olism and energetic cost of thermoregulation in wild turkeys. J. Wildl. Manage. 52:133–137.

HAYES, S. R., AND J. A. GESSAMAN. 1980. The combined effects of air temperature, wind and radiation on the resting metabolism of avian raptors. J. Therm. Biol. 5:119–125.

HILL, R. W. 1972. Determination of oxygen consumption by use of a paramagnetic oxygen analyzer. J. Appl. Physiol. 33:261–263.

KASPARIE, J.A.J. 1983. Some physiological and behavioral responses of the Great Horned Owls (*Bubo virginianus*) to winter conditions. M.A.thesis. Univ. of Missouri, Columbia.

KIBLER, H. H., AND S. BRODY. 1944. Metabolic changes in growing chickens. J. Nutr. 28:27.

MCINVAILLE, W. B., AND L. B. KEITH. 1974. Predator-prey relations and breeding biology of the Great Horned Owl and Red-tailed Hawk in central Alberta. Can. Field-Nat. 88:1–20.

ORIANS, G., AND F. KUHLMAN. 1956. Red-tailed Hawk and Great Horned Owl populations in Wisconsin. Condor 58:371–385.

PETERSEN, L. 1979. Ecology of Great Horned Owls and Red-tailed Hawks in Southeastern Wisconsin. Wis. Dep. Nat. Resour. Tech. Bull. No. 111.

PROSSER, C. L. 1973. Comparative animal physiology. W. B. Saunders Company, Philadelphia.

RIDDLE O., G. C. SMITH, AND F. G. BENEDICT. 1934. Seasonal and temperature factors and their determinations in pigeons of percentage metabolism change per degree of temperature change. Am. J. Physiol. 107:333.

SMITH, K. G., AND H. H. PRINCE. 1973. The fasting metabolism of subadult Mallards acclimatized to low ambient temperatures. Condor 75:330–335.

WASSER, J. S. 1986. The relationship of energetics of falconiform birds to body mass and climate. Condor 88:57–62.

ZAR, J. H. 1973. Using regression techniques for prediction in homeotherm bioenergetics, p. 115–133. *In* J. A. Gessaman [ed.], Ecological energetics of homeotherms: a view compatible with ecological modeling. Utah State Univ. Monogr. Ser. 20.

ANALYSIS OF A DIALECT BOUNDARY IN CHACO VEGETATION IN THE RUFOUS-COLLARED SPARROW[1]

S. C. LOUGHEED, A. J. LOUGHEED, M. RAE, AND P. HANDFORD
Department of Zoology, University of Western Ontario, London, Ontario, Canada N6A 5B7

Key words: Dialects; vocalizations; Rufous-collared Sparrow; Zonotrichia capensis.

Examinations of the relationship between culturally transmitted traits, like bird song, and ecological attributes are particularly important in the study of avian song dialects. Correlation between habitat and bird song is the foundation of the genetic adaptation hypothesis developed by Nottebohm (1972). In the genetic adaptation hypothesis, a dialect functions as a recognition signal among individuals of a local population which is adapted to a particular habitat and which is genetically distinct from neighboring populations in different habitats (Payne 1981). Such ecological correlates may also reflect adaptation of song characteristics to acoustic properties of different habitats (the acoustic adaptation hypothesis, e.g., Wiley and Richards 1982). There are a number of studies in which correlations between bird song and habitat have been examined. For example Baker et al. (1982) found no relationship between four dialects in *Zonotrichia leu-*

cophrys nutalli and the coastal scrub vegetation of their study area, although the dialect populations appeared to be genetically differentiated to some degree. Hunter and Krebs (1979) suggested that differences in territorial songs of *Parus major*, the Great Tit, between dense forest and open woodland were, in part, due to differences in acoustic characteristics of their respective habitats.

