RELATIONS BETWEEN LEWIS' AND RED-HEADED WOODPECKERS IN SOUTHEASTERN COLORADO

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THE Lewis' Woodpecker (*Asyndesmus lewis*) and the Red-headed Woodpecker (*Melanerpes erythrocephalus*) are nearly ecological equivalents in western and eastern North America, respectively (Bock, 1970). Both species prefer open breeding habitat such as savannah or old burns, where they rarely excavate for wood-boring insects, but instead hawk for insects on the wing (e.g., Beal, 1911; Bent, 1939). During the winter both species harvest, store, and aggressively defend caches of acorns, corn, or similar mast (Kilham, 1958; Bock, op. cit.). Both are partially migratory but may be resident in suitable habitat, and they show generally opportunistic habits by moving into areas where food is temporarily abundant (e.g., an oak woodland rich in acorn mast).

These woodpeckers have never to our knowledge been studied in sympatry, although there is limited potential overlap of their breeding ranges in central Montana, eastern Wyoming, Colorado, and New Mexico (A.O.U. Check-list, 1957). In June, 1969, we discovered substantial populations of Lewis' and Red-headed Woodpeckers nesting together along the Arkansas River and adjacent farmlands in Crowley and Otero counties, on the plains of southeastern Colorado. This paper presents information on the ecology and behavior of the two species in sympatry. By way of further comparison we carried out a structural and functional analysis of their vocalizations during the breeding season.

METHODS

Data on habitat selection and interspecific aggression were gathered by direct observation. Rates of aggressive encounters were calculated during 1465 minutes of nest observation on 15 days (Table 1). An additional 23 hours were spent driving farm and levy roads in the study area, censusing breeding pairs. Calls were recorded with a Uher 4000 Report-L tape recorder on Scotch 1.5 mil 175 Tenzar tape at 19 cm/sec. The microphone used was a pistol-type Electro-Voice Model 644 which limited the recording system to a frequency range of 40 to 10,000 hertz. The sonagrams were made at the University of Colorado Sound Laboratories using a Kay Electric 6061A Sona-Graph, set for a narrow band analysis of 45 hertz.

RESULTS

Habitat Selection.—Lewis' and Red-headed Woodpeckers nested in two habitats in the study area. The first was the bottomland along the river itself. This area consisted of an overstory of mature cottonwoods (*Populus sar-*

FIG. 1. Breeding habitat of Lewis' and Red-headed woodpeckers in southeastern Colorado—cottonwood riparian woodland. Photograph taken in August, 1970, on the Arkansas River, Crowley County, Colorado.

gentii) mixed with a variety of shrubs, herbs, and smaller trees, especially willow (*Salix* sp.) and tamarisk (*Tamarix pentandra*). Ground fires are common as an agricultural attempt to reduce shrubs and increase grass production. The result is that much of the habitat is open and park-like (Fig. 1). Both species nested in dead or partially decayed cottonwoods and foraged extensively on the ground or by flycatching in clearings between the trees. The second breeding habitat was farmland (Fig. 2). Here the woodpeckers nested in cottonwoods along roads or around buildings and foraged for emergent insects largely in or over adjacent cultivated fields.

A census of breeding pairs indicated that while habitat preferences did overlap, Lewis' Woodpeckers nested significantly more often in the agricultural areas (34 of 36 nests) while Red-headed Woodpeckers were more common in the river bottomlands (19 of 27 nests; significant differences at $\alpha = 0.05$, using the Chi-square test). This demonstrated habitat difference is consistent with two additional factors related to the life histories of these species. First, while the Red-headed Woodpecker is strictly a bird of the breeding season in southeastern Colorado some of the Lewis' Woodpeckers

FIG. 2. Breeding habitat of Lewis' and Red-headed woodpeckers in southeastern Colorado—farmland. Photograph taken in August, 1970, in Crowley County, Colorado.

were permanent residents in our study area (Hadow, MS), storing and utilizing corn as a winter food supply. This may explain the larger numbers of Lewis' Woodpeckers which we observed in agricultural areas, where the birds nested at or near their winter storage sites.

In addition, we found that even those Lewis' Woodpeckers breeding in the riparian bottomlands nested near a woodland border and foraged to a large degree by hawking insects high over adjacent open fields, as well as in the woodland area. Red-headed Woodpeckers were not restricted to the margins of the forest, but nested wherever there were clearings amongst the cottonwoods. *Melanerpes* rarely executed the high prolonged hawking flights even when near open fields. It would appear that while both species prefer open habitat conducive to aerial maneuvering and therefore do share habitats, *Asyndesmus* is very much the specialist or extremist of the two, particularly with regard to the extended hawking flights so characteristic of this species.

