

SIGNIFICANCE OF OLD-GROWTH FOREST TO THE HAWAI'I 'ĀKEPA

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Abstract. The Hawai'i 'Ākepa (*Loxops coccineus coccineus*) is an endangered Hawaiian honeycreeper that nests obligately in tree cavities of 'ōhi'a-lehua (*Metrosideros polymorpha*) and koa (*Acacia koa*). Comparative evidence from cavity-nesting birds elsewhere suggests that the distribution and abundance of the Hawai'i 'Ākepa may depend on large trees. During a seven-year study of the bird at Hakalau Forest National Wildlife Refuge, 54 trees were used by the birds. I documented size and growth form of these trees and compared them to trees randomly selected and to large trees that were inventoried. The trees used by the birds are the largest 'ōhi'as, which are in the rarest size classes, and large koas. The 'ōhi'a and koa trees fit many criteria of old-growth forest. Particularly striking is the association of cavities with large trees. Growth form is also important since cavities occur almost exclusively in monopodial (single-trunked) 'ōhi'as, and the birds use cavities in monopodial koa trees over those in sympodial (multiple-trunked) trees. Regeneration of old-growth forest involves both the transition of large trees into cavity trees and the growth of seedlings into a monopodial form. Disturbance to the forest over the last 100 years has generated problems at both scales of regeneration. Trees with cavities are likely falling at a faster rate than cavities develop in smaller trees, and increased light levels in the understory and at edges of the forest appear to promote sympodial growth in seedlings.

Key Words: *Acacia koa*; distribution and abundance; Hawai'i 'Ākepa; koa; *Loxops coccineus coccineus*; *Metrosideros polymorpha*; 'ōhi'a; old-growth forest; regeneration; tree cavities.

Old-growth forests have specific relevance to both evolutionary and conservation biology. Free from human or natural disturbance for a much longer time than second-growth forests, old-growth forests appear to be unique environments in which some resident species evolved their life histories and behaviors (Wesołowski 1983, Piotrowska and Wesołowski 1989). These forest types are often associated with conservation hot spots where some species have their highest densities. Spotted Owls (*Strix occidentalis caurina*), Red-cockaded Woodpeckers (*Picoides borealis*), and Marbled Murrelets (*Brachyramphus marmoratus*) are prominent avian examples for old-growth coniferous forests (Forsman et al. 1984, James 1991, Ralph et al. 1995a). The macroecological approach to the study of correlation between distribution and abundance suggests a hot spot exists because the niche requirements of the species in it are best met (Brown 1984, Brown et al. 1995, Terborgh 1995). This is best illustrated by temporal changes in a population of Acorn Woodpeckers (*Melanerpes formicivorus*) in New Mexico associated with a decline in old, partly dead cottonwood trees (*Populus angustifolia*) used as stable granaries for storing acorns (Ligon and Stacey 1996).

The most extensive forest type on the main Hawaiian islands consists of 'ōhi'a-lehua (*Metrosideros polymorpha*, hereafter referred to as 'ōhi'a), frequently in association with koa (*Acacia koa*) as a co-emergent (Scott et al. 1986, Wagner et al. 1990a,b). However, the concept of

old-growth forest has not yet been applied to this or any other forest type in Hawai'i. There may be several reasons for this including (1) inability to age 'ōhi'a and koa trees based on growth rings (Sastrapradja 1965, Burgan 1970, Wick 1970); (2) elimination of large trees by repeated hurricanes (Shaw 1981, Schroeder 1993) and by humans as forests were destroyed (Kirch 1982a); (3) steep topography, which would limit tree size for biomechanical reasons of soil support (Garwood et al. 1979, Sidle et al. 1985, Mattheck 1991) and exposure to wind (Telewski 1995), or for physiological reasons of water stress caused by exposure to wind and excessive drainage (Kozłowski and Pallardy 1997a); and (4) growth in soils on older islands with fewer nutrients (Crews et al. 1995, Vitousek et al. 1995). In addition, on the volcanically active island of Hawai'i, elimination of forests by lava flows (Carson et al. 1990) and youth of regenerating forests on lava do not provide the pattern for recognizing old-growth forests. The phenomenon of "'ōhi'a dieback," where cohorts of mature trees but not saplings die synchronously (Mueller-Dombois 1987), also does not promote the concept of old-growth forest with large live specimens standing and large dead specimens on the ground (Franklin et al. 1981, 1986).

The Hawai'i Forest Bird Survey (Scott et al. 1986) was the first comprehensive attempt to analyze the distribution and abundance of native forest birds in relation to features of habitat. However, there was no formal incorporation of variables that could identify old-growth forest.

Scott et al. (1986) indicate that tree diameter was measured at selected stations, but these data were not incorporated as variables in the habitat response analysis designed to identify aspects of habitat that were associated with high and low densities of birds. Rather, forest development was indexed as tree biomass, calculated as crown cover (in percent) times canopy height (m). For many aspects of the survey this was appropriate, as in other studies attempting to estimate canopy volume for comparative purposes (Sturman 1968, Karr and Roth 1971, Sabo 1980, Rice et al. 1983). However, dense stands of tall, thin trees could have the same value of tree biomass as thinner stands of large (in diameter) trees of similar height but with wider canopies. Such stands could even have higher estimated tree biomass than areas with more widely separated trees that are large in diameter and of the same height. Without formally incorporating variables of tree diameter, there would be no way in which old-growth forest, based on the presence of large trees, could be identified.

