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BURDENS OF THE PICID HOLE-EXCAVATING HABIT

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Woodpeckers (Picidae, some 200 species) are well known for their woodpecking, drumming, and other habits, but obviously their ability to excavate their own nesting and roosting cavities in wood, sometimes well-rotted, but often in sound wood, is of major importance in their biological "success." That the hole-nesting habit is advantageous is evident not only from the wide distribution, relative abundance, and number of species of woodpeckers, but from the great number of species of other bird families that are unable to excavate their own cavities, and seize upon every opportunity to avail themselves of woodpecker holes. Indeed, some species in at least some situations are so dependent upon woodpecker holes that their abundance and distribution may be affected by the occurrence and availability of such nesting sites; immediately to mind come such American species as the Tree Swallow (*Tachycineta bicolor*) various species of *Myiarchus* flycatchers, and the Elf Owl (*Micrathene whitneyi*) and Old World species such as flycatchers of the genus *Ficedula*, many starlings of diverse genera, and pygmy owls, genus *Glaucidium*. Von Haartman (1971) demonstrated that the population density of hole-nesting birds could be dramatically increased by providing nesting boxes where holes were uncommon or lacking in managed forests, and he showed that such birds are substantially more numerous in unmanaged forests that have holes available than in similar, but managed forests. Holes are so much in demand that the woodpeckers are under heavy pressure from 1 or another species that tries to usurp their cavities from the moment the woodpecker excavation reaches the point of usability (see Tracy 1933:118–119, Szlivka 1957, 1960, Blume 1968, Kilham 1968, 1969, 1972a:37).

It is important to note several points about woodpeckers and their holes. Virtually all picids require individual roosting cavities (Blume 1968, Short 1974a, in press), and these usually are in separate trees. Sometimes woodpeckers may roost outside holes, if none are available, but the prevalence of widespread, year-round excavation of new holes for roosting suggests that the birds are safer in holes, hence it is selectively advantageous for them to have a roosting hole. Further, individuals may have several alternate holes (Blume 1968); they may switch occasionally, and can do so if a cavity is lost, or they are frightened and forced to evacuate a cavity. Based upon my experience with over half the woodpeckers of the world (see, e.g., Short 1971a, 1973, and also such works as Blume 1962, 1968), most species

excavate a new nesting cavity yearly. The male of a pair often shifts from his roosting cavity to the nest for roosting after it is fully excavated (he may shift back again to the prior hole after nesting, see discussion of *Picoides leucotos* in Blume 1968). It follows that ideally each woodpecker territory should have a number of available holes and certainly a number of trees suitable for excavating holes. Ideally there should be several alternate roosting holes per bird. The availability of numerous holes is especially advantageous after the young of the year are fledged, for fledglings are particularly vulnerable (see Blume 1968:54) until the time when they can excavate their own cavities. The presence of suitable, unoccupied cavities for roosting probably enhances survival of the young birds during this crucial phase of life. Finally, it follows that the unavailability of trees suitable for excavating holes, or the occupation of woodpecker holes by other animals may influence the suitability of a territory for a woodpecker pair. Pressures caused by lack or occupancy of holes may be varied, and subtle. For example, the female of a nesting pair presumably must have a roosting hole on or near the territory of her mate—loss of her roosting cavity, if suitable trees for excavation are at a premium, conceivably could interfere with breeding activities, even rendering nesting impossible, if, for example, she was forced to roost too far from the nest to reach it readily. A scarcity of trees suitable for excavating presents a problem compounded by competition for the existing, already excavated holes in an area.

I here review some of the problems woodpeckers face in competition for their nesting and roosting holes, and I treat the adaptations of the woodpeckers to overcome or minimize these problems.

