American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2467 SEPTEMBER 28, 1971

The Evolution of Terrestrial Woodpeckers

By Lester L. Short[1]

ABSTRACT

Woodpeckers are very specialized for arboreal life. Despite their specializations for climbing, nesting, and foraging in trees, more than 12 species forage regularly on the ground and three are essentially terrestrial. Terrestriality has evolved as a secondary feature, and aspects of terrestrial adaptation, as well as of possible preadaptive ancestral woodpecker features that have benefited ground woodpeckers, are discussed. The evolution of walking from hopping, the adoption of ground nesting, the trends toward brown color and dorsal barring, the reduced massiveness of the skull, the development of a curved, long, thin bill, and other morphological adaptations are also discussed. Behavioral adaptations include the evolution of voices that are louder and carry farther, "flash" color patterns, greater sociality, reduction of sexual recognition markings, and other adaptations. Preadaptations include ant-eating habits, and the ability of the woodpeckers to excavate cavities for nesting. Ground-foraging but arboreally nesting woodpeckers are variously intermediate between arboreally specialized woodpeckers and the fully terrestrial *Geocolaptes olivaceus* of Africa, and *Colaptes rupicola* and *C. campestris* of South America. The arboreal specializations of the ancestors of ground woodpeckers have benefited them in adapting to terrestrial life.

INTRODUCTION

If a layman were considering birds that he might expect to find in open grasslands, he probably would not think of woodpeckers as a possibility. During the course of their evolution, woodpeckers have become highly

[1] Curator, Department of Ornithology, the American Museum of Natural History; Adjunct Professor, City University of New York.

TABLE 1

GROUND FORAGING WOODPECKERS[a]

Species	Range	Nesting	Locomotion on Ground
Colaptes rupicola	South America	T	W, H
Colaptes campestris	South America	T, A	W, H
Geocolaptes olivaceus	Africa	T	H, W
Colaptes fernandinae	Cuba	?A	?H
Colaptes auratus	North America	A	H
Colaptes melanochloros	South America	A	H
Colaptes punctigula	South America	A	H
Colaptes atricollis	South America	A	?H
Campethera bennettii	Africa	A	H
Picus viridis	Eurasia	A	H
Picus canus	Eurasia	A	H
Picus sp.[b]	Asia	A	?H

[a] Arranged from more terrestrial at top to more arboreal toward bottom of list. *Symbols:* T–terrestrial, A–arboreal, W–walking, H–hopping.

[b] As many as five species have been seen on the ground, but it is unknown to what degree they forage there.

modified for a life of climbing, foraging, and nesting in trees. Their feeding apparatus, including bill, tongue, skull and associated muscles and glands; their locomotory apparatus, including legs, toes, and claws, with their muscles and tendons; and other internal and external features, show the effects of marked adaptation to an arboreal existence. Nevertheless, among the approximately 200 species of woodpeckers (comprising the subfamily Picinae, the family Picidae), more than a dozen forage more or less regularly on the ground, and three of them are able to exist in open grasslands (table 1).

Woodpeckers that nest in trees but feed on the ground occur in all continents inhabited by woodpeckers, namely the Americas, Europe, Asia, and Africa. Such woodpeckers include 10 or more species of the genera *Colaptes*, *Campethera*, and *Picus* (table 1; relationships of these genera are indicated in fig. 1). The species that are fully terrestrial, that is, those that can forage and nest in country devoid of trees are: the Andean Flicker (*Colaptes rupicola*) of the northern Andes Mountains (fig. 2) of South America; the Campo Flicker (*C. campestris*, including "*campestroides*") of the campos and pampas (fig. 3) of lowland South America, and the African Ground Woodpecker (*Geocolaptes olivaceus*) of the dry grasslands (fig. 4) of southern Africa. The present report explores some

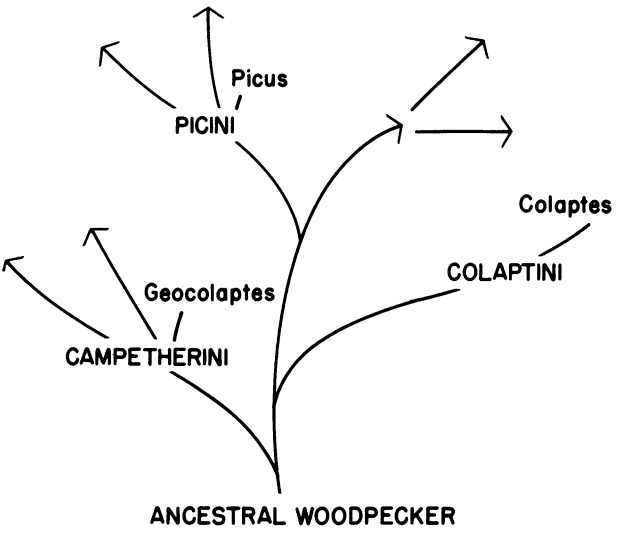

FIG. 1. Phylogenetic diagram following unpublished studies of Bock and Short, showing relationships among ground-foraging genera of woodpeckers.

parameters of terrestrial adaptation in woodpeckers, and of the evolution of ground woodpeckers. The ecology, behavior, and systematics of ground woodpeckers are discussed in more detail elsewhere (Short, MS for *Colaptes rupicola* and *C. campestris*; Short, In press for *Geocolaptes olivaceus*).

FOOD AND THE EVOLUTION OF GROUND FORAGING

All the genera of woodpeckers to which the ground-foraging species belong largely subsist on ants gleaned from the surface of bark, leaves, blossoms, and the ground. They also tap and drill to take food from beneath the surface. Ant-eating woodpeckers are especially common in the tropics, as I have discussed elsewhere (Short, 1970a). However, these woodpeckers occur to some extent in temperate regions as well, and, indeed, ground-dwelling species are found principally in the temperate zone and the temperate-tropical zone border. Woodpeckers utilize diverse species of ants for food, including carpenter ants of the genera *Crematogaster*, *Camponotus*, and others. Many of these ants forage in trees and on the ground, and they build either terrestrial or arboreal nests. Hence it is not unexpected that woodpeckers feeding on ants in trees occasionally will follow prey from high in the tree along the trunk and branches to their bases, even onto the ground (of course, there are several species of

FIG. 2. Habitat of Andean Flicker in puna grassland 18 km. NW Huallanca, western Huánuco, Peru, elevation about 14,300 feet. Large rock in foreground used as singing perch by this species.

arboreal woodpeckers that eat few or no ants and are seen occasionally on the ground as when following a morsel of food falling from a tree).