Interspecific Aggression.—One pair of *Asyndesmus* which we found in cottonwood bottomland nested in 1969 and 1970 within 35 meters of an established pair of *Melanerpes*. This afforded an opportunity to look for any signs of interspecific aggression and territoriality. The two pairs were discovered on 6 June 1969, when both were incubating. We returned to the

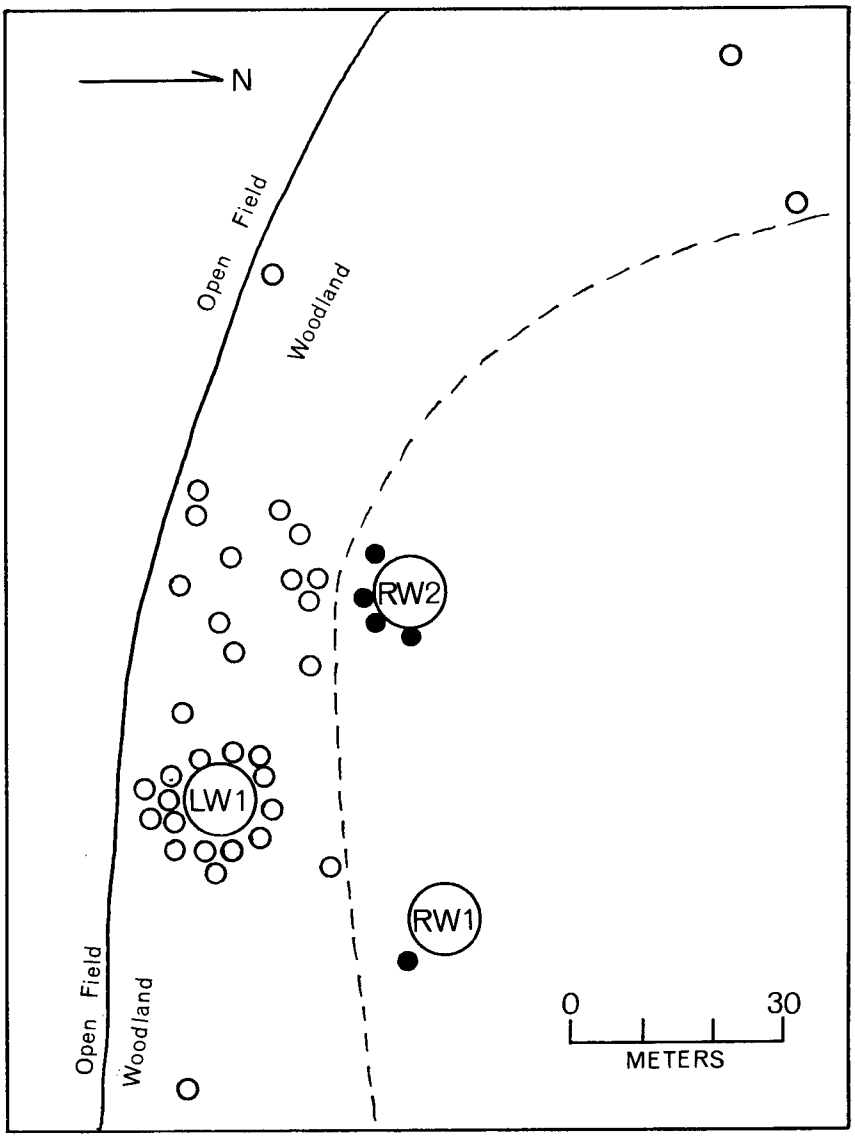

FIG. 3. Interspecific territoriality and aggression between breeding pairs of Lewis' and Red-headed woodpeckers, Arkansas River, Crowley County, Colorado. LW1 = Lewis' Woodpecker nest tree; RW1 = Red-headed Woodpecker nest tree; RW2 = partially excavated and abandoned Red-headed Woodpecker nest tree (1970 only). Open circles = locations of interspecific encounters in which Lewis' Woodpeckers dominated; closed circles = locations of encounters in which Red-headed Woodpeckers dominated. Solid line indicates border between woodland (north) and pasture (south); dashed line indicates territorial boundary between the two nesting pairs.