COMPETITION FOR NESTING AND ROOSTING SITES

Woodpeckers seem to "recognize" potential nest-competitors, perhaps through experience, and to distinguish such nest-competitors from species that do not pose this threat. Intense reactions may occur, as between Black-backed Woodpeckers (*Picoides arcticus*) and Tree Swallows (Short 1974b), throughout the breeding season, even when there is no direct threat to the nesting hole. The Black-backed Woodpeckers attack Tree Swallows that perch anywhere in the vicinity of the former's nest (they also attack individuals of *Colaptes auratus*, *Sphyrapicus varius*, *Picoides villosus* and *P. tridactylus*), and in turn the Tree Swallows attack and harass any Blackback that chances to land in a stub in the open where Tree Swallows are foraging in numbers. On the other hand, if sufficient cavities are available, woodpeckers may nest very close to competitors that are tolerated with little or no interaction (see, e.g., Eates 1937, Hoyt 1957, Szlivka 1960, Skutch 1969, Reller 1972).

The introduced Starling (*Sturnus vulgaris*) has spread across the North American continent partly at the expense of non-picid hole-nesters such as the Eastern Bluebird (*Sialia sialis*), and probably with some detrimental effects on woodpeckers such as the Northern Flicker (*Colaptes auratus*) and Red-headed Woodpecker (*Melanerpes erythrocephalus*), although it mainly uses natural cavities in trees, human edifices and structures, and old, abandoned woodpecker holes. Well-adapted by its sheer persistence to evict woodpeckers and other birds, Starlings win many although not all battles for woodpeckers' holes (see, e.g., Bent 1939, Szlivka 1957, Stickel 1963, Kilham 1968). The severity of the competition is indicated by occasional death of woodpeckers or Starlings in their conflicts over nest-sites (Shelley 1935).

Other non-picid competitors may or may not be as aggressive as Starlings, but usually show persistence in their efforts. The tityras (*Tityra semifasciata* and *T. inquisitor*, Skutch 1969) are successful in usurping nests of several melanerpine woodpeckers by filling the woodpeckers' holes with leaves and debris whenever the woodpeckers are absent; the latter eventually may give up removing the leaves and abandon the nest. Skutch (1969) also noted the aracari toucans (*Pteroglossus* sp.) as severe competitors for the holes of woodpeckers, and they may prey upon young woodpeckers as well. Tarboton (1976) indicated his strong suspicion that Crested Barbets (*Trachyphonus vaillantii*), a competitor for holes occupied by wrynecks (*Jynx ruficollis*) in South Africa, may kill the young wrynecks if there are young in the nest when they commence their takeover. Not only toucans and barbets, but other tropical birds such as parrots, hornbills, and even some ovenbirds (*Xenops*) and dendrocolaptids (fide P. O'Brien) often usurp woodpecker nests, and owls and hole-nesting falcons may do so. Mammals such as flying squirrels and other squirrels, monkeys, and others evict woodpeckers (and other hole-nesting birds) from holes they have excavated or occupied. Predatory mammals and snakes may eat the eggs or young of woodpeckers, then settle for a time in the nesting cavity.

The intensity of competition for newly excavated holes may be greater than that for older cavities since the former are clean. Older holes develop a microfauna often including parasites and other vermin that may make such holes less than attractive. Newly excavated holes lack pests, and thus may be preferred by woodpeckers and their competitors. Tracy (1933), Szlivka (1957, 1960), Blume (1968), Kilham (1968, 1972a), and Skutch (1969) provided data emphasizing the takeover or attempted takeover of woodpecker nests just at the point of completion. There are many cases of woodpeckers excavating 2, 3 or even more cavities and losing them just at completion of excavation (see Szlivka 1957, Stickel 1963, Kilham 1968, and Jackson 1977).