Some anomalies in the habitat response analysis might be attributed to the absence of a variable that could represent old-growth forest. The Hawai'i 'Ākepa (*Loxops coccineus coccineus*) is a Hawaiian honeycreeper (Drepanidinae) that exists exclusively in 'ōhi'a or 'ōhi'a-koa forests on the island of Hawai'i (Scott et al. 1986). The bird forages mainly in the terminal foliage of 'ōhi'a (Perkins 1903) and is unique among forest birds in being able to extract caterpillars from the inside of 'ōhi'a leaf buds (Richards and Bock 1973, Freed et al. 1987a). The main 'Ākepa populations, in the Hāmākua study area on Mauna Kea and in the Ka'ū study area on Mauna Loa (Fig. 1), varied in their response to habitat variables (Scott et al. 1986). The 'Ākepa in the Ka'ū site showed no relationship between density and tree biomass, whereas the 'Ākepa in the Hāmākua site showed a negative relationship between density and tree biomass. A negative response could occur if the birds were more likely to be detected, or were more abundant, in highly disturbed forest with large trees than in second growth forest with smaller trees. It is possible that large 'ōhi'a trees in a pasture may be more important to the niche of the Hawai'i 'Ākepa than dense stands of smaller 'ōhi'a trees with native understory. A second variation in response was that birds in the Ka'ū site were negatively associated with koa, whereas birds in the Hāmākua site were positively associated with koa. This pattern could occur if large koa trees were associated with large 'ōhi'a trees in the Hāmākua but not the Ka'ū study site. In fact, the southeastern portion of the Ka'ū site with the most 'Ākepa has large 'ōhi'a but no koa, where-

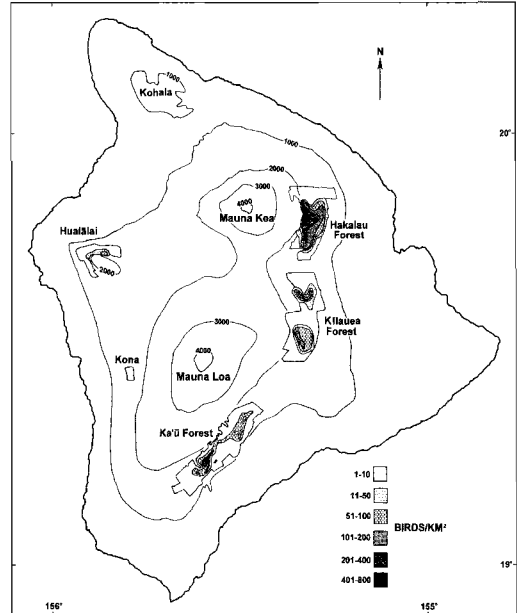


FIGURE 1. Distribution and abundance of Hawai'i 'Ākepa on the island of Hawai'i based on Hawai'i Forest Bird Survey (Scott et al. 1986). Contour lines at 1,000 m. Birds were found at Hakalau Forest, Ka'ū Forest, Kona, and Hualālai; distribution is represented by irregular enclosures. Hakalau Forest and Kilauea Forest were within the Hāmākua study area of the survey. Ka'ū Forest was within the Ka'ū study area. Pua 'Ākala study site in current study is located at the highest Hawai'i 'Ākepa density (solid black) in Hakalau Forest. Hart (*this volume*) compared 'Ākepa at Pua 'Ākala with those in a site of reduced density north of Pua 'Ākala.

as the northwestern portion with koa has few 'Ākepa (Jacobi 1978, Scott et al. 1986).

The location of nests of the Hawai'i 'Ākepa may be the link between the density of birds and the presence of large trees in old-growth forests. The 'Ākepa appears to be the only honeycreeper that nests obligately in cavities in trees (Scott et al. 1980, Freed et al. 1987b, Lepson and Freed 1995), and all reported nests were located in large trees (Sincock and Scott 1980, Collins 1984, Lepson and Freed 1997). A variety of cavities were used, including holes in trunks or branches, snags, and even open areas where the bark and wood had separated (Sincock and Scott 1980, Collins 1984, Freed et al. 1987b). There are no primary cavity-nesting (excavating) birds such as woodpeckers in Hawai'i. Therefore, cavities must form naturally in trees, and large trees might be much more likely than small trees to form cavities, as has been found with *Eucalyptus* in Australia (Lindenmayer et al. 1991a, 1993; Bennett et al. 1994). Studies of secondary cav-

ity-nesting birds, which use existing cavities, indicate that nests are located in cavities in large trees (Saunders et al. 1982, van Balen et al. 1982, Wesolowski 1989). No study of relationship between cavities and tree size has occurred in Hawai‘i.

As part of a long-term study of the breeding biology and mating system of the Hawai‘i ‘Ākepa, I documented ‘ōhi‘a and koa trees used by the birds as nest sites and compared the trees used as nest sites with other trees available in the same study area. This provided a basis for establishing the nonrandom use of trees in the forest. In addition, I investigated the relationship between cavities and tree size. This relationship is the basis for identifying old-growth forest in Hawai‘i and the critical role that exceptionally large trees have in the nesting niche of the Hawai‘i ‘Ākepa.

METHODS

The relations among tree size, tree form, presence of cavities, and use of cavities for nesting by Hawai‘i ‘Ākepa were studied in the Pua ‘Ākala Tract of Hakalau Forest National Wildlife Refuge. This section of the refuge has the highest density of ‘Ākepa on the windward slope of Mauna Kea (Fig. 1). The study site within the tract was a 500 × 600 m area at an elevation of 1,900 m. The land had been partially cleared and extensively grazed by cattle for over 100 years (Tomonari-Tuggle 1996). As a result, the site has a parkland-like structure of large ‘ōhi‘a and koa trees, with introduced grasses as the primary understory species in cleared areas. Within this structure are sections of less altered forest with an understory of native ferns and *Rubus hawaiiensis*, and a midstory of native woody trees and shrubs, mainly *Cheirodendron trigynum*, *Myrzine lessertiana*, *Coprosma ochracea*, *Vaccinium calycinum*, *Ilex anomala*, and *Styphelia tameiameia*.