The occurrence of vocal dialects in the Rufous-collared Sparrow, *Zonotrichia capensis*, has been well documented (Nottebohm 1969, 1975; King 1972; Handford and Nottebohm 1976). The typical song of *Z. capensis* consists of an introductory theme with between one and five whistled notes, followed by a trill, a series of similar, brief notes (Nottebohm 1975). Nottebohm (1975) and Handford (1981, 1988) have demonstrated a consistent association between the rate of the terminal trill (the dialect-discriminating variable) and vegetation over a large area in northwestern Argentina. However, there have been few fine-grained analyses of dialect boundaries (Nottebohm 1975, Handford and Nottebohm 1976). In these studies, dialect boundaries were usually sharply demarcated and located in areas where vegetation types changed rapidly.
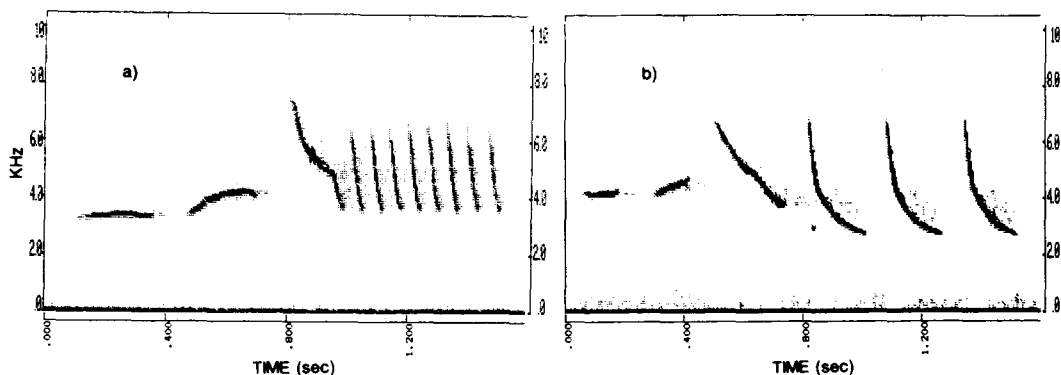
Here we provide a detailed description of a dialect

FIGURE 1.   Two representative sonograms of the two *Z. capensis* dialects discussed in the text: (a) a rapid trill lowland chaco song and (b) a slower trill montane chaco song.

boundary in different vegetation types than those described by Nottebohm (1975) and Handford and Nottebohm (1976): lowland and montane chaco thornscrub (see Handford 1988 for a detailed description of the vegetation in this region).

MATERIALS AND METHODS

A total of 43 individuals was recorded along 26.4 km of provincial Route 2, southeastern Catamarca province, Argentina, between the outskirts of the villages of Icaño (28°54'S, 65°19'W, altitude 400 m) and Ancasti (28°49'S, 65°30'W, altitude 810 m). The eastern edge of the study area, around Icaño, is occupied by lowland chaco, a subtropical xeric to mesic thornscrub. Ascending westwards toward the village of Ancasti, the vegetation changes into montane chaco, with a more continuous and higher upper canopy. There is no sharp division between the two vegetation types, and much of the area has been disturbed by human activity and overgrazing by livestock. Twenty-one *Z. capensis* were recorded on 17 February 1988, 16 on 31 December 1988, and six on 1 January 1989. Dialect boundaries have been shown to be temporally stable with respect to form and location (Handford 1988). Chaco breeding season (based on dates of fresh, complete egg clutches) lasts approximately 3 months, starting in late December/early January lasting until March (King 1973). We have pooled the song data from two successive breeding seasons. Songs were recorded with a Sennheiser MKH816 "shotgun" microphone and a Uher CR260 AV tape recorder. Kilometer readings were taken by odometer (km zero at the western village limit of Icaño) and altitudes were taken from a Thommen 2000 altimeter-barometer at each site. Additionally, photos and notes were taken along the transect so that vegetation correlates with song variation could be assessed. Other observed bird species were noted to determine whether the avifauna was typical of the vegetation under study. Recordings were analyzed using a Uniscan II spectrum analyzer (Multigon Industries) and trill intervals were calculated (see Fig. 1). Diurnal song of *Z. capensis* in an individual is highly stereotyped (Handford and Nottebohm 1976); thus, we used only one sonogram per individual for trill analyses.