The effects upon woodpecker populations of nest losses to the various competitors are difficult to evaluate, and appropriate data are sparse. Troetschler's (1976) studies of the Acorn Woodpecker (*Melanerpes formicivorus*) of western North America, only exposed to Starlings for the past few decades, indicate substantial impact on that woodpecker. Almost all of the nests excavated early in the season (presumably at a time most optimal for the woodpecker) in some areas, are lost to Starlings and consequently the average timing of hatching of young woodpeckers has shifted to later in the season. Flickers may in some areas, be affected similarly, and so too are Great Spotted Woodpeckers (*Picoides major*) in Europe (Blume 1968). Nests excavated by Great Slaty Woodpeckers (*Mulleripicus pulverulentus*) in Malaya were repeatedly usurped, or the woodpeckers driven away, by hornbills or mammals (Short 1973). Thus, the seemingly very long breeding season of this species reported by various authors seems due to the initial, and perhaps repetitive loss of the nest (which may take 3 weeks or a month to excavate, after a suitable site is located—up to 6 or so weeks may be lost if the nest is usurped just after excavation is completed, and even more time is lost if nesting has progressed to the egg-laying, incubation, or nestling period). In the case of repetitive nest-hole losses of woodpeckers to Starlings, mentioned above and involving at least several picids (e.g., *Melanerpes carolinus*, Stickel 1963; *Picoides syriacus*, Szlivka 1957; *P. villosus*, Kilham 1968; and *P. borealis*, Jackson 1977), it is obvious that several re-excavations and new breeding attempts in succession substantially delay nesting, pushing it beyond the presumably optimal period of the initial endeavor. Tropical woodpeckers particularly seem prone to lose their initial nest; Skutch (1969) and Short (1970) treated a number of instances in the Neotropics, Short (1973) discussed some cases in Asian picids, and Short (pers. obs.) has seen losses of Nubian (*Campethera nubica*) and Bearded woodpecker (*Dendropicos namaquus*) nests to various African starlings, and, as noted above, Tarboton (1976) reported that barbets usurp wryneck nests in southern Africa.

Woodpeckers of course are among the potential and actual nest competitors of other picids. (I exclude from consideration intraspecific competition, and competition between allospecies in zones of contact, as this is almost equivalent to intraspecific competition.) Such nest usurption often occurs during the excavation period, 1 woodpecker, usually representing a larger species simply driving away the other, usually smaller woodpecker, enlarging its excavation, and nesting therein. I have seen this in such species as the Hairy to the Downy woodpecker (respectively *Piocides villosus* and *P. pubescens*; see also Kilham 1962). Other examples include enlargement of nests of *Picoides minor* by *P. major* (Tracy 1933), of *P.*

borealis by *Melanerpes carolinus* (Ligon 1971), and of *Melanerpes pucherani* by *Dryocopus lineatus* (Kilham 1972a). The episode described by Tracy (1933) illustrates the intensity of the interaction, for the larger species (*Picoides major*) persisted in enlarging the cavity of *P. minor* despite strong attacks by the latter, and the interference of the human observer on behalf of *minor* (the success of *major* was but temporary, for subsequently it lost the enlarged cavity to Starlings). This competitive pressure may explain the tendency for small picids, especially, to favor sites that barely permit the dimensions of their nesting (or roosting) cavity, i.e., sites that larger species cannot use. Some small species prefer to excavate into the underside of thin branches, as does *Melanerpes rubricapillus* (Kilham 1972a), again in situations unlikely to attract a large woodpecker.

More difficult to understand is the actual enlargement of cavities of smaller woodpeckers by larger picids involving sites that the larger birds either cannot or usually do not use. A White-bellied Black Woodpecker (*Dryocopus javensis*) methodically enlarged an intended nesting cavity of the much smaller *Picus puniceus*, the Crimson-winged Woodpecker, in Malaya (Short 1973). The *puniceus* cavity was in a branch much too small to afford a cavity that could accommodate *javensis*, yet the latter gradually rendered it unsuitable for *puniceus*, enlarging the opening until it was far too big, and the cavity exposed. The larger woodpecker did not feed during its excavating. One could consider this to be a competitive reaction, but there is virtually no overlap or possible direct competition between these picids, either in foraging (feeding modes and sites differ, Short 1973), or in nesting and roosting sites. Dennis (1971) and Jackson (1978) also described the habit of Pileated Woodpeckers (*Dryocopus pileatus*) of enlarging Red-cockaded Woodpecker (*Picoides borealis*) holes that the pileateds only occasionally are able, or choose, to use.