TABLE 1

RATES OF AGGRESSIVE INTERACTION AMONG AND BETWEEN *ASYNDESMUS LEWIS* AND *MELANERPES ERYTHROCEPHALUS* NESTING IN A COTTONWOOD GROVE ON THE ARKANSAS RIVER, CROWLEY COUNTY, COLORADO. (Based upon 252 encounters recorded during 1465 minutes of nest observation in 1969 and 1970.)

Stage of nesting cycle and dates	Minutes of observation	Rate per hour and number( ) of aggressive encounters[1]		
		Asyndesmus-intraspecific	Interspecific	*Melanerpes*-intraspecific
Early courtship;[2] 12–13 May 1970	135	—	1.3(3)	—
Advanced courtship; 16–18 May 1970	390	0.6(4)	4.0(26)	29.4(191)
Melanerpes nest excavation; *Asyndesmus* incubation; 23–30 May 1970	540	—	0.8(7)	0.7(6)
Both species incubating; 5–10 June 1969	90	—	—	—
Both species feeding young; 29 June 1970	90	—	0.7(1)	—
Both species with partially fledged broods; 12–13 July 1969	220	0.3(1)	3.0(11)	0.5(2)

[1] Does not include interactions between members of the same pair.

[2] Our first observations in 1970 were on 12 May, when both species were involved in early courtship; however, we cannot be certain when courtship began. It is apparent from the table that the *Asyndesmus* were somewhat ahead of *Melanerpes* in their nesting activities.

area on 12 July when both species had partially fledged broods. In 1970 observations were made during courtship, incubation, and fledging periods. During a total of 1465 minutes of observation at this site we recorded the numbers and locations of intra- and interspecific encounters between these two pairs and other transient individuals (Table 1; Fig. 3). Encounters almost always involved one bird physically supplanting another, accompanied by aggressive postures (see Kilham, 1958; Bock, 1970) and vocalizations (see below).

Table 1 shows the numbers and rates of inter- and intraspecific aggressive encounters during different stages of the nesting cycle. The number of encounters involving Red-headed Woodpeckers was very high due to the large number of this species present in the study area. Particularly during the courtship period in 1970 (Table 1) the resident pair of *Melanerpes* was involved in an almost continual series of encounters with transient conspecific individuals. On three occasions strange Lewis' Woodpeckers also

appeared and were displaced when they landed at the Lewis' Woodpecker nest tree.

Of particular interest in this study is the fact that the resident pairs were equally intolerant of each other and all intruders of both species. This intolerance, coupled with the large number of transient *Melanerpes*, resulted infrequent interspecific encounters during the courtship period (Table 1). Later in the season when the transient *Melanerpes* disappeared the two established pairs came to occupy more or less mutually exclusive foraging areas (Fig. 3). The Lewis' Woodpeckers foraged east and west along the woodland edge and south over an adjacent open field, while the Red-headed Woodpeckers usually operated further back in the cottonwoods, with the result that there was very little interspecific contact. The birds seemed to recognize a territorial boundary (Fig. 3). The rate of interspecific encounters rose again at the end of the breeding season in 1969, when the young were fledging. Ten of the 11 observed encounters (Table 1) occurred when the parent Red-headed Woodpeckers flew into a cluster of cottonwoods west of the Lewis' Woodpecker nest (Fig. 3) to feed one of their recently fledged young which had flown there. The Lewis' Woodpeckers were especially protective of this area and drove out the Red-headed Woodpeckers when they approached.

The Lewis' Woodpeckers dominated in 43 of 48 interspecific encounters, although this may have been a result of the fact that most encounters took place when *Melanerpes* approached the *Asyndesmus* nest tree and foraging area. The Red-headed Woodpeckers were dominant on five occasions when Lewis' Woodpeckers approached their nest sites (Fig. 3).

Structural Analysis of Vocalizations.—In addition to drumming, Lewis' and Red-headed woodpeckers each gave three distinct calls during the breeding season. Sonagrams and descriptions of these calls are given in Table 2 and Figure 4.

Analysis of the vocalizations indicates that the *churr* of the Lewis' Woodpecker is intermediate in structure between the *churr* and rasp-calls of the Red-headed Woodpecker. The *churr* of both species has harmonic structure; the emphasis in *Melanerpes* is on the first harmonic, but in *Asyndesmus* it is on the wide, noisy second harmonic, which covers a frequency range more comparable to that of the *Melanerpes* rasp-call. The chatter and squeak of the Lewis' Woodpecker are similar, short, more musical notes which have no apparent structural counterpart in the Red-headed Woodpecker.