Ground-foraging woodpeckers are generally found in open woodland, savanna, and on the edges or in open places of forests. Given ant-foraging habits, no special problems are presented by occasional ground-foraging at or near the bases of trees, for various arboreal ant-seeking woodpeckers (e.g., species of *Celeus*), as well as partly terrestrial species, regularly forage low on tree trunks. I suspect that species that feed frequently on the ground have evolved from forest species that tended to feed low in forest trees, because of greater efficiency (time would be wasted in moving to the tops of high trees from the ground). However, no comparative data are available for an evaluation of this hypothesis, as, for example, comparisons of *Colaptes* with close relatives among *Piculus*, of *Geocolaptes* or *Campethera bennettii* with its campetherine near-relatives, or of the wholly arboreal close congeneric relatives of the partly terrestrial *Picus viridis* and *P. canus*.

The wholly terrestrial woodpeckers evolved in open country, under selection pressures favoring terrestrial adaptation (see fig. 1 in Short, 1971a).

FIG. 3. Habitat of Campo Flicker in pampas grassland, Corrientes, Argentina, elevation about 600 feet.

Particular climatic conditions such as the recent increased aridity in many parts of the world caused some constriction of woodlands. Some restricted woodlands, including those containing various ant-eating, largely or entirely arboreal woodpeckers, became savanna-like with trees ever more widely scattered. In such a situation woodpeckers able to forage on the ground would be favored. Those surviving, gradually came to feed more and more on the ground. Some restricted savanna woods may have disappeared gradually. As trees diminished in number, ground-foraging woodpeckers in such areas made the critical shift to nesting terrestrially, and thus evolved the ground woodpeckers. Once freed from a dependence on trees, terrestrial woodpeckers were able to spread throughout neighboring grasslands. This independence from trees, complete though it is in the terrestrial species, does not mean that these woodpeckers shun trees. On the contrary, scattered bushes, or planted eucalyptus trees serve as perches for singing or displaying ground woodpeckers in Africa and in South America, and such trees may be important perches during times of danger. I have observed even the African Ground Woodpecker and the Andean Flicker perched in trees, although rarely. The Campo Flicker uses trees, when available, for nesting. In fact utilizing trees (and termite mounds and fence posts) for nests in the lower, flatter pampas regions may

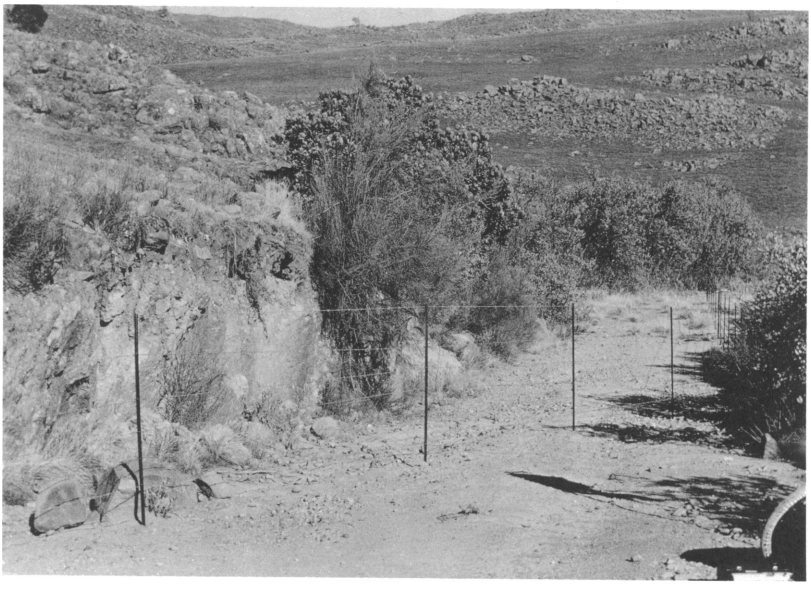

FIG. 4. Habitat of African Ground Woodpecker in highveld grassland near Dullstroom, Transvaal, South Africa, elevation about 7000 feet. A nest was found in the bank at the left behind the fence. Foraging was on slopes in background.

allow the bird to occupy grasslands that would otherwise be too wet (from spring flooding) for nesting in the ground!

Ancestral, ant-eating habits have been retained in all the ground-foraging[1] woodpeckers except the Andean Flicker. This terrestrial species inhabits the high Andean puna grasslands (fig. 2) at elevations up to 16,000 feet. Ants appear to be scarce at high elevations, and in any event they do not comprise a major part of the diet of the Andean Flicker. Instead this woodpecker probes the ground, often flicking dirt from side to side with its bill, obtaining various insect larvae, especially of the orders Lepidoptera and Coleoptera.

It should not be construed that the other ground-foraging woodpeckers subsist entirely on ants the year round. Ant-eating species, both terrestrial and arboreal, take other foods as well, even in the breeding season. When not breeding they may consume other foods to a greater extent, especially fruits and berries. The ability of the migratory North American Flicker

[1] "Ground-foraging" includes the wholly and partly terrestrial woodpeckers, whereas "ground woodpeckers" includes only wholly terrestrial species herein.

(*Colaptes auratus*) to locate such foods is the reason for occasional birds to remain quite far north in the winter, even enduring snow. Ground-foraging woodpeckers are opportunist enough to take spiders and insects besides ants that they may encounter, even though ants comprise their staple food for much of the year. Adult woodpeckers feeding on ants in the breeding season gain several biological advantages from this habit; 1) they can obtain for their young large numbers of food items in a short time as ants are colonial and therefore available in numbers; 2) given their ability to store and regurgitate food when feeding the young, these woodpeckers can carry large quantities of food at one time, and need make fewer trips to the nest, thereby reducing the danger of attracting attention to the nest site; and, 3) young ground-foraging woodpeckers may rapidly gain independence from their parents because ant-foraging is relatively simple—the adult birds lead the young to sites where ants abound and the young can readily commence feeding on their own.