The greatest degree of competition among woodpeckers would appear to be between similarly-sized species, and particularly between similarly-sized congeneric woodpeckers that overlap in foraging habits (see, e.g., *Picoides macei* and *P. canicapillus in* Short 1973); these are apt to have similar nesting requirements as well as similar foraging sites, hence contact between them will be frequent. I have described (Short 1971b) an instance of intense, direct interspecific aggression and territoriality between the usually non-interactive Hairy Woodpecker and Nuttall's Woodpecker (*Picoides nuttallii*) in a situation involving a rather poor, ecologically simple habitat that was, however, abundantly occupied by the smaller *P. nuttallii.* A pair of Hairy Woodpeckers appeared, out of their normal habitat, and were engaged constantly in conflicts with persistent, numerous Nuttall's Woodpeckers, interfering with the Hairy Woodpeckers' endeavors at nesting. The

degree of contact may influence strongly the relative competition between woodpeckers for nesting sites. Indeed it is in primary tropical forests with dense, wet vegetation, rendering the woodpeckers difficult to see and muffling the sounds of their workings, that the greatest number (up to 13) of picid species can coexist (Short 1978).

ADAPTATIONS RELATING TO COMPETITION FOR HOLES

Considering the specialization of woodpeckers for obtaining insects below the surface of tree-bark, one might expect that tropical woodpeckers could tolerate the loss of nesting holes rather easily, i.e., they should be able to find insect food in trees, and thus to nest as easily at one as at another time of the year. This might be the case for a few highly specialized "woodpecking" species, but in fact most picids nest at that time of year when food is most readily available and easily accessible in quantities sufficient to feed and raise their young. Many woodpeckers that feed by excavating much of the time into the bark may nest when certain insects are available at the surface, and forage then by gleaning for insects to feed their young (e.g., 4 sympatric species of *Picoides* in southern California, Short 1971b). Thus, woodpeckers are apt to breed at an optimal time of the year, as are most birds, and this especially is likely wherever there is a distinct or even partial seasonality affecting rainfall, vegetation, and food supply. Temperate zone woodpeckers are strongly seasonal breeders. For most woodpeckers a delay in nesting is apt to be detrimental, hence the ability to excavate and defend a nesting cavity is very advantageous.

Woodpeckers usually become very attached to the nest site as the excavation nears completion, and from that time until the young have hatched and are partly developed, 1 or the other parent usually can be found near the nest. When an adult is within the cavity the chance of a nest-competitor dislodging it from the nest is slim (Lawrence 1967, Kilham 1968, Skutch 1969), but persistent efforts by some competitors often are rewarded once they are able to enter the nest during an infrequent absence of both woodpeckers. Nevertheless constant surveillance of the nest and occupation of the hole by the woodpeckers from the time the nest is completed, though egg-laying, incubation, and hatching periods, until such time as the nestlings can climb to (and thus, by their presence, "protect") the nest entrance, help to reduce nest losses to competitors.

Loss of the nest to competitors that happens despite actions of the woodpeckers to retain it may be followed by rather rapid renesting. This is facilitated by several activities that, if not influenced by selection favoring rapid renesting, at least preadapt woodpeckers for such action. Most picids excavate 1 or more roosting cavities during the course of the year,

usually at times other than during the breeding season. Almost every adult woodpecker has 1 or several roosting cavities or evasion holes (Blume 1962, 1968) to which it can retire at night in relative safety. As noted above, once nesting commences the male parent occupies the nesting cavity from the time it is sufficiently complete to make this feasible until the young near the time of fledging. Since the shift of the nesting male from its roosting cavity to the (usually newly constructed in most picids, see, e.g., Blume 1962, 1968, Lawrence 1967) nesting hole frees the roosting site, that cavity is potentially available for renesting. Other roosting cavities of members of a pair also are available for renesting. Such cavities require minimal enlarging or modification, hence the renesting will be much more rapid than would occur if a new cavity had to be excavated.

Furthermore, during the initial period of nest excavation the woodpecker may start several holes before finally deciding on that to be used for nesting. Other partially worked holes usually are found in any woodpecker's territory, leftovers from abortive nesting or roosting hole construction. Some of these may be suitable for full excavation, and to the extent that they have been excavated earlier, time will be saved in renesting (for the importance of such holes see Blume 1968:39 for *Picoides major*, and ibid:75 for *P. medius*). It is logical that hole-working that human observers might interpret as irrelevant behavior or even "play" is selectively advantageous in providing initial holes that, in an emergency (need for roosting or nesting hole) can be completed more rapidly than a new construction.