Functional Analysis of Vocalizations.—The functional significance of Lewis' Woodpecker vocalizations has been discussed previously (Bock, 1970). Breeding males give *churr*-calls to proclaim territories or nest sites and to attract mates. The chatter-call serves an aggressive function during

TABLE 2

STRUCTURAL ANALYSIS OF LEWIS' AND RED-HEADED WOODPECKER VOCALIZATIONS. (Compare with sonagrams in Fig. 4.)

	Melanerpes calls		
	churr-calls (a)[1]	rasp-call (b)	low-call (c)
Duration of a single note (sec)	0.25–0.30	0.30–0.45	0.12–0.16
Composition	single or in bursts; irregular intervals	bursts, 0.14–0.15 sec apart	bursts, 0.14–0.18 sec apart
Fundamental frequency (kilohertz)	0.9 to 1.5 to 0.9[2] 1.5 to 2.2 to 1.9	no clear harmonics; energy between 2.0 and 5.0	no clear harmonics; energy between 1.3 and 3.0
Harmonic structure	5 harmonics; emphasis on first	no clear harmonics	no clear harmonics
	Asyndesmus calls		
	churr-call (d)	chatter-call (e)	squeak note (f)
Duration of a single note (sec)	0.40–0.55	0.07–0.09	0.07–0.13
Composition	single or in bursts; irregular intervals	bursts, 0.03 to 0.05 sec apart	single or in irregular bursts
Fundamental frequency (kilohertz)	1.5	about 1.2, up to 1.5 or 1.9, and back	1.3 to 1.6, rising to 1.6 or 1.8, and back
Harmonic structure	4 to 5 harmonics; emphasis on 2nd	3 to 4 harmonics; emphasis on 2nd or 3rd	3 to 4 harmonics; emphasis on 2nd

[1] Letter in parentheses corresponds to sonagram in Figure 4.
[2] There are two fundamental frequencies, each with its own harmonics. This is an example of what Greenwalt (1968) calls an "internal duet," each side of the syrinx producing a different sound.

inter- as well as intraspecific encounters throughout the year; males usually give chatter-calls prior to copulation, perhaps as an expression of intra-pair hostility. Squeak notes connote alarm such as would be caused by a predator approaching a nest. Lewis' Woodpeckers rarely drum, and then strictly during the courtship period.

Though Kilham (1958) has referred to vocalizations of wintering Red-headed Woodpeckers, calls associated with nesting have not been described in depth. We recorded the behavioral contexts of vocalizations given by the *Melanerpes* population breeding along the Arkansas River in 1969 and 1970

TABLE 3

RED-HEADED WOODPECKER VOCALIZATIONS AND CORRELATED BEHAVIORS. (Based upon the results of 1465 minutes of nest observation in 1969 and 1970 on the Arkansas River, Crowley County, Colorado.)

Communication	Behavior			
	Copulation	Intraspecific encounter	Interspecific encounter	No identified behavior
Churr-call (n = 39)	3	22	4	10
Rasp-call (n = 42)	2	28	7	5
Low-call (n = 32)	25	5	2	0
Drum (n = 46)	7	22	6	11

(Table 3). Since the species is sexually monomorphic, we could determine the sex of a calling individual with certainty only during courtship bouts.

Rasp-calls were associated with aggressive encounters, and were given in almost all intraspecific contacts, as well as during conflicts with Lewis' Woodpeckers when Red-headed Woodpeckers were dominant. They seemed to be given by all birds. We feel that this call connotes general aggressiveness, and is not territorial per se.

Twenty-five of 32 low calls were given by males prior to copulation (Table 3), indicating that this vocalization might be an invitation to or initiator of sexual behavior. However, its structural similarity to the aggressive rasp-call (Fig. 4; Table 2) and the fact that it also occurred during some intra- and interspecific encounters, suggests that both vocalizations may occur in an aggressive context, and that the low call can be a reflection of intra-pair hostility, or lower aggression levels between unpaired birds.