LOCOMOTION ON THE GROUND

Movements of woodpeckers on the ground differ, of course, from their usual tree-climbing movements. Upward or downward movement of a woodpecker on more or less vertical trunks and branches is by means of a "hitching" movement akin to hopping (see Spring, 1965). Virtually all woodpeckers also progress along horizontal branches, and when so doing their hopping resembles that which they might employ on the ground, except for greater clasping with the claws and a definite inward twisting of the feet so that the feet clasp inwardly when the horizontal branch is very small relative to the size of the woodpecker. However, the mode of progression in trees varies considerably from species to species, even within a genus (e.g., *Campephilus*, see Short, 1970a, 1970b). Despite this variation, the movements of woodpeckers in trees can be categorized generally as hopping, in that both legs act simultaneously in propelling the bird. In contrast walking involves alternate movement of the legs.

Ground-dwelling birds of diverse avian families either walk or hop on the ground, depending on the nature of the terrain and the density of the vegetation. Broken, rocky terrain, and dense, clumped vegetation favor hopping whereas level terrain favors walking. Among the partly terrestrial woodpeckers, *Colaptes auratus*, *C. pitius*, *C. punctigula*, *C. melanochloros*, *Picus viridis*, *P. canus*, and *Campethera bennettii* progress on the ground entirely, or almost entirely (see below) by hopping. The African Ground Woodpecker mainly hops (fig. 5), but it sometimes walks. Over short distances the Andean Flicker and the Campo Flicker both mainly walk (fig. 6), but

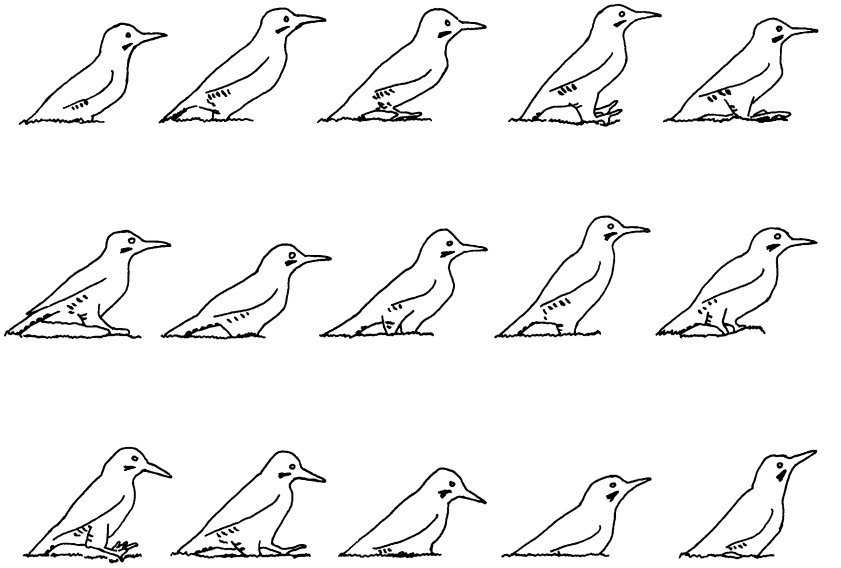

FIG. 5. Hopping of male African Ground Woodpecker. Note simultaneous movement of legs. Traced from 16 mm. motion picture frames. Starting at top left, view left to right, top to bottom, ending at bottom right.

they hop (fig. 7) when moving great distances or on uneven terrain. All three species known to walk usually live in open treeless country. The partly terrestrial woodpeckers that hop but rarely or never walk when on

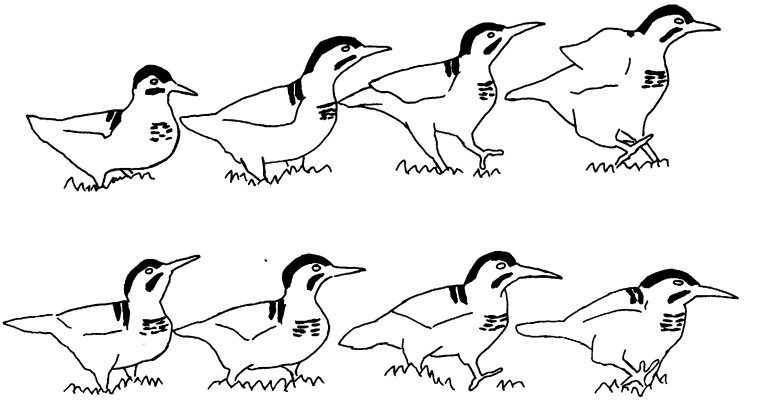

FIG. 6. Male Andean Flicker walking. Note alternating use of legs. Traced from 16 mm. motion picture frames. View left to right and top to bottom.

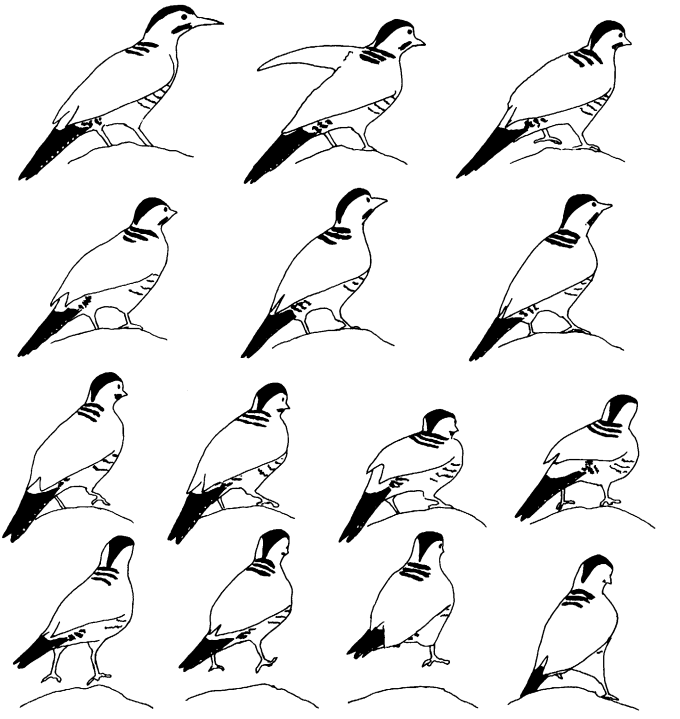

FIG. 7. Male Campo Flicker on ant hill. View top to bottom and left to right. Bird takes one step at top, then second step (right foot). At next to bottom, right, it bounds, through bottom sequence, thrusting with both legs synchronously. Traced from 16 mm. motion picture frames (sequence over one second interval at 24 frames per second).

the ground invariably are restricted to woodland edges or open country with trees nearby. Nesting habits appear correlated with the ability to walk rather than hop; the woodpeckers that walk can nest in the ground, whereas species that only hop on the ground require trees in which to nest.