Seasonal adjustments might be expected as means of avoiding both picid and non-woodpecker competition for nesting sites. There is no evidence that such adjustment occurs in relation to non-picids. As regards woodpecker competition, Kilham (1972b) showed that *Campephilus melanoleucos* and *Dryocopus lineatus*, 2 similar-appearing woodpeckers, nest at different times of the year where he studied them in Panama, but data from juvenile specimens of both suggest some seasonal overlap in Panama, and in Mexico *C. guatemalensis* (a close relative of *C. melanoleucos*) may nest at the same time of year, and even in the same tree simultaneously with *D. lineatus* (Shaughency, *in* Short in press). It is unlikely that very great shifts in seasonality are possible in most picids. Since many woodpeckers are resident, permanently territorial species that may excavate roosting cavities at any time of the year, interspecific contact, and competitive interactions are not confined to the breeding season. For example, competitive interactions between Indian *Picoides macei* and *P. canicapillus* affect foraging activities whenever the birds meet (Short 1973, 1975). Hence a radical shift in breeding seasons for purposes of avoiding nest-site competition

would not seem to accomplish sufficient avoidance or insure that the nesting site would not be lost to picid competitors.

The ability of woodpeckers to excavate cavities in wood is shared by other groups of birds (barbets, kingfishers, parids) only to the extent that the woodpeckers use well-rotted, dead wood. Excavation in live trees having hard wood is advantageous to some extent in reducing nest losses to competitors larger than the woodpeckers that perform the excavation. Non-picids larger than the woodpeckers are unable to enlarge the opening of a cavity (see Lawrence 1967:104) in live or very hard dead wood. Non-picid hole-nesters smaller than woodpeckers, such as tits, some flycatchers and others usually do not offer competition to woodpeckers, except in the case of *Passer* (Szlivka 1960). Competitors that often are successful and pose a serious threat are those larger than the picids, such as falcons, perhaps owls (see Graber et al. 1977:10; owls also are predators of woodpeckers), hornbills, toucans, rollers, and others. It follows that any excavation of a roosting or nesting cavity by a woodpecker ought to be as small as possible to discourage potential predators. There is abundant evidence that the smaller woodpeckers particularly excavate holes with openings as small as possible e.g., pied woodpeckers, Lawrence 1967, Blume 1968; sapsuckers, Lawrence 1967; piculets, Short 1970, in press). Excavations in live wood offer an advantage for the owner even in the case of competition from other woodpeckers in that any enlargement must be accompanied by loud sounds of excavating that are sure to attract the owner's attention, whether or not it can prevent the enlargement. Not only do most woodpecker holes have small entrances, but the woodpeckers excavate, in live trees and hard dead trees, a tunnel penetrating some distance into the wood before dropping down into a chamber. Thus, a potential usurper larger than the woodpecker not only would have to enlarge the entry, but would face the difficult and awkward task of enlarging a section of tunnel through hard wood. In addition to the small entry and tunnel, it is advantageous as well if the stub used is not much larger than that needed for the sized woodpecker involved. Of course small stubs bearing woodpecker cavities are apt to break in storms (see especially Skutch 1969), so the selective advantage accruing from use of a small stub (large nest competitors would find the site unsuitable, but see the above-mentioned cases of enlargement of unsuitable cavities by large woodpeckers) is to some extent balanced by selection favoring choice of a sturdy site to minimize loss of the nest by breakage of the stub.

The particular site of a nest may discourage potential nest-hole competitors. Like many small barbets (genus *Tricholaema*, 3 species, pers. obs.), *Melanerpes rubricapillus* favors sites on the underside of rather small branches for its excavations. Many though not all birds find it difficult to

cling to the underside of a small branch, to say nothing of fending off the picid owners, working on the wood from an upside-down position, and carrying nesting material into the nest chamber.