‘Ākepa nesting had been studied within the site for 7 years (Lepson and Freed 1995, 1997). I measured the diameter at breast height (dbh) in cm using a dbh tape of the 54 ‘ōhi‘a and koa trees that had been used by the birds. The diameter of the part of the tree that contained the cavity was estimated as a percentage of dbh based on comparing units of a ruler subtended by the part and by the trunk at dbh height viewed from a similar distance. I also identified the growth form as the height of first forking in relation to the measurement of standard dbh (height of 1.3 m). Trees that forked above this height were considered single-trunked (monopodial). Trees that forked below this height were considered sympodial, with co-dominant trunks (forks). Size of sympodial trees was measured below the fork. In addition, the diameter of each fork was measured. These trees are the basis of comparison with other trees sampled in this study.

The size of trees available to the birds was determined by sampling trees in the same study area. Sampling stations were located 50 m apart along transects 50 m apart, based on a randomly selected initial starting point near the corner of the study area. At each of the 133 stations where a tree was within 20 m of the

TABLE 1. TYPES OF CAVITIES USED AT 71 NEST SITES BY HAWAI‘I, ‘ĀKEPA

Cavity entrance	Proportion
Smooth hole	0.34
Rough crack	0.24
Rough hole	0.20
Smooth crack	0.11
Niche	0.04
Long crack	0.01
Unknown	0.06

station, the dbh and trunk type was determined for the closest tree with dbh above 5 cm. At 16 of these stations, the closest tree in each of four quadrants was measured. This resulted in a sample of 162 ‘ōhi‘a and 10 koa trees. *Ilex*, *Coprosma*, and *Cheirodendron* together resulted in four trees. Sizes of ‘ōhi‘a and koa available and used were compared to illustrate the significance of large and old trees to the breeding niche of the bird.

The relationship among tree size, growth form, and presence of cavity was determined by inventorying large trees within a 200 × 500 m subarea. Sections of the subarea were investigated in relation to prominent landmarks to ensure complete coverage. All trees >60 cm dbh, the smallest tree size known among the 54 trees used by nesting ‘Ākepa, were measured in the inventory. In addition, some specimens were included that were measured and found to be <60 cm dbh. Diameter at breast height, growth form, presence of cavity, and use of cavity by ‘Ākepa were documented for each tree in the inventory. Trees used by the birds in previous years were already marked. The inventory included 229 trees (172 ‘ōhi‘a, 57 koa).

Unless indicated otherwise, all statistical analyses of metric variables were done using a two-sided t-test, and tests of proportions involved a binomial test.

RESULTS

CHARACTERISTICS OF CAVITIES AND TREES

The birds used cavities with several types of entrances (Table 1, Fig. 2). The sample size of 71 cavities in 54 trees reflects the fact that about one-third of the trees had more than one cavity present and used, but never during the same breeding season. The holes and cracks were cavities formed by openings within the wood. The niche cavity was an opening formed by the separation of the bark away from the wood, as was reported for an ‘Ākepa nest in the Ka‘ū Forest Reserve on Mauna Loa (Freed et al. 1987b). Both rough and smooth openings were used equivalently (0.44 and 0.45, respectively), indicating that the type of opening does not appear to be important. The heights above ground of cavities used ranged from 1.5 to 19.5 m (mean 10.2 m). This wide range suggests that the presence of a cavity may be more relevant than its height above the ground. The range includes the

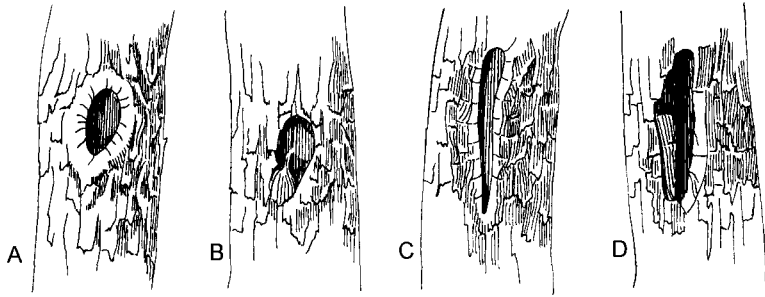


FIGURE 2. Four major types of openings of cavities used for nesting by Hawai'i 'Ākepa. A = smooth hole, B = rough hole, C = smooth crack, D = rough crack. Ontogenetic differences are discussed in text.

highest nest known for 'Ākepa (Collins 1984, Freed et al. 1987b); however, height of the first 'Ākepa nest discovered in the Ka'ū Forest Reserve by Sincov and Scott (1980) was the lowest at 1 m.

The birds used only large trees for nest sites. For 'ōhi'a, the trees used are on average more than twice the size of trees available based on the random sample ($P < 0.001$; Fig. 3); for koa, there was no significant difference ($P = 0.42$; Fig. 4). However, the random sample of koa contained only one tree < 75 cm dbh (10%), unlike the random sample for 'ōhi'a, in which 77% of trees were < 75 cm dbh. The rarity of smaller koa trees appears to be the result of cattle ranching for the last 100 years and faster growth and possibly shorter life of koa (Cooray and Mueller-Dombois 1981, Spatz and Mueller-Dombois 1981). I have observed cows seek young koas as food with the result that koa regeneration has probably been suppressed over the past century (Baldwin and Fagerlund 1943). Nevertheless, all nests were located in enormous 'ōhi'a and koa trees, averaging 1 m dbh with a minimum of 60 cm dbh. Trees of this size would be expected in an old-growth forest, thus revealing the essential role of such a forest in the niche of the 'Ākepa.