The retention of the hopping habit by the terrestrial woodpeckers seems attributable to the fact that hopping is more efficient than is walking among rocks or on otherwise uneven ground. Both the African Ground Woodpecker and the Andean Flicker invariably frequent broken terrain with rock outcrops. Their activities center about rocky places. Typically these woodpeckers fly to a vantage point on some rock immediately after they arrive in a foraging area. They move down to the ground to com-

mence foraging, but at any sign of danger fly onto the rocks (partly terrestrial woodpeckers show the same behavior, but oriented about trees rather than rocks). The Andean Flicker is less dependent on rocks than is the African Ground Woodpecker, and it may forage on flat ground up to a half-mile or more from rock outcrops. The African Ground Woodpecker seems restricted in occurrence to the immediate vicinity of rocks or banks of earth. Related to this difference is the fact that the Andean Flicker walks much of the time, whereas the African Ground Woodpecker usually hops. The other species of woodpecker that walks, the Campo Flicker, inhabits generally flat, open terrain in lowlands. Despite the suitability of such terrain for walking, hopping has its advantages here (fig. 7) as well, and thus has been retained. The campos and pampas inhabited by the Campo Flicker tend to have many termite mounds and ant hills, which are visited by these woodpeckers, and the vegetation tends to be tall and dense (in contrast the high grasslands where the Andean Flicker occurs, and the highveld home of the African Ground Woodpecker have less dense and clumped grass and are interspersed with more bare ground), favoring the retention of hopping.

Woodpeckers that progress entirely by hopping may appear to walk when they change their course as they move across the ground. Such shifts in direction not only may explain reports of walking in "hopping species" (e.g., in *Picus viridis*, see Yapp, 1962), but they help to understand the evolution of walking from hopping. Bennett's Woodpecker (*Campethera bennettii*) is shown hopping normally in figure 8, and in figure 9 it is depicted changing its direction as it hops. Apparent "walking" involves a thrust by one leg, and a counter-balancing movement of the other leg (that toward the direction in which the bird turns). The legs are asynchronous for one to two steps until the bird is faced in the new direction. Then both legs thrust simultaneously again as the bird reverts to its normal hopping mode. The rapid shift back to hopping as soon as a straight course is attained, and the differential action of the two legs in the momentary step (the inner leg balances briefly and the outer leg thrusts horizontally to the outside as well as vertically and ahead) indicate that the mode of locomotion basically is hopping, not mixed hopping and walking. This is not simply a matter of semantics, for walking and hopping differ fundamentally. A hopping bird supports its body with both legs at each hop, and it thrusts with both legs. A walking bird must support and balance its body on one leg in addition to "shoving off" alternately with each leg. Since the momentary "step" of a hopping bird making a turn has its thrust partly to the side, and the vertical and horizontal thrust of one leg assist the other leg in balancing the body, the

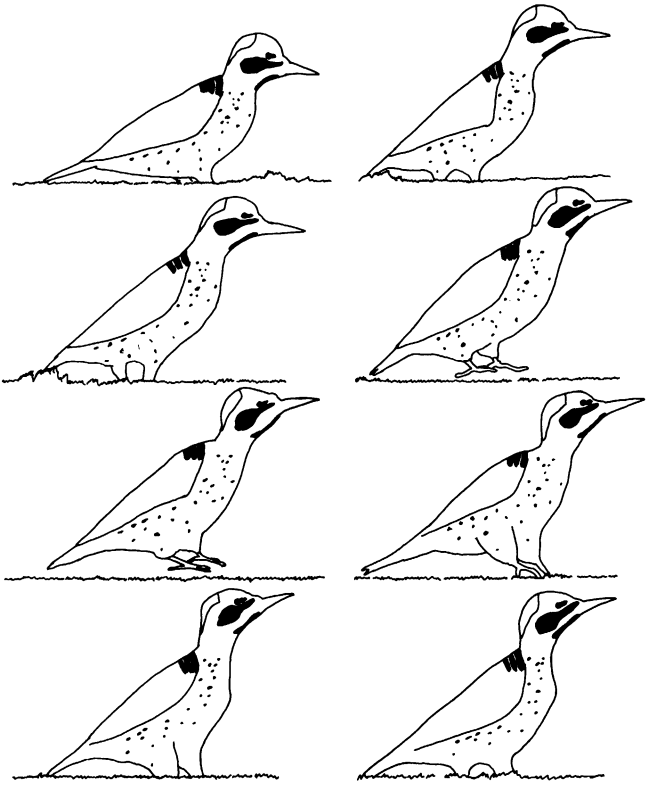

FIG. 8. Hopping female Bennett's Woodpecker. Note synchronous thrust of legs. View from top to bottom, and left to right. Traced from 16 mm. motion picture frames.

action is not functionally like walking. It is perhaps noteworthy that wild birds lacking one leg invariably represent species that progress by walking (and hence are "preadapted" for supporting their body on one leg), not by hopping.

