaction	1

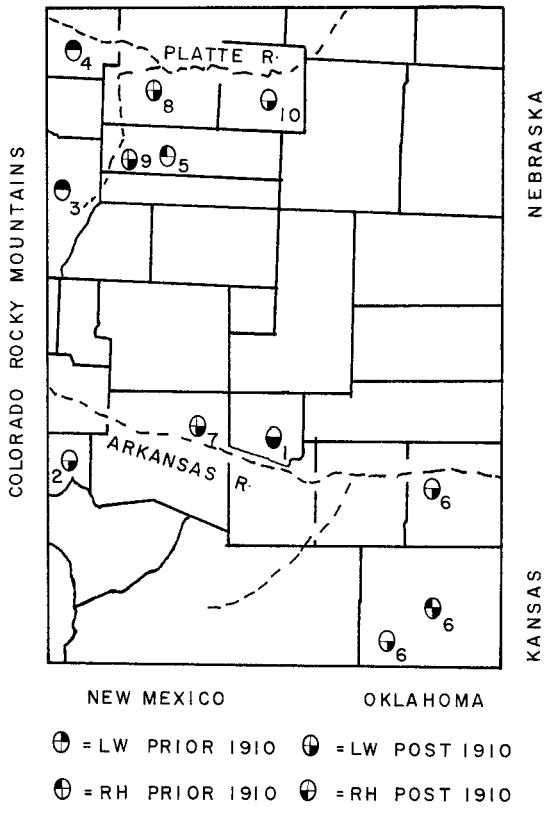

FIGURE 10. Location of some Lewis' (LW) and Red-headed Woodpecker (RH) sitings on a map of southeastern Colorado. The locations were cited in the following studies: (1) this study (King's Center); (2) this study (Branstine's); (3) Dille, 1903; (4) Richards, 1908; (5) Hersey and Rockwell, 1909; (6) Warren, 1906; this study; (7) Henderson, 1920; (8) Bergtold, 1919; (9) Bergtold, 1920; (10) C. E. Bock, pers. comm., about 1970.

the eastern Rocky Mountain foothills. In Colorado *Asyndesmus* were common near Durango (Gilman 1907), in Mesa County (Rockwell 1908), near Steamboat Springs (Warren 1908), and in southeastern Montrose County (Warren 1908). Hersey and Rockwell (1909) found no Lewis' Woodpeckers in Adams County, but Red-headed Woodpeckers were common summer residents. Dille (1903) and Richards (1908) found them breeding commonly in coniferous forest down to about 5500 ft elevation in the eastern foothills of the Rockies. Warren (1906) found no *Asyndesmus* in Baca County, Colorado, at Lamar, Springfield, or in the "cedars" at the extreme southwestern edge of the county.

Asyndesmus apparently began to extend its breeding range eastward onto the plains along the Platte and Arkansas river drainages soon after 1910 (fig. 10). Bergtold (1919) found a Lewis' Woodpecker nesting in the Platte River valley 20 miles NE of Denver, citing this as evidence of a range extension. He found one *Asyndesmus* wintering in Denver (Bergtold 1920), the first in 8 years of winter observation. Henderson (1920) found one *Asyndesmus* nest in the Arkansas valley near Boone, Colorado, in June 1917, and cited it as further evidence for a range extension. I found *Asyndesmus* resident in large numbers on the plains near Ordway, Colorado, from 1969 through 1972, and with C. E. Bock and others saw over 100 in the "cedars" of southwestern Baca County [actually a Gambel's oak, pinyon pine (*Pinus edulis*), juniper complex] in April and October 1971, and in March 1972. We also found six *Asyndesmus* wintering on the outskirts of Lamar, Colorado, in October 1971.

I feel that the preceding two paragraphs constitute evidence for a large extension, at least in winter range, since the turn of the century. The maturation of cottonwoods around ranch buildings, which provided storage and nesting sites, and irrigated corn, which provided storable mast, probably were at least part of the cause. We found that *Asyndesmus* bred almost exclusively in cottonwood clumps around ranch buildings (Bock et al. 1971), but only if the trees contained dead branches or rotten areas where nest holes could easily be excavated. *Asyndesmus* is poorly adapted for drilling (Spring 1965; Bock 1970). Corn is an essential component of the winter habitat because it is the only storable mast found east of the foothills in the Arkansas valley.

While I feel that *Asyndesmus* has only recently become resident on the plains of southeastern Colorado, there are two other possibilities: (1) that *Asyndesmus* resided at their present locations, but were overlooked by observers in the early 1900s; or (2) that current populations of *Asyndesmus* represent temporary concentrations in areas of high food density which were absent prior to about 1920. The first of these possibilities seems unlikely because populations such as I have described are very conspicuous, especially when the birds are flycatching. Isolated breeding pairs of Lewis' Woodpeckers might have been overlooked on the edge of riparian woodlands, but they could not have wintered there until recent agriculture provided corn for mast stores. Concentrated winter populations in the riparian woodlands along the Platte and Arkansas rivers prior to modern agriculture were unlikely for the same reason. Although the existence of temporary breeding

concentrations is hard to disprove, it seems unlikely that such concentrations would have gone unnoticed, or that riparian woodlands would be suitable habitat for such concentrations (Bock et al. 1971).