ASSOCIATION BETWEEN CAVITIES AND TREES

The presence of cavities in 'ōhi'a in the inventory area and the use of trees with cavities by 'Ākepa was related to the size of tree. Only monopodial trees are considered for the analysis of 'ōhi'a. Within the set of large 'ōhi'a trees that were inventoried, cavity trees are an average of 20 cm greater in dbh than 'ōhi'a trees without cavities ($P < 0.001$), and cavity trees used by the birds for nesting are about 14 cm greater in dbh than unused cavity trees ($P = 0.04$; Fig. 5). It appears that the birds are tracking the largest 'ōhi'a trees in the forest, a finding further supporting the hypothesis of old-growth forest niche for the 'Ākepa.

There is a similar relationship between tree size and presence of cavity for koa. Within the set of large koa trees sampled, trees with cavities were an average of 35 cm larger in dbh than non-cavity koa trees ($P < 0.001$; Fig. 6). However, unlike 'ōhi'a, there was no significant difference in the size of koa trees with cavities that were used and those with cavities that were unused ($P = 0.80$; Fig. 6). The birds do not appear to be tracking the largest koa trees in the forest.

The difference between 'ōhi'a and koa may be compared directly. Within the inventory area, there were 48 'ōhi'a and 33 koa trees with cavities. Although the proportions of use of these trees by the birds are not significantly different ($P = 0.72$), within the limited sample of 15 trees used, the direction favors 'ōhi'as (0.21) rather than koas (0.15). This, plus the tracking of large 'ōhi'a trees, is consistent with the dependence of the bird on 'ōhi'a rather than koa in its distribution.

Both 'ōhi'a and koa trees varied in the height of forking below and above the 1.3 m height of dbh. A mixture of monopodial and sympodial large trees is a characteristic of the forest. Approximately 50% of the large 'ōhi'a trees in each of the size classes in the inventory area are monopodial (overall 52%; Fig. 7). More koa are monopodial (79%; $P < 0.001$), suggesting that large 'ōhi'a trees have a more variable growth form than large koas, presumably reflecting differences in apical dominance between the species. In my random sample of 164 'ōhi'as, 80% of the trees were monopodial. However, of the 28 trees in this sample with dbh > 60 cm, 64% were monopodial, statistically indistinguishable from the area sample ($P = 0.17$). An interesting finding is that within the random sample of 'ōhi'a, trees < 60 cm dbh were more likely to be monopodial than trees > 60 cm dbh (84% versus 64%; $P = 0.034$). As will be discussed below, this may reflect differences in early growth conditions for the trees of different ages.

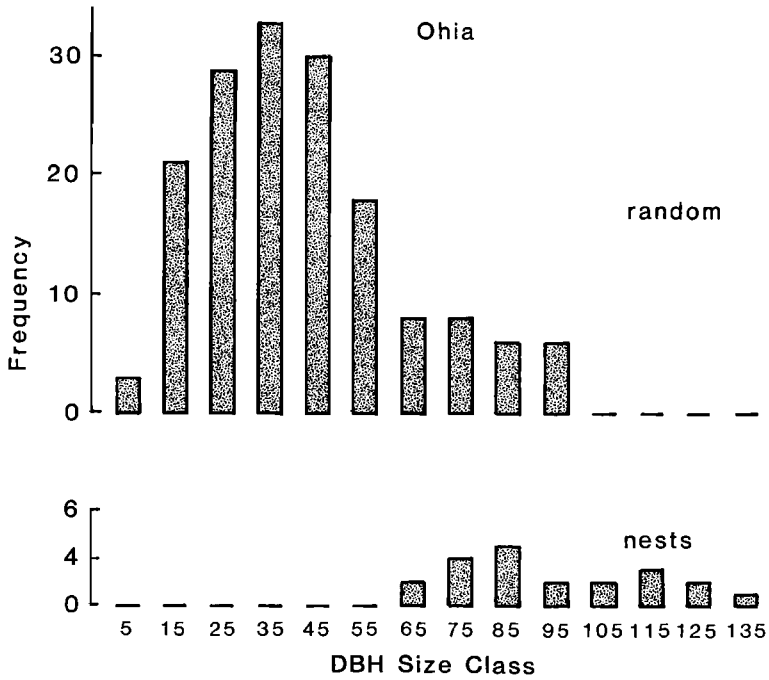


FIGURE 3. Diameter at breast height (DBH size class in cm, midpoint shown) of ‘ōhi‘a trees sampled throughout the study area (upper) and those used as nests in the same area (lower).