STRUCTURAL ADAPTATIONS

Woodpeckers are highly modified structurally for their "woodpecking" habits. Of course, there are many degrees of arboreal, "woodpecking" specialization, with the greatest modifications shown by such diverse forms as the three-toed woodpeckers (*Picoides*, part), and the magnificent, virtually extinct ivory-billed woodpeckers (*Campephilus imperialis*, *C. principalis*). The terrestrial woodpeckers, and those that are partly terres-

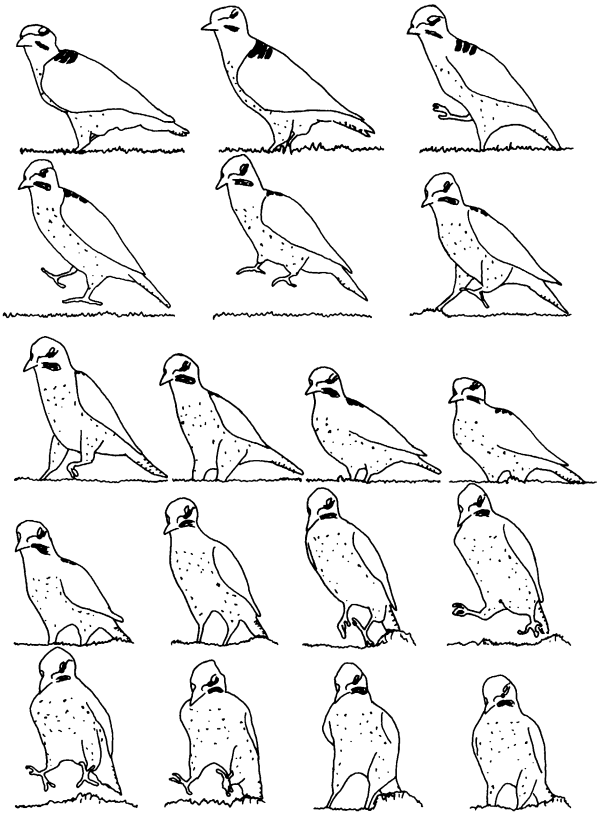

FIG. 9. Pivoting and hopping male Bennett's Woodpecker. View top to bottom, left to right. Note bird leaning on left foot (top), thrusting asynchronously, landing first on right foot as it pivots, then thrusting synchronously as it hops on straight course (toward camera, at bottom). Traced from 16 mm. motion picture frames.

trial are not related to such highly specialized forms. Rather, their relationships (fig. 1) are with less arboreally specialized woodpeckers of the Colaptini (species of *Colaptes*), the Picini (species of *Picus*), and the Campetherini (*Campethera bennettii* and *Geocolaptes olivaceus*). There is no evidence that the ground woodpeckers and ground-foraging woodpeckers are the most primitive woodpeckers. That they are secondarily derived from more strongly arboreal ancestors is indicated by: 1) the indirect, rather than direct interrelationship of ground woodpeckers, and the genera they represent—i.e., the various ground woodpeckers are poly-

phyletic, and hence independently derived; and, 2) the close relatives of woodpeckers, namely the piculets and the wrynecks (comprising the other two subfamilies of the Picidae, respectively the Picumninae and Jynginae, in addition to the Picinae), are more arboreally specialized than are the ground woodpeckers. On the other hand the ground-foraging woodpeckers represent genera and tribes that are rather closely related, that is,

FIG. 10. Comparison of woodpecker skulls, dorsal view. From left: *Campephilus melanoleucos*, highly specialized "woodpecking" species from South America; *Dryocopus lineatus*, a moderately specialized, Neotropical woodpecker; *Picus viridis*, a partly terrestrially foraging, arboreal woodpecker; and, *Geocolaptes olivaceus*, the terrestrial African Ground Woodpecker. Note the shift from left to right in lessening of: width of bill, especially area between nostrils; skull massiveness; and, projection of orbital ring. Not all to scale.

they evolved from the stem-group of unspecialized woodpeckers (see fig. 1; the Picini share an ancestor in common with *Celeus* and its relatives, these are descended from a stock that was ancestral, too, to the Colaptini, and all of these share an ancestor in common with that of the Campetherini).

Woodpeckers have moderately heavy to very heavy, thick skulls. Two special features of woodpeckers are an indented, in-curved frontal area (at the base of the bill), and a broad-based, chisel-tipped bill. Ground woodpeckers show no trace of an in-curved frontal area, although among the ground-foraging species *Picus viridis* and *P. canus* show evidence of it (it is more strongly developed in the more arboreal species of *Picus*). The bills of ground woodpeckers, although somewhat chisel-tipped, tend

to be more sharply pointed, and the culmen is curved, as in arboreal ant-foraging picids, not straight as in more specialized woodpeckers. Ground woodpeckers also have bills that are narrow at the base, and narrow across the culmen between the nostrils (fig. 10). The nostrils of "woodpecking" species often are reduced to lateral slits, the bill being very wide at the base, and, especially, wide across the culmen between the nostrils. The broadened bill base probably forms a stable platform for the driving of the tip of the bill, preventing slipping or breakage of the bill when it strikes the often uneven surface of a tree (*fide* W. Bock). The bills of the ground woodpeckers are not used for pecking a hard surface, but rather as implements for probing and digging in relatively soft earth, hence they tend to be longer, narrower, and less chisel-shaped. The skulls of ground woodpeckers are also less massive than those of specialized woodpeckers (fig. 10), or even of related ground-foraging woodpeckers. The orbital ring of bone is thin and does not flare out, there is thinner bone between the orbits, and bony projections of the skull (e.g., the frontoparietal ridges, the flanges on the opisthotic bones) are generally less developed in ground woodpeckers than in "woodpecking" species (fig. 10). The latter woodpeckers require greater protection of the brain and other vital structures from shock, support for the head, and attachment areas for the muscles that "drive" the bill during "woodpecking." Finally, the foramen magnum of ground-foraging, and especially of ground woodpeckers tends to be directed posteriorly, rather than ventrally as in specialized arboreal woodpeckers. Thus, the head of terrestrially feeding species is held more horizontally, that is more parallel with the body, in contrast to arboreally specialized woodpeckers that hold the head more perpendicular to the body.