There were probably a few transients and perhaps a few breeding birds in the area prior to the range extension, since there are a few specimens from western Kansas (Tordoff 1956) and Cimarron County, Oklahoma (Sutton 1967) collected during the 1920s. Transients are not unknown for the Lewis' Woodpecker, as one was found wintering in central Wisconsin in January 1972 (Donald 1972). This also probably explains the female specimen in the University of Kansas Museum (KU 7890), taken near Lawrence, Kansas, in November 1908 (Tordoff 1956) and other Kansas specimens from this period.

The situation may be quite different in the "cedars" of southwestern Baca County, Colorado. This area is immediately adjacent to Cimarron County, Oklahoma, where Sutton (1967) reported scattered sightings of Lewis' Woodpeckers "during all seasons from 1921 to 1931." Those birds, like those which I studied in Baca County, could have been resident since they could use acorns for winter mast stores. Cottonwoods, present in thin stands along the small streams of the region, would have provided more suitable nesting habitat for *Asyndesmus* than would the dense riparian woodland along the Platte and Arkansas rivers. *Asyndesmus* numbers have been shown to fluctuate dramatically, probably in response to fluctuating acorn crops (e.g., Bock 1970; migration section, this study). This may explain why Warren (1906) found no *Asyndesmus* in Baca County even though they were in nearby Cimarron County, Oklahoma, less than 20 years later. Possibly, *Asyndesmus* populations in southeastern Colorado are derived from two sources: the eastward movement along the major east-west river drainages; and a northeast movement which originated in New Mexico and spread north and east through the northwest tip of Oklahoma into Baca County, Colorado.

The range-extension of *Asyndesmus* along the Platte and Arkansas rivers appears to have restricted the breeding range of the ecologically similar Red-headed Woodpecker in southeastern Colorado. The latter apparently bred commonly on the plains in the early 1900s (Warren 1906; Hersey and Rockwell 1909), and into the transition zone of the eastern Rockies (Dille 1903). Leopold (1919) found them breeding in telegraph poles in New Mexico and suggested that they might have dispersed along the route of the railroads across the open plains to near Albuquerque, New Mexico. We found them to be quite common near Ordway, Colorado (Bock et al. 1971), but they bred almost exclusively in riparian woodlands where *Asyndesmus* was absent, and never in small cottonwood clumps around ranches which were preferred *Asyndesmus* habitat. *Asyndesmus* had the advantage in nest-site competition because residents maintained nesting sites all year; migrant *Asyndesmus* established nesting territories before migrant Red-headed Woodpeckers arrived; and breeding Red-headed Woodpeckers were almost always subordinant to *Asyndesmus* in aggressive encounters (Bock et al. 1971). These circumstantial lines of evidence suggest that *Asyndesmus* has displaced *M. erythrocephalus* from the uplands to the riparian vegetation where flycatching is difficult, thus placing the former at a disadvantage.

SUMMARY

Lewis' Woodpeckers were partially migratory in southeastern Colorado. About half of the birds that bred on the plains remained resident, storing corn kernels during the winter. The others migrated west to the foothills of the Rocky Mountains in October and amassed stores of Gambel's acorns. Birds in both locations defended their stores both inter- and intraspecifically.

Plains-wintering *Asyndesmus* relied less upon their stores as a source of winter food (¼ vs. ¾ of total feeding time) and more upon flycatching and gleaning for insects. Probably insects were the preferred food at both locations, but were more frequently available on the plains than in the foothills due to milder weather. Corn kernels were available and stored all winter on the plains; acorns were seldom stored after November in the foothills.

Competition for the Lewis' Woodpecker's mast stores, quantified by measuring the frequency and intensity of aggressive encounters at these stores, was more intense in the foothills than on the plains. There were more species of competitors (10 vs. 4), greater frequency of aggressive encounters (1.41 vs. 0.26 per hr), and greater density of conspecifics in the foothills. Competition was intense when stores were first established in the foothills, and during December at both locations. Aggressive-encounter frequency was

higher on "snowy" days than on "non-snowy" days in the foothills because of an increased rate of intrusion by heterospecifics and increased aggressiveness of the defending *Asyndesmus*. Lewis' Woodpeckers responded more aggressively to flickers and conspecifics than to passerine intruders. Differential aggressiveness in defense of stores is adaptive since the greatest energy expenditure is made defending stores against the greatest potential competitors, and under the conditions of most intense competition.

It would seem adaptive for Lewis' Woodpeckers nesting on the plains to remain resident because of milder weather, reduced competition, increased food availability, and reduced energy expenditure in migration and the establishment and defense of winter territories. Approximately half of a population of *Asyndesmus* breeding near Ordway, Colorado, was migratory, and this may be related to a range extension of this species eastward along the Arkansas River. This extension may have occurred since the turn of the century, permitted by conditions that include the maturation of cottonwoods around ranches providing nesting and storage sites, and the cultivation of corn providing storable mast for the birds. Competition between Lewis' and Red-headed Woodpeckers, the result of contact following the range extension, seems to have reduced the breeding range of the latter in the area of contact to riparian woodlands where the former is at a disadvantage because flycatching is difficult in dense vegetation.

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