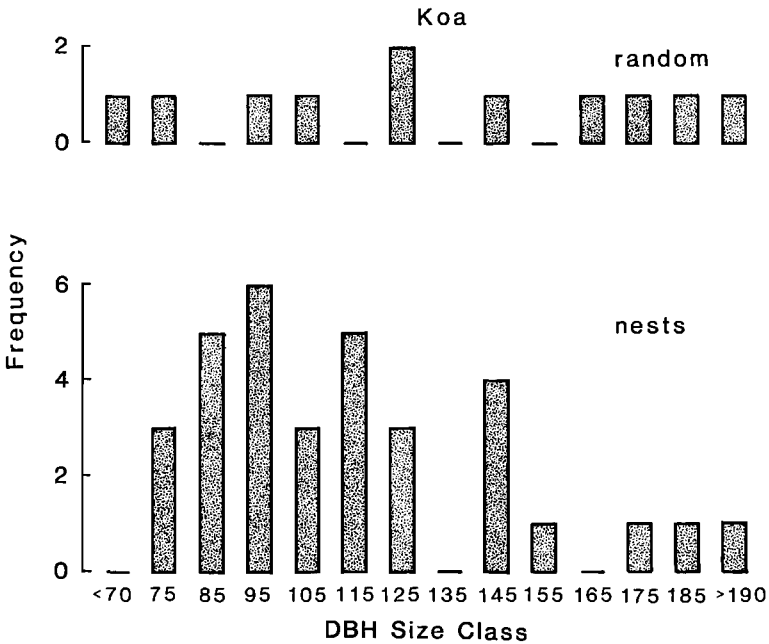


FIGURE 4. Diameter at breast height (DBH size class in cm, midpoint shown) of koa trees sampled throughout the study area (upper) and those used as nests in the same area (lower).

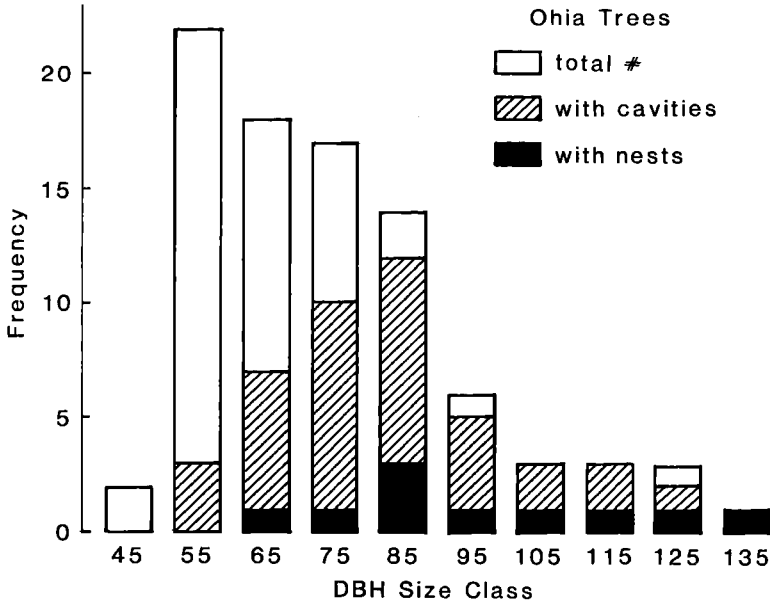


FIGURE 5. Diameter at breast height (DBH size class in cm, midpoint shown) of large ‘ōhi‘a trees within inventory area. Height of the bar represents the total number of trees. Diagonal hatching is overlaid on that bar to show the trees with cavities, and the solid fill is further overlaid to show the trees with cavities that were used by Hawai‘i ‘Ākepa.

Sympodial ‘ōhi‘a trees, whose diameter was measured below the bifurcation, were not significantly smaller than monopodial ‘ōhi‘a trees within the inventory area ($P = 0.51$; Figs. 3, 5). However, only 2 of the 83 sympodial trees had cavities visible to researchers, in contrast to the 46 of 89 monopodial trees in the same area

(Fisher exact test, $P < 0.001$). Among the 21 ‘ōhi‘a trees used by ‘Ākepa in the entire study area, only one was sympodial, which was consistent with the rarity of cavities in trees of this form.

The situation with koa is more complex. Sympodial koa trees in the inventory area were an

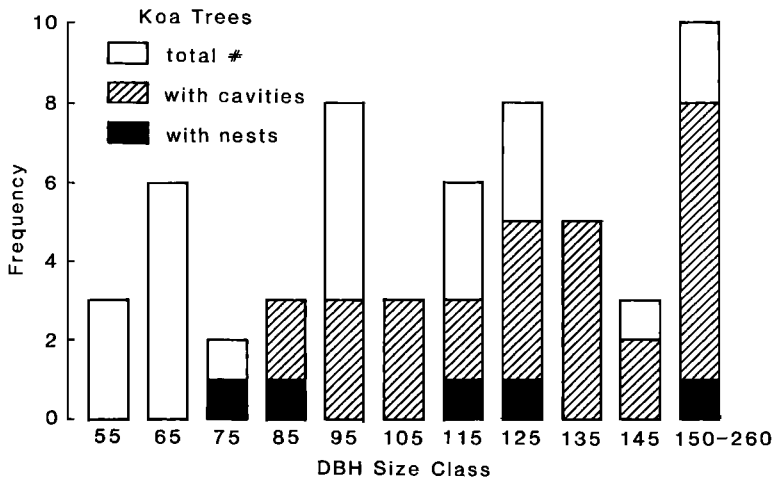


FIGURE 6. Diameter at breast height (DBH size class in cm, midpoint shown) of large koa trees within inventory area. Height of the bar represents the total number of trees. Diagonal hatching is overlaid on that bar to show the trees with cavities, and the solid fill is further overlaid to show the trees with cavities that were used by Hawai‘i ‘Ākepa.