The tongue of ground woodpeckers is long and extensible, as are the tongues of their arboreal ant-foraging relatives. The hyoid bones supporting the tongue are very long, curving around the skull, over the head and even out to the nostrils beneath the ramphotheca in flickers and the Green Woodpecker (*Picus viridis*). The well-barbed, sticky coated tongue can be extended 2 inches or more (*Colaptes auratus*) into corridors in ant nests (personal observ.). The salivary glands producing the fluid coating the tongue are even more massive in terrestrial flickers (*Colaptes rupicola*, *C. campestris*) than in their less terrestrial relatives (personal observ.). Several ants can be obtained at one flick of the tongue. These ants can be stored in the enlarged, saclike esophagus (at least in species of *Colaptes*, personal observ.), which can hold vast numbers of ants, ant eggs, larvae, and pupae. These are fed to the young by regurgitation. Hence, large amounts of food can be fed to the young with relatively few trips to the nest.

TABLE 2

SOME RATIOS FROM MUSEUM (SKIN) SPECIMENS OF TERRESTRIAL WOODPECKERS AND THEIR ARBOREAL RELATIVES[a]

Species	Habits	Tail / Wing	Bill / Wing	Tarsus / Wing
Piculus rivolii	A	0.725	0.173	0.182
Colaptes melanochloros melanochloros	A, (T)	0.745	0.150	0.175
Colaptes melanochloros perplexus	A, T	0.655	0.175	0.189
Colaptes auratus chrysocaulosus	A, T	0.754	0.195	0.183
Colaptes auratus auratus	T, (A)	0.695	0.188	0.182
Colaptes campestris campestroides	T	0.692	0.176	0.191
Colaptes rupicola puna	T	0.668	0.254	0.178
Picus puniceus	A	0.678	0.185	0.184
Picus viridis	T, A	0.620	0.210	0.186
Campethera taeniolaema	A	0.638	0.152	0.176
Campethera bennettii	A, T	0.566	0.178	0.182
Geocolaptes olivaceus	T	0.685	0.210	0.202

[a] Both sexes averaged, 10 birds of each sex taken at one time of year in most cases. *Symbols:* A–arboreal, T–terrestrial; parentheses indicate little of that type of foraging.

Other anatomical modifications of ground woodpeckers remain to be established, or to be more fully understood. It appears that ground-foraging woodpeckers have longer bills than their more arboreal relatives (table 2). This is true of the more terrestrial forms (e.g., *perplexus*, *leucofrenatus*) of *Colaptes melanochloros*, the more terrestrial species of *Picus*, and of *Geocolaptes olivaceus* and *Campethera bennettii* compared with other species of *Campethera*. *Colaptes rupicola* has an extremely long bill (table 2), and it feeds wholly terrestrially. Ground woodpeckers tend to have longer tarsi than their arboreal relatives,[1] but the evidence is equivocal (table 2). Arboreal woodpeckers, however, may vary greatly in the use of their legs during climbing, and structural parallelism may result between terrestrial and certain arboreal woodpeckers even though their legs function differently in locomotion. Whatever differences exist in the action of the legs in various woodpeckers perhaps are apt to be reflected more by differences in the size and arrangement of the muscles, than in the proportions and conformation of the bones. The tail too is apt to be utilized diversely in woodpeckers (Short, 1970c), so that clear-cut differences between ground woodpeckers and typically arboreal woodpeckers are not apparent.

[1] Ground woodpeckers of the tribes Campetherini and Colaptini also attain the largest size (by weight) in those tribes.

However, it does appear that there is a tendency for ground woodpeckers to have shorter tails than their more arboreal relatives. This is shown by tail/wing ratios of the similarly sized (by weights) *Colaptes m. melanochloros*, which is arboreal, and *C. m. perplexus*, which is arboreo-terrestrial (table 2). Both forms have wings of approximately the same length, but the terrestrially foraging *perplexus* has a considerably shorter tail. The more arboreal *Colaptes auratus chrysocaulosus* too has a longer tail than does *C. a. auratus* which is continental, and forages mainly on the ground (table 2), although the former is larger and probably has relatively shorter wings as well. A factor relating to this difference possibly is a functional difference in use of the tail when landing on the ground by terrestrially foraging forms, versus landing against a tree trunk by arboreal foragers. Obviously functional analyses of these structures are needed to provide data that can be used in answering diverse questions about the structural adaptations of ground woodpeckers.

COLOR PATTERNS

Terrestrial woodpeckers have tended to lose the often bright, well-marked plumage patterns of their arboreal relatives in favor of more subdued patterns which in many cases include dorsal barring (in brown or black), and ventral barring or spotting. Various flickers, especially *Colaptes rupicola*, *C. pitius*, and *C. fernandinae*, and the African Ground Woodpecker are good examples. The more terrestrial forms are in each case brown, and their arboreal relatives greenish. This holds even within species; the *melanolaimus* group of *Colaptes melanochloros* is browner than the *melanochloros* group, and within *Colaptes auratus*, usually brown dorsally, the more arboreal *C. a. chrysocaulosus* of Cuba occasionally shows some green dorsal coloration (Short, 1965). These shifts in color presumably are associated with different forces of natural selection due to predation, since predators feeding on the terrestrial and arboreal species differ in their very different environments. Ground woodpeckers usually exhibit "flash" patterns such as white rump patches, bright yellow (or pink) under-wing and under-tail surfaces, and ventral, rather than dorsal areas of bright color, such as pink (*Geocolaptes*), or yellow (*Colaptes campestris*). Within *Colaptes melanochloros*, the partly terrestrial *melanolaimus* group has a whitish rump and a gold breast patch, whereas the arboreal *C. m. melanochloros* has no rump patch and no breast patch. These patterns may serve as warning signals, or otherwise in communication with conspecific individuals while the birds are in flight as well as during courtship and aggressive displays. These markings ordinarily are not visible, and the dull

pattern of their upper parts then affords protection by blending with the earth and grass in which they feed.