RESULTS AND DISCUSSION

Observed avifaunal elements of this transect were consistent with, or typical of, chaco (this according to Olrog 1979, Olrog and Capllonch 1986, Narosky and Yzurieta 1987): *Ortalis canicollis, Columba maculosa, Zenaida auriculata, Columbina picui, Campephilus leucopogon, Xiphocolaptes major, Empidonomus aurantioatrocristatus, Todirostrum margaritaceiventer, Stigmatura budytoides, Turdus amaurochalinus, Coragyps atratus,* and *Cathartes aura.*

Along the transect, approximately 15 km west of Icaño, the vegetation was sparse (due more to destructive human activity than to natural characteristics of the vegetation). The area was dominated by cacti (primarily of the genus *Opuntia*) and numerous low scrubby trees (*Prosopis, Acacia,* and *Zizyphus*). Over the next 3 or 4 km, the vegetation gradually changed. From about 20 km west of Icaño towards Ancasti the vegetation assumed the character of montane chaco. In this zone the upper canopy was much more obvious. Numerous larger trees were in evidence including the palo borracho (*Chorisia*) and horco quebracho (*Schinopsis*), as well as large arborescent cacti of the genus *Cereus.*

Handford (1988) showed that in northwestern Argentina trill interval in lowland chaco varied between approximately 60 and 80 msec, while that in montane chaco varied between 120 and approximately 220 msec. The present study results were consistent with these findings (near Icaño: $\bar{x} = 57.6$ msec, $n = 18$, SD = 7.6 msec; near Ancasti village: $\bar{x} = 143.9$ msec, $n = 17$, SD = 19.3) (see Fig. 1). From the outskirts of Icaño to the site 19 km along Route 2, the songs were typical of lowland chaco. Similarly, along 5.1 km of Route 2 east of Ancasti, the dialect was the typical slow trill found in montane chaco. The change from one trill type to the other takes place over a distance of 2.3 km (see Fig. 2), and this change is associated with the change in vegetation.

Throughout much of the vast area of lowland chaco to the east, north, and south of the present study site, the trill rates of *Z. capensis* remain remarkably consistent (Nottebohm 1975, Handford 1981). Additionally, Handford (1988) has reported that in one broad ecotone between lowland chaco and Monte desert scrub
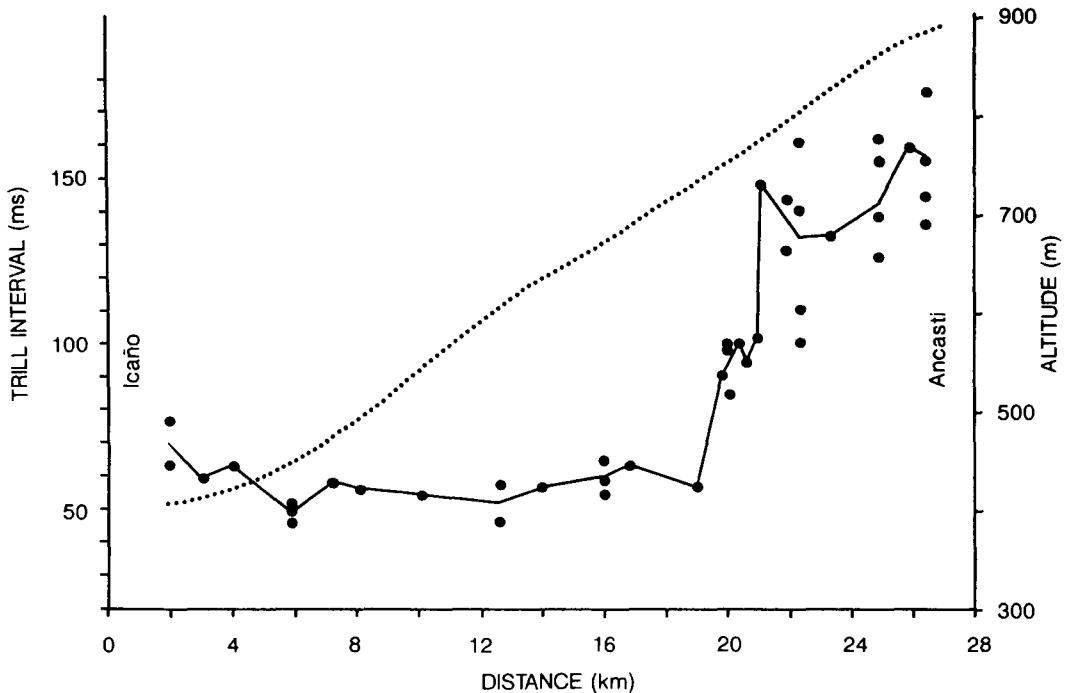
FIGURE 2.   Trill interval profile (in the case of more than one individual for a site the line passes through the median) from Icaño to Ancasti in Catamarca province, northwestern Argentina (geographic coordinates in text) crossing a boundary between lowland and montane chaco (solid line). Dotted line represents altitude profile over the same transect.