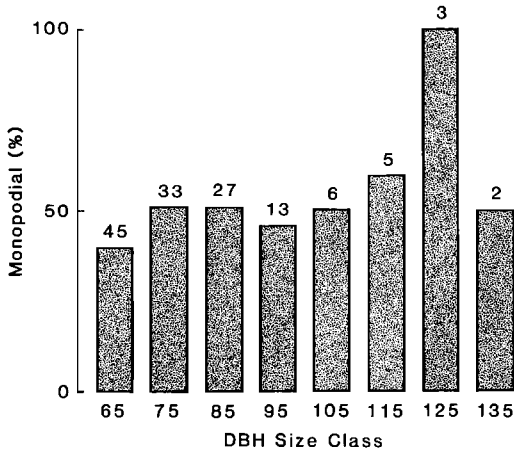


FIGURE 7. Proportions of ‘ōhi’a trees of different size (midpoint shown) that were monopodial within the inventory area. (DBH is diameter at breast height.)

average of 33.1 cm greater in diameter than monopodial trees ($P = 0.015$). In addition, 10 of 12 (0.83) sympodial koa trees had cavities in contrast to 23 of 45 (0.51) monopodial trees (Fisher exact test, $P = 0.055$). Among the 33 koa trees used by ‘Ākepa in the entire study

area, only 2 were sympodial. A higher proportion of sympodial koa trees than sympodial ‘ōhi’a trees had cavities (10 of 12 koa versus 2 of 83 ‘ōhi’a with cavities in the inventory area; Fisher exact test, $P < 0.001$), indicating that sympodial koa trees with cavities were underutilized by the birds (Fisher exact test, $P < 0.001$).

‘Ōhi’a and koa trees differ in the pattern of growth form, size of tree, and presence of cavity. The relationship among these variables seems to be based on the size of the forks in the sympodial trees. Only rarely, even in the largest sympodial ‘ōhi’a trees, are forks of diameter >63 cm (Fig. 8), the diameter of the smallest monopodial trees with cavities used by ‘Ākepa. It appears then that the growth form of the tree, determined as height of first forking, influences the likelihood that a cavity will develop. Sympodial ‘ōhi’a trees appear to be larger than they really are with respect to cavity formation, since the forks available for cavity formation are smaller than the measured diameter on the short main trunk. In contrast, as documented above, sympodial koas are larger than monopodial koas, and all sympodial koas had at least one fork that fell within the size range of monopodial koas with cavities ≥ 70 cm in diameter.

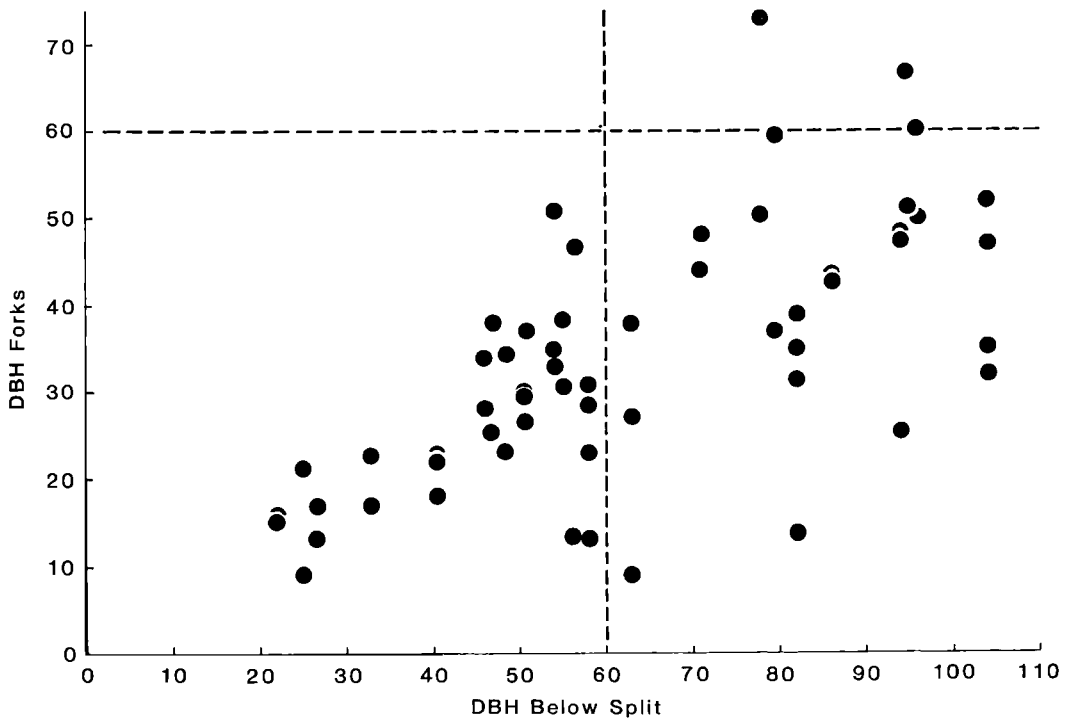


FIGURE 8. Diameter of forks (cm) in relation to size of trunk below the first fork (cm) in sympodial ‘ōhi’a trees. (DBH is diameter at breast height.)

TABLE 2. PORTIONS OF TREE OF 71 CAVITIES USED AS NEST-SITES

Location of cavity	Proportion
Branch	0.48
Trunk	0.24
Fork	0.15
Snag	0.10
Unknown	0.03

Cavities in trees used by the Hawai'i 'Ākepa were found in a variety of locations (Table 2). Almost one-half of cavities used were in branches and approximately one-quarter were in primary trunks, reflecting the rarity of cavities in forks and the rarity of snags. Parts of trees with cavities used must generally be >20 cm in diameter, based on median and first quartile displayed in Figure 9.

Particularly relevant is the size of branches with cavities. There is a significant relationship between the size of the branch (or snag) with cavities and the size of the primary trunk of the tree for 39 trees (linear regression, $P = 0.015$; Fig. 10). While larger trees have larger branches, absolute branch or snag size appears to be important since over two-thirds of the cavities used were in parts with a diameter >20 cm ($P = 0.005$).