The nesting of many tropical, and some other forest and woodland picids outside the forests or woods (see Skutch 1969, Short 1973), i.e., in isolated trees in pastures or other areas adjacent to woods, not only reduces predation by arboreal predators but also limits nest-hole competition from more secretive forest and woodland species that do not leave these areas. These advantages often seem to outweigh the greater exposure of the isolated trees to wind and lighting, and of the woodpeckers to aerial predators as they fly across open areas to the nesting site. From personal experience I have found (Short in press) that many forest and woodland picids frequently seek out trees standing apart from forests in which to excavate nests. These woodpeckers include even such interior forest birds as Asian *Dinopium rafflesii* and South American *Campephilus melanoleucos*, as well as many other species (divergent examples that come to mind are: *Piculus aurulentus*, *Veniliornis spilogaster* and *Dryocopus lineatus* from the Neotropics; *Picoides obsoletus*, *Dendropicos xantholophus* and *Campethera cailliautii* of Africa; and *Picus puniceus*, *Reinwardtipicus validus*, and *Dryocopus javensis* of Asia). Arboreal competitors (some also are predators) for holes that are excluded from competition by placement of a woodpecker's nest in an isolated tree outside the forest include various mammals (squirrels, monkeys) and also some hornbills, owls and other birds that find that situation unsuitable. Some woodpeckers (as well as other birds) especially may choose trees near human habitation, a situation which excludes certain "shy" or persecuted aerial and arboreal predators and nest competitors (although perhaps adding others, such as non-forest starlings in Africa and elsewhere).

A few picids reduce competition for nest holes by excavating their nesting cavities in occupied ant or termite nests, either raised above the ground or in trees. All the woodpeckers that use these sites subsist to a large extent on ants and termites. Such species are *Celeus brachyurus* of Asia (Short 1973; almost exclusively nesting in termite or ant nests), *Campethera nivosa* of Africa (Chapin 1939) and *Piculus chrysochloros* and *Celeus lugubris* in South America (Short 1970). The nature of the substrate and presence of the ants or termites would seem to deter both predators and thinner-skinned (picids have tough, thick skin) nest-competitors, but not the picid excavators. Studies of the nesting of such woodpeckers are needed to gain data on these matters, but intuitively it seems that relief from such pressures was a factor in the evolution of such nesting habits.

Red-cockaded Woodpeckers (*Picoides borealis*) keep resin flowing about their nesting and roosting holes by pecking and tapping activities. This

perhaps reduces predation by snakes and other enemies (Jackson 1978); possibly it may make it difficult for some competitors to usurp and use their holes, but this remains to be shown.

A final group of adaptations might be considered, namely social adaptations. Woodpeckers generally are aggressive birds (Blume 1968, Short 1974a), and this aggressiveness is displayed interspecifically (Short 1973, 1974b, 1975) as well as intraspecifically. Such aggression helps the woodpeckers to defend their nests, at least sometimes with success, against persistent potential usurpers (e.g., Starlings) incapable of excavating their own nests and against birds that may be of larger size (e.g., I have seen nesting *Picoides pubescens* drive away larger *P. villosus*, and *P. arcticus* keeps *Colaptes auratus* from proximity to its nest, Short 1974b). Despite intense aggression between competitors for nesting sites, such competitors at least occasionally appear "satisfied" once they have secured a nesting site, and there are many reports of nesting in proximity of usually aggressive nest-hole competitors with some, little or no aggression between them. Some examples are: (1) the nesting of *Picoides mahrattensis* and the parrot *Psittacula krameri* in the same tree with some attacks on the latter by the former (Eates 1937); (2) nesting of Northern Flickers and Pileated Woodpeckers on opposite sides of the same stub, the latter acting at times to drive the former away (Hoyt 1957); (3) the usurping of the nest of a pair of *Picoides syriacus* by *Passer montanus* and subsequent harmonious and successful nesting of *syriacus* in a newly excavated adjacent cavity that connected with that of the *Passer* (Szlivka 1960); (4) nesting in the same stub harmoniously of the usually interactive *Melanerpes chrysauchen* and *M. rubricapillus* (Skutch 1969); (5) nesting .6 m apart of *Melanerpes erythrocephalus* and *Colaptes auratus*, the former being dominant, with conflicts only when both species happened to visit the nest simultaneously (Reller 1972); and (6) nesting 1.4 m apart of *Melanerpes carolinus* and *Picoides borealis*, although the former usually is very aggressive to the latter (Jackson 1978).