occurring over 100 km, *Z. capensis* dialects change over a much smaller distance (maximum of 20 km). The present dialect frontier is not exactly coincident with an equally sharp change in vegetation; we do believe, however, that this transect substantiates Handford's (1988) and Nottebohm's (1975) general findings with regard to trill dialects and, moreover, provides a further illustration of the association between dialect boundaries in this species and borders between natural vegetation types.

This work was supported by a Natural Sciences and Engineering Research Council of Canada Operating Grant to P. Handford. We wish to acknowledge two anonymous reviewers for their helpful comments.

LITERATURE CITED

BAKER, M. C., D. B. THOMPSON, G. L. SHERMAN, M. A. CUNNINGHAM, AND D. F. TOMBACK. 1982. Allozyme frequencies in a linear series of song dialect populations. Evolution 36:1020–1029.

HANDFORD, P. 1981. Vegetational correlates of variation in the song of *Zonotrichia capensis*. Behav. Ecol. Sociobiol. 8:203–206.

HANDFORD, P. 1988. Trill rate dialects in the Rufous-collared Sparrow, *Zonotrichia capensis*, in northwestern Argentina. Can. J. Zool. 66:2658–2670.

HANDFORD, P., AND F. F. NOTTEBOHM. 1976. Allozymic and morphological variation in population

samples of Rufous-collared Sparrow, *Zonotrichia capensis*, in relation to vocal dialects. Evolution 30:802–817.

HUNTER, M. L., AND J. R. KREBS. 1979. Geographical variation in the song of the Great Tit (*Parus major*) in relation to ecological factors. J. Anim. Ecol. 48: 759–785.

KING, J. R. 1972. Variation in the song of the Rufous-collared Sparrow, *Zonotrichia capensis*, in northwestern Argentina. Z. Tierpsychol. 30:344–373.

KING, J. R. 1973. The annual cycle of the Rufous-collared Sparrow (*Zonotrichia capensis*) in three biotypes in northwestern Argentina. J. Zool. (Lond.) 170:163–188.

NAROSKY, T., AND D. YZURIETA. 1987. Guia para la Identificacion de las Aves de Argentina y Uruguay. Asoc. Ornitolgica del Plata. B. Aires.

NOTTEBOHM, F. 1969. The song of the chingolo, *Zonotrichia capensis*, in Argentina: description and evaluation of a system of dialects. Condor 71:299–315.

NOTTEBOHM, F. 1972. The origins of vocal learning. Am. Nat. 106:106–140.

NOTTEBOHM, F. 1975. Continental patterns of song variability in *Zonotrichia capensis*: some possible ecological correlates. Am. Nat. 109:605–624.

OLROG, C. C. 1979. Lista y distribucion de las Aves Argentinas. Opera Lilloana, XI. Fundacion Miguel Lillo. Tucuman, Argentina.

OLROG, C. C., AND P. CAPLLONCH. 1986. Bioorni-
tologia Argentina. Historia Natural. Suppl. No. 2.
PAYNE, R. B. 1981. Population structure and social
behavior. Models for testing the ecological signif-
icance of song dialects in birds, p. 108–120. *In* R.
D. Alexander and D. W. Tinkle [eds.], Natural
selection and social behavior: recent research and
new theory. Chiron, New York.