DISCUSSION

Large 'ōhi'a and koa trees are clearly part of the ecological niche of the Hawai'i 'Ākepa. The large trees that have cavities are rare and for

'ōhi'a are almost exclusively monopodial in growth form. Here I will relate these findings to more general issues associated with the distribution and abundance of the Hawai'i 'Ākepa, attempt to identify characteristics of forests with large 'ōhi'a and koa trees that could be considered old-growth, and identify problems in regeneration of old-growth 'ōhi'a-koa forest based on variation in growth form of 'ōhi'a.

DISTRIBUTION AND ABUNDANCE OF THE HAWAI'I 'ĀKEPA

The dependence of the Hawai'i 'Ākepa on large trees with cavities can be considered the Big Tree Hypothesis concerning the distribution and abundance of the bird. The hypothesis has the potential to explain otherwise puzzling aspects of these phenomena both historically and recently. Early naturalists reported that the bird had a spotty distribution on the island, but that it was locally common in certain areas (Wilson and Evans 1890–1899, Rothschild 1893–1900, Henshaw 1902a, Perkins 1903). According to the Big Tree Hypothesis, the areas in which the bird was locally common were forests with large trees with cavities. On active volcanoes such as Mauna Loa, Kīlauea, and Hualālai (Fig. 1), big trees would most likely be present in areas that had escaped lava for extensive periods of time, and also escaped fire and high winds. Kohala and Mauna Kea (Fig. 1), as inactive volcanoes, would have consistently older substrates free from lava. However, geographical heterogeneity of tree size could still be generated by tree fall

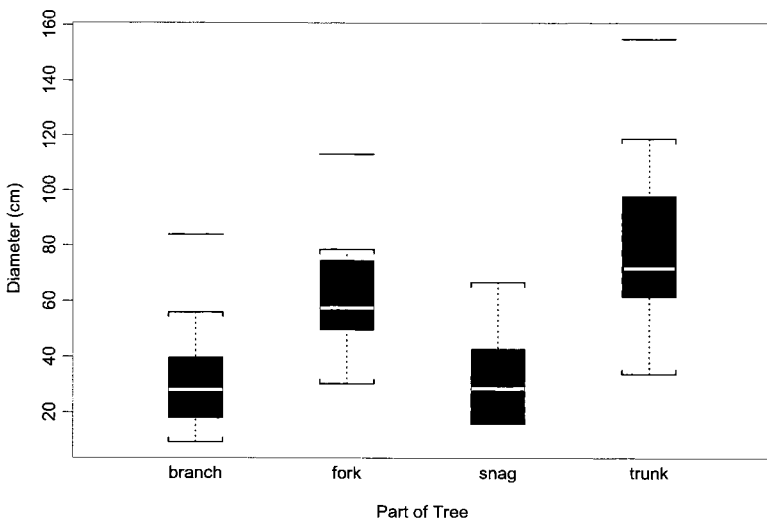


FIGURE 9. Diameter of part of tree with cavity that was used by Hawai'i 'Ākepa. Horizontal white line is the median, top and bottom of shaded box represent first and third quartiles. Brackets show range. Isolated black lines represent outliers.

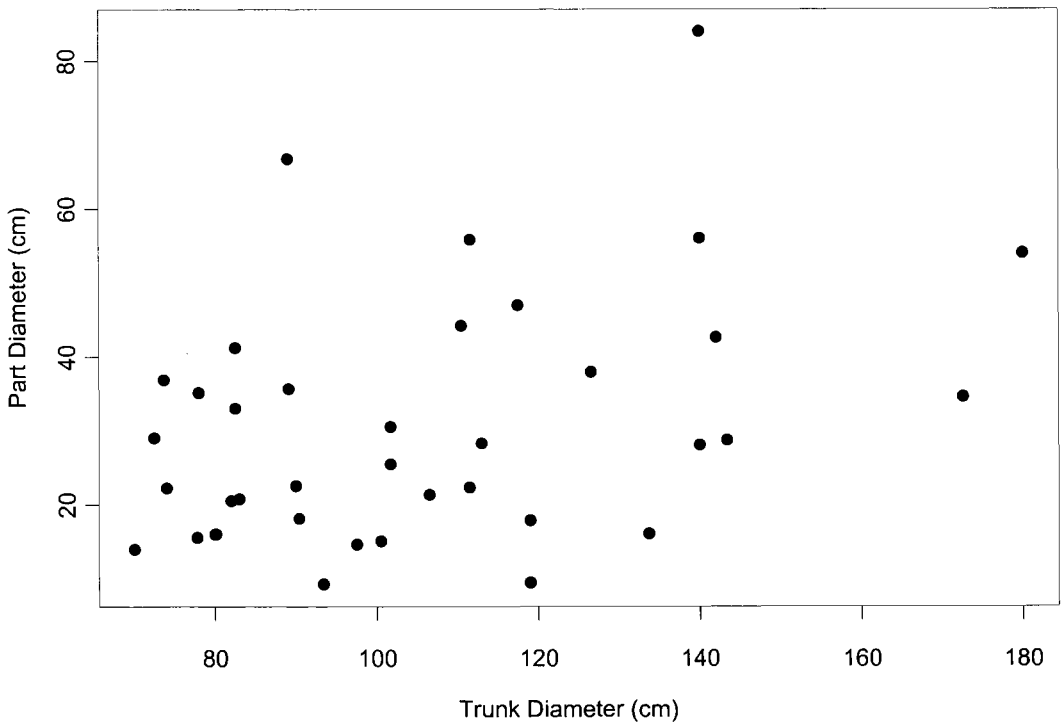


FIGURE 10. Diameter of branches and snags with cavities used by Hawai'i 'Ākepa in relation to size of trunk (diameter at breast height).

associated with high wind, torrential rains, and perhaps fire.