Churr-calling occurred with all behaviors listed in Table 3, but most frequently with intraspecific encounters and in the "not identifiable" context. It should be emphasized that *churr*-calls occurred *prior to* and *not during* aggressive encounters and copulations (unlike rasp-calls). That is, *churr*-calls seemed to advertise the territory to intruders and potential mates, and the readiness to copulate to the mate. The number of *churr*-calls in the "unidentified" category (Table 3) further supports the general advertisement interpretation of the call, as no obvious stimulus was necessary to elicit it. Only males gave *churr*-calls during courtship bouts, and it seems likely that this is strictly a male call, as is the case with the Lewis' Woodpecker *churr*-call (Bock, 1970).

The final communication is the drum or roll, which is a burst of very closely spaced taps occurring singly or in groups of two or more. The drum has been interpreted for many other species of woodpeckers as a proclama-

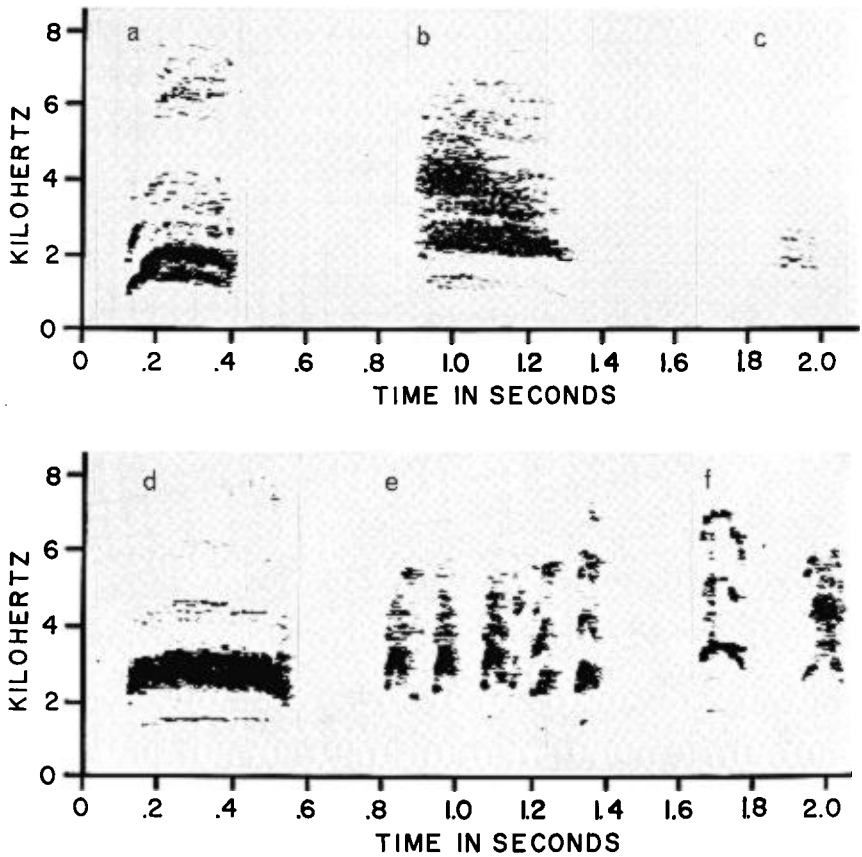

FIG. 4. Sonagrams of Lewis' and Red-headed woodpecker vocalizations recorded during June, 1970, along the Arkansas River, Crowley County, Colorado. a = *Melanerpes churr*-call; b = *Melanerpes* rasp-call; c = *Melanerpes* low-call; d = *Asyndesmus churr*-call; e = *Asyndesmus* chatter-call; f = *Asyndesmus* squeak note. See Table 2 for call descriptions.

tion of territory (e.g., Kilham, 1959, 1961, 1966; Lawrence, 1967; Bock, 1970), and this also appears to be the case for the Red-headed Woodpecker. The similarity of the distribution of drums and *churrs* in Table 3, suggests that they share the functions of territorial advertisement and invitation to copulation.

To summarize: with the exception of the *Asyndesmus* alarm note, Lewis' and Red-headed woodpeckers have functionally equivalent vocal repertoires. There is one call given only by males which advertises the territory and nest site to rivals and mates (*churr*-calls), and there is a second vocalization given

by both sexes connoting aggression during intra- and interspecific encounters (chatter, rasp, and low-calls).