Color markings relating to sexual recognition are among the most distinct and obvious of woodpecker color patterns, and they usually are located on the head of the woodpecker. The patterns can function in two ways, namely as sexual recognition marks and as species recognition marks. Noble's (1936) studies of sexual recognition in *Colaptes auratus* clearly demonstrated the simple functioning of one distinct color marking, in this case the moustache or malar stripe, as the feature of sexual recognition in this species. Unlike many birds, in which sexual recognition assumes importance only in the breeding season, woodpeckers tend to recognize each other sexually throughout the year. Sexual recognition markings serve as signals utilized in the dominance relationships of nonbreeding, as well as of breeding birds. Invariably, male woodpeckers assert dominance over females in encounters during the nonbreeding period. Additionally, head patterns, including those used in sexual recognition, may provide species specific recognition signals which prevent interspecific hybridization (see Short, 1971b, regarding this possible function of the varying size of the red nuchal patch in males of various species of *Picoides*).

Several factors influence these sexual and species recognition features in ground woodpeckers. One factor is the rather great sociality, for woodpeckers, observed in ground woodpeckers (Short, 1970a, In press, MS, respectively treating various species of *Colaptes*, *Geocolaptes olivaceus*, and, again, species of *Colaptes*). Birds associating closely in groups the year round perhaps have less need for strong color markings in sexual recognition, depending instead upon behavioral cues for sexual recognition. A second factor is the need for reduction of bright color patterns, particularly dorsally, in terrestrially feeding species. Such patterns would attract the attention of potential predators. At any rate, selection favoring protective coloration may be responsible for the reduction and even the elimination (*Colaptes rupicola* in part, *C. campestris*, *C. pitius*) of the red nuchal patch in flickers, and perhaps for some of the reduction in the malar patch of males in the various ground woodpeckers. A third factor is the virtual absence of closely related species within the ranges of the ground woodpeckers. That is, selection against interbreeding, which might enhance or maintain certain color patterns, has been reduced in most ground woodpeckers because they are not sympatric with related species. Sympatry of the entirely terrestrial species is nonexistent. On the other hand, there is some sympatry of one ground woodpecker, *Colaptes campestris*, with a related ground-foraging woodpecker, *C. melanochloros* (this may account

for the fact that *C. campestris* is the most patterned of the ground woodpeckers). *Colaptes campestris* and *C. melanochloros* associate in feeding on the ground in a manner suggesting that the less terrestrial *melanochloros* benefits from this association (Short, 1969). Several ground-foraging woodpeckers are sympatric. The two known cases are: *Picus viridis* which is broadly sympatric with its close relative, *P. canus*, in Europe, although there is some ecological separation, the latter being more arboreal (personal observ.); and *Colaptes fernandinae*, sympatric with the more arboreal *C. auratus* in Cuba, with some ecological separation—the two species are not closely related. Several rather closely related species of *Picus* (e.g., *P. canus*, *P. vittatus*, *P. xanthopygius*) occur sympatrically in Asia but it is not known to what extent they forage on the ground.

Ground woodpeckers have reduced sexual markings and no conspicuous dorsal color marks. The inconspicuous malar stripe of *Geocolaptes* males can be detected only at close range. A malar stripe is present in both sexes of *Colaptes campestris*, but the red marking of the male is conspicuous only at very close range; the malar is even less conspicuous in the black-throated northern race of that species, because it blends into the throat. *Colaptes rupicola* has a relatively inconspicuous gray-black malar stripe, flecked with red posteriorly in males, again visible only from a short distance. The ground-foraging *C. fernandinae* and *C. pitius* are the least patterned, brownest, and most barred of all ground-foraging woodpeckers. The former is sympatric with *C. auratus*, which probably only recently entered Cuba (hence *fernandinae* evolved in allopatry), and *C. pitius* is sympatric with no related species. Males of *fernandinae* have a moderately conspicuous malar stripe, but males of *pitius* have almost lost all the malar pattern.

The gregarious habits of ground woodpeckers facilitate sexual recognition through behavioral cues and the use of relatively inconspicuous color markings. The lack of sympatry with closely related species seems to have permitted reduction of strong sexual and other color markings in ground woodpeckers. Selection from predation seems responsible at least partly for the shift to brown coloration, the strong tendency toward barring and streaking, the reduction of conspicuous colors and markings dorsally, the reduction of sexual markings, and the development and enhancement of "flash" signals. These signals probably also are favored by long-distance visibility in open country.

BEHAVIORAL ADAPTATIONS

Ground woodpeckers show behavioral features correlated with their

assumption of terrestriality. Some of these relating to color patterns and sexual recognition have been discussed above. In addition to "flash" colors, which become conspicuous only during displays, are special movements such as wing-flicking (see fig. 7), which are more prevalent in ground-dwelling flickers (e.g., in *Colaptes campestris*) than in their semi-terrestrial relatives. These movements can be seen at some distance in open terrain, and they make the bird conspicuous only when it is appropriate for some behavioral reason. The open, often windy nature of the environment of ground woodpeckers has favored high-pitched, yelping, repetitive calls that can be heard at long distances. The three ground woodpeckers have such strongly developed calls. The yelping call of the African Ground Woodpecker is remarkably like that of the Andean Flicker, whereas the arboreal near-relatives of these species have dissimilar calls with far less carrying power (Short, In press, and MS).

Most woodpeckers are solitary, territorial birds pairing only during the breeding season. If they do remain paired the year around, the mated birds either maintain loose contact only, or they remain in close contact but are territorial toward conspecific individuals. Ground woodpeckers are among the most social woodpeckers. Importantly, they are more social than are their arboreal close relatives. Andean Flickers occur in groups of three to 15 birds, and they nest in loose or occasionally in dense colonies in banks, road cuts, and rocky cliffs. The Campo Flicker is slightly less social but it may nest in loose colonies, and groups of three or four birds or more and are seen throughout the year. The African Ground Woodpecker is less social, but nonetheless trios of adults are frequently observed and two pairs may nest in proximity.

The habits of ground woodpeckers are discussed elsewhere (Short, In press, MS), but a few highlights concerning special behavioral features of each of them will illustrate the adaptations and adaptability of these birds.

The Andean Flicker nests and roosts in small colonies, as noted above. These flickers forage in loose groups often numbering 10 or more birds. In their high Andean home (fig. 2) they have developed the habit of burrowing into abandoned and sometimes even occupied adobe huts of Indians (fig. 11). This occurs mainly during the summer "rains"—paradoxically, precipitation in the form of snow often is more common in summer than in winter at high altitudes near the Equator where precipitation is greater in summer. Apparently the flickers roost in these holes, but do not nest in them. Some collapsing buildings are pock-marked with several score of these flicker holes, which normally penetrate the surface, then turn abruptly to one side.