Sociality itself is uncommon in picids, being mainly confined to terrestrial *Colaptes* and *Geocolaptes*, and to some melanerpine woodpeckers (Short 1970, 1971a, 1972, 1974c). These social picids are generalized in habits, and can concentrate in numbers because of their extensive simple habitat (open grasslands for *Colaptes, Geocolaptes*) or their omnivorous habits (especially melanerpine species). More "typical" woodpeckers that work the bark or wood for insect foods usually cannot concentrate in numbers, but must spread themselves through their habitat to insure sufficient foraging sites for individual and family needs. The social species have the advantage of numbers of adult individuals about the colony at all times (e.g.,

Colaptes rupicola, Short 1972; *Melanerpes striatus*, Short 1974c), available to protect the nesting bank or tree. The semi-social *Picoides borealis* shows this to come extent, but adults tend to feed and to visit the nest in groups, so adults are not present about the nest most of the time (Jackson, pers. comm.). In *Melanerpes cruentatus* (Short 1970) and *M. formicivorus* (MacRoberts and MacRoberts 1976) a number of adults beyond 1 pair are involved at a nest, and the nest is attended almost constantly. These habits doubtless afford greater protection to the nests than can be provided by a solitary pair of woodpeckers.

SUMMARY AND CONCLUSIONS

Woodpeckers excavate their own nesting cavities in hard or soft wood. Competitors for these cavities are numerous, and adversely affect the nesting efforts of many woodpeckers. Even other woodpeckers may usurp the partial or completed excavation of another woodpecker. However, picids show a number of adaptations that tend to reduce or minimize the loss of nests to competitors, such loss interfering as it does with the timing of nesting, and, when nesting sites are in short supply, with its success.

Losses that do occur are minimized by the ability of woodpeckers to renest rapidly, given suitable nesting sites. One factor in rapid renesting is the availability of other partly completed or completed holes (e.g., holes begun but discarded early in the nesting season, roosting holes) that can be used for renesting with minimum modification.

The avoidance of losses takes many forms, some of which are related as well to avoiding predation. Woodpeckers are closely associated with the nesting site from the time of excavation until the nestlings are active about the nest entrance, hence competitors are kept out of the cavity. There is little evidence for seasonal adjustment of breeding activities for temporal avoidance of competition with picid competitors, and no evidence regarding such adjustments to non-woodpecker competitors. Many woodpeckers use live wood in excavating their nest holes, and to the extent that they do so most competitors larger than the woodpecker are prevented from using the cavity because they are physically unable to alter (enlarge) it. Such holes often have deep tunnels from the entrance into the center of the tree, and the entrance itself usually is barely large enough to admit the woodpecker, hence large competitors must face difficulty not only in entering the cavity, but in sufficiently enlarging the tunnel, which usually penetrates hard wood. Picids, too, tend to choose as small a stub or tree as will permit construction of the nest, hence competitors of larger size will be unable to use the nest. Another tactic is to place the nest on the underside of a (small) branch, demanding great agility of potential competitors if they are to be successful. Some forest woodpeckers often choose a nesting tree outside the forest, precluding competition from arboreal mammals and reducing nest-site competition from hornbills and other secretive forest species. Human habitations outside the forest also are often the scene of woodpecker nesting efforts, again reducing competition from more secretive forest species, usually larger than the woodpecker, and sometimes hunted or otherwise persecuted by man. A few woodpeckers nest in ant or termite nests that are unsuitable for most nest-competitors. Social adaptations include the general aggressiveness of woodpeckers that aids them in retaining nests that are sought by competitors, and, in a few species, increased sociality that allows more individuals to defend the nest site or colony. These adaptations, when added to the basic capability of woodpeckers to excavate their own holes, several

times in succession when forced to do so, account for the success woodpeckers have had in achieving a nearly cosmopolitan distribution in diverse habitats.

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