DISCUSSION AND CONCLUSIONS

Orians and Willson (1964:737), in a discussion of interspecific territoriality in birds, observed that "the exclusion of other species from territories strongly suggests that securing an adequate quantity of some limited resource has given selective advantage to the behavior." The limited and shared resource could be either food or nest sites, but if the latter, then territorial defense should be focused only on the nest site. Many of the interspecific encounters we observed between Lewis' and Red-headed woodpeckers did occur at their nests. However, the Lewis' Woodpeckers also drove off Red-headed Woodpeckers which persisted in flying into cottonwoods some distances east and especially west of their nest tree (Fig. 3). These trees were the main hawking perches for the Lewis' Woodpeckers. Furthermore the two resident pairs rarely transgressed the territorial boundary shown in Figure 3 once nesting had begun and transient birds had dispersed (Table 1). This behavior is in decided contrast to that directed toward other hole-nesting species in the area. For example, Starlings (*Sturnus vulgaris*) were common yet the woodpeckers reacted aggressively to these birds only when the Starlings actually attempted to enter their nest cavities. Although there were sizeable breeding populations of flickers (*Colaptes auratus*) in our study area, we observed only two interactions between flickers and the other woodpeckers; in both instances a flicker was displaced when it landed in the Lewis' Woodpecker nest tree. We conclude that the interspecific aggression and territoriality between Lewis' and Red-headed woodpeckers is a result of similar feeding ecology as well as nest-site requirements.

Selander and Giller (1959) discovered interspecific territoriality between the ecologically similar Golden-fronted Woodpecker (*Centurus aurifrons*) and Red-bellied Woodpecker (*C. carolinus*). In the same area, however, one pair of Red-bellied Woodpeckers held a territory which completely overlapped the range of a pair of Red-headed Woodpeckers. They suggested that in the second instance differences in habitat utilization and feeding behavior precluded the evolution of interspecific territoriality.

Johnson (1963) has emphasized the importance of possible common ancestry and the retention of similar acoustic and/or display behaviorial releasers between two species showing interspecific territoriality. *Centurus aurifrons* and *C. carolinus* have virtually identical vocalizations (Selander and Giller, 1959) and similar plumages, especially in comparison to the distinctively colored Red-headed Woodpecker. The possibility exists that interspecific territoriality shown by the *Centurus* species was solely or partially

the result of shared releasers, while the dissimilar *C. carolinus* and *Melanerpes* did not respond to heterospecific sign stimuli.

Resolution of these alternate ecological (Orians and Willson, 1964) and evolutionary (Johnson, 1963) explanations for the causes of interspecific territoriality seems possible in our study. First, the feeding ecologies of these species are very similar. Second, the territorial *churr*-calls of Lewis' and Red-headed woodpeckers, while generally alike, do show significant structural differences (Fig. 4; Table 2) and are readily distinguishable even to the human ear; furthermore, plumages associated with aggressive displays are totally unlike. Therefore it seems certain that the interspecific aggression shown by these species is a direct result of competition for shared resources and not similarity of territorial defense mechanisms.

SUMMARY

Lewis' and Red-headed woodpeckers for the first time were recorded nesting sympatrically, on the plains of southeastern Colorado. There was habitat overlap, although the Lewis' Woodpeckers nested primarily in farmlands while Red-headed Woodpeckers were more common in riparian woodland along the Arkansas River.

Two pairs which nested within 35 meters of each other in 1969 and again in 1970 were interspecifically aggressive and territorial.

Analysis of breeding vocalizations indicated that, with the exception of the Lewis' Woodpecker alarm note, the two species have functionally equivalent and in some ways structurally similar vocal repertoires; these consist of one call given only by males which advertises territory and nest site to rivals and mates, and a second type of call probably given by both sexes connoting general aggressivity during intra- and interspecific encounters.

It seems certain that the interspecific aggression shown by these species is a direct result of competition for shared resources and not similarity of territorial defense behaviors.

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ANNOUNCEMENT

The Australian Advisory Committee has decided that the XVI International Ornithological Congress will be held at the Australian National University in Canberra in the period 12 August to 17 August 1974.

Applications for membership will be accepted until 1 March 1974, and applications for the presentation of papers should reach the Secretary-General not later than 1 February 1974. It is probable that, apart from the those presented by invitation in a Symposium, there will be some selection of the papers that are actually read, and accordingly it is essential that each offer of a paper should be accompanied by a summary of about 200 words.

Further information can be had by writing: Dr. H. J. Frith, Secretary-General, XVI International Ornithological Congress, P. O. Box 84, Lyneham. A.C.T. Australia 2602.