The lowland Campo Flicker occurs in groups scattered throughout the campos of Brazil and pampas of Argentina (fig. 3), especially where there are termite nests. This species nests in banks, or in termite nests, or it readily will utilize fence posts and trees bordering open country where they are available. As noted above, the ability to use trees or posts for nesting probably renders more open country habitat available to

FIG. 11. Andean Flicker holes in old adobe building, La Raya Pass, south of Cuzco, Peru, elevation 13,500 feet. Holes excavated at different times over many years are used for roosting at night.

these flickers in the nesting season, when the subsurface of the ground may be saturated with water from the spring rains. Nests are not placed very close together, but they may be in adjacent trees, or within 100 m. apart in termite nests. Foraging areas are not defended and several pairs often feed together.

The African Ground Woodpecker, restricted in its highveld grassland habitat to the vicinity of dongas and to broken terrain (fig. 4), wanders about in small groups in the nonbreeding season. The birds probe in the dirt among rocks or grassland adjacent to rocks, picking up great numbers of ants. They nest in groups of several pairs, or in solitary pairs which may have a third "helper" associated at the nest. The nests are shallow, a

meter or less in depth, and favored nesting sites in banks may be used for several or many years.

PREADAPTATION

In addition to their adaptations for terrestrial life, ground woodpeckers of course retain many structural and behavioral features of arboreal woodpeckers. It is appropriate to ask whether any, or some, of these particularly have preadapted ground woodpeckers for successfully invading the open country (see Bock, 1959, 1963, for discussion of preadaptation and for woodpecker examples). As we have seen (above), ant-foraging habits preadapted ground woodpeckers for obtaining food in open country. This habit of many woodpeckers has more subtle aspects. For instance, woodpeckers are remarkably thick-skinned, tough birds that are tenacious of life, as anyone who has collected and prepared specimens is aware. Part of their "toughness" undoubtedly relates to their climbing and woodpecking habits, that is, to structural adaptations for "shock-absorption" in woodpecking and for muscle action (and counteraction in balancing) relating to woodpecking, and to maintaining a suitable platform for this action. I suspect that the ant-foraging habit itself, involving the capture of aggressive, biting and stinging insects, was a factor in the evolution of the thick skin of woodpeckers (honey-guides, Indicatoridae, relatives of the woodpeckers that feed at the nests of bees also have a thick skin). At any rate, there may be as yet undefinable attributes of the "toughness" of woodpeckers which preadapted them for successful occupation of grasslands.

Of course the ability of woodpeckers to excavate their own nesting cavity is a fundamental feature responsible in large measure for their success in the trees, and this certainly has preadapted them for life in open country. Bock and Miller (1959) have shown that the zygodactyl foot of woodpeckers is basically a perching, and not a specialized climbing, foot. Although certainly not a preadaptation for terrestriality, the zygodactyl foot is not so specialized as to be a hindrance to terrestrial existence. The entire "woodpecking" array of characteristics, from bill and associated muscles and glands to leg action while pecking has been readily converted both to nest construction and to foraging in the earth, with the modifications noted above. These and other possible adaptations and preadaptations of terrestrial woodpeckers are in need of further study.

CONCLUSIONS

Far from arboreally specialized ancestors being a drawback to adoption

of terrestrial habits, the ground-dwelling woodpeckers have adapted well to life in open country. Equipped with their ancestral structures and habits, and with some modifications of these, they have successfully exploited a new niche. Their success is evident in their being a conspicuous and familiar element of every grassland that they inhabit. Ground woodpeckers evolved from ant-foraging, only moderately arboreally specialized, woodpeckers. The African Ground Woodpecker, and the terrestrial flickers evolved independently, although they are distantly related. The potential for the evolution of further ground woodpeckers exists in species of *Colaptes* in North America, and of *Picus* in Eurasia. However, the evolution of ground woodpeckers is dependent upon speciation under a peculiar set of circumstances, which apparently occurs rarely.

My studies were made possible by the help of many friends on three continents, and by the National Science Foundation (Grant GB-5891).

LITERATURE CITED

Bock, W. J.
1959. Preadaptation and multiple evolutionary pathways. Evolution, vol. 13, pp. 194–211.
1963. Evolution and phylogeny in morphologically uniform groups. Amer. Nat., vol. 97, pp. 265–285.

Bock, W. J., and W. De W. Miller
1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. Amer. Mus. Novitates, no. 1931, pp. 1–45.

Noble, G. K.
1936. Courtship and sexual selection of the flicker (*Colaptes auratus luteus*). Auk, vol. 53, pp. 269–282.

Short, L. L.
1965. Variation in West Indian flickers (Aves, *Colaptes*). Bull. Florida State Mus., vol. 10, pp. 1–42.
1969. The foraging association of Green-barred Flickers and Campo Flickers in Argentina. Wilson Bull., vol. 81, pp. 468–470.
1970a. Notes on the habits of some Argentine and Peruvian woodpeckers (Aves, Picidae). Amer. Mus. Novitates, no. 2413, pp. 1–37.
1970b. The habits and relationships of the Magellanic Woodpecker. Wilson Bull., vol. 82, pp. 115–129.
1970c. Reversed sexual dimorphism in tail length and foraging differences in woodpeckers. Bird-Banding, vol. 41, pp. 85–92.
1971a. Woodpeckers without woods. Nat. Hist. Magazine, vol. 80, no. 3, pp. 66–74.
1971b. The systematics and behavior of some North American woodpeckers, genus *Picoides*. Bull. Amer. Mus. Nat. Hist., vol. 145, art. 1, pp. 1-118.
[In press.] Notes on South African woodpeckers. Ostrich.

[MS.] The systematics and behavior of South American flickers (Aves: *Colaptes*).

SPRING, L.

1965. Climbing and pecking adaptations in some North American woodpeckers. Condor, vol. 67, pp. 457-488.

YAPP, W. B.

1962. Birds and woods. London, Oxford Univ. Press, 308 pp.