WILEY, R. H., AND D. G. RICHARDS. 1982. Adapta-
tions for acoustic communications in birds: sound
transmission and signal detection, p. 132–182. *In*
D. E. Kroodsma and E. H. Miller [eds.], Acoustic
communication in birds. Vol. 1. Academic Press,
New York.

OBSERVATIONS ON FOOD HABITS AND SOCIAL ORGANIZATION OF ACORN WOODPECKERS IN COSTA RICA[1]

MARK T. STANBACK

Hastings Natural History Reservation and Museum of Vertebrate Zoology,
University of California at Berkeley, Berkeley, CA 94720

Key words: Acorn Woodpecker; cooperative breed-
ing; foraging; food caching; Costa Rica; Quercus cos-
taricensis.

Intraspecific comparisons of ecology and behavior
across habitat gradients are excellent sources of infor-
mation concerning the adaptive significance of social
traits. Here I report observations on (1) group size, (2)
foraging behavior, and (3) acorn use in a Costa Rican
population of Acorn Woodpeckers (*Melanerpes for-
micivorus*). Acorn Woodpeckers, a species well-known
at higher latitudes for acorn storage and cooperative
breeding, range from Oregon to the Colombian Andes
(Koenig and Mumme 1987). Throughout this area, these
birds are found in association with oak woodland.
However, aspects of the ecology of this species vary
considerably between the north temperate and equa-
torial portions of its range.

From 16 to 19 March 1988, I observed Acorn Wood-
peckers (*M. f. striatipectus*) near the village of San Juan
de Chicua (9°57'N, 83°50'W) on the slopes of Volcan
Irazu, Cartago Province, Costa Rica. The site was ap-
proximately 2,800 m in elevation and was dominated
by remnant oak forest and pasture. I made observa-
tions on six different woodpecker groups in the area,
concentrating on two groups and activities at a heavily
visited fruiting oak.

GROUP SIZE

Throughout their range Acorn Woodpeckers live in
groups of varying sizes; groups of five to 10 birds are
found in both California and Colombia (Koenig and
Mumme 1987, Kattan 1988). Several suites of obser-
vations support the hypothesis that the birds at Volcan
Irazu were group living: (1) I observed at least three

adult birds in all of the six territories that I found. (2)
At one territory, five adult birds were seen sitting and
foraging together without aggressive encounters. (3) I
once observed at least 11 birds foraging in a single oak
tree. Though all 11 probably did not form a single
group (chasing and displacement were common), groups
of up to four birds were commonly observed sitting
together in surrounding trees. At one point I observed,
after a single alarm note, a group of eight birds depart
the fruiting oak tree simultaneously and in the same
direction. (4) While roost watching at one of my focal
groups I saw on one night six and on the second night
five birds engage in preroost activities. On this latter
night four, possibly five, birds roosted together in the
same cavity.

As all of these observations were made prior to the
breeding season, these groups were unlikely to have
consisted of parents and dependent young. Rather,
Acorn Woodpeckers at Volcan Irazu appear to live in
groups with an observed range of three to at least eight
individuals. Across much of their range, Acorn Wood-
pecker groups are comprised of multiple mate-sharing
breeders and nonbreeding helpers, the latter being 1-
to 4-year-old nondispersing young of the breeders
(Koenig and Mumme 1987). I did not ascertain wheth-
er nonbreeding helpers, mate sharing, or both occur in
the groups observed in Costa Rica.

FORAGING BEHAVIOR

The foraging behavior of this species varies across its
range in expected and unexpected ways. In California,
Acorn Woodpeckers eat both fresh and stored acorns,
sap, buds, catkins and, especially, insects hawked from
the air (MacRoberts and MacRoberts 1976, Koenig
and Mumme 1987). Considering this catholic diet, it
is not surprising that in the tropics individuals probe
for insects in bromeliads, drink flower nectar, and are
partially frugivorous (Leck 1972, Stacey 1981, Kattan
1988). I report here on a foraging mode often practiced