An attempt to document historical forest structure is difficult at best with species with growth rings from which ages of standing trees can be estimated (Harper 1977). The lack of distinct annual growth rings in 'ōhi'a and koa, as in many other tropical trees (Kozlowski and Pallardy 1997b), makes it even more difficult. However, both large 'ōhi'a and koa trees become nursery logs when they fall over and begin to decompose (Scowcroft 1992). In principle, it would be possible to document the presence of large trees in an area in the past by including dead nursery logs as well as live specimens, and including large trees that show evidence of past nursery logs through their stilt-like roots arranged around an opening. An interesting project in historical biogeography would be to determine if the distribution of large trees (standing and as logs) was as spotty as the distribution of the bird.

The Big Tree Hypothesis can also account for current patterns of distribution and abundance. For example, Scott et al. (1986) identified a series of distributional anomalies for the Hawai'i 'Ākepa. These were defined as unexpectedly low abundance in areas with presumably the ap-

propriate tree biomass. Such anomalies were identified as elevational and lateral. Elevational anomalies, where the birds were rare in suitable habitat at lower elevations, could be generated by less visible factors such as *Culex* mosquitoes as vectors and pathogens such as malaria (*Plasmodium*) and poxvirus (*Poxvirus avium*) (Scott et al. 1986). An increasing body of evidence supports this interpretation of elevational anomalies since both the mosquito and *Plasmodium* fare better at lower and warmer elevations (van Riper et al. 1986, Atkinson et al. 1995, Jarvi et al. *this volume*). However, disease is much less likely as an explanation for the lateral anomalies within an elevation. A specific prediction of the Big Tree Hypothesis is that large trees will be rarer where the Hawai'i 'Ākepa is rarer, consistent with other studies of hole-nesting birds (von Haartman 1971).

The Kīlauea Forest Reserve is the only other site on the island of Hawai'i where both bird densities and tree sizes have been measured. Consistent with the Big Tree Hypothesis, 'Ākepa densities there were lower than at Pua 'Ākala during the Hawai'i Forest Bird Survey (Scott et al. 1986), and sizes of 'ōhi'a and koa reported in Cooray and Mueller-Dombois (1981) do not achieve those documented here. The possibility

exists that the lower 'Ākepa densities at the Hakalau tract of Hakalau Forest National Wildlife Refuge, documented by Hart (*this volume*), may be associated with lower densities of large trees.

OLD-GROWTH FOREST AND CAVITIES

Habitat quality and critical resources are fundamental aspects of management. Given the attention that old-growth forests have received in the journal *Conservation Biology* during the last 10 years, it is pertinent to consider the forest at Pua 'Ākala as potentially indicative of old-growth in Hawai'i. While the focus on old-growth will be with respect to the Hawai'i 'Ākepa, it is also relevant to note a general correlation in distribution and abundance between the 'Ākepa and other endangered birds of 'ōhi'a-koa forest (Scott et al. 1986). This suggests that old-growth forests may be important to endangered forest birds such as Hawai'i Creeper (*Oreomystis mana*) and 'Akiapōlā'au (*Hemignathus munroi*). While the Hawai'i 'Ākepa depends on large trees for nest sites, it is possible that the bark of large trees may support more arthropods for the Hawai'i Creeper and the wood more insects for the 'Akiapōlā'au than that of smaller trees. At minimum, large trees provide larger patches of foraging substrate that could reduce travel costs of foraging birds.

There are two approaches to defining old-growth forest. The process approach is based on stand development (Oliver and Larson 1996). Events since the last major disturbance are the key in distinguishing transitional old-growth and true old-growth. There may be relic large trees that germinated before the last major disturbance. Stands that still contain such trees, with younger trees growing upward, could be considered transitional old-growth. In contrast, with sufficient time, the relic large trees may have germinated after the last major disturbance and the entire stand would consist entirely of trees that grew upward from beneath. This is considered true old-growth. While much work has been done on stand development of 'ōhi'a and koa on younger substrates (Mueller-Dombois 1987), it is impossible to know the conditions under which the large 'ōhi'a trees at Pua 'Ākala germinated relative to a major disturbance. However, charcoal from underneath lava flows in the region has been dated at approximately 5,000 years (Wolfe et al. 1997). Volcanic rocks closer to the summit have been aged between 65,000 to 4,000 years ago (Wolfe et al. 1997). At least with respect to geological events, there has been sufficient time for true old-growth conditions to occur.

The second approach to defining old-growth

forest is based on structure (Oliver and Larson 1996). Criteria include many large, old trees, often at a wide spacing; standing dead trees as snags; large logs on the ground; and long time free from human disturbance (Franklin and Waring 1979; Franklin et al. 1981, 1986). Pua 'Ākala has all of these characteristics but with human disturbance. Logging, or clearing and burning for cattle ranching, has occurred more outside of the forest than inside. Disturbance inside the forest is due primarily to the direct effects of cattle. As herbivores, cattle have a major impact on the understory and regeneration but little impact on established trees. The time scale of disturbance by cattle, 100 years, has not been long enough to modify the structure of the emergent canopy. Studies of 'ōhi'a (Porter 1973) and koa (Spatz and Mueller-Dombois 1981) growth indicate that the large emergent canopy trees are much older than 100 years. Also, cattle would have no effect on the presence of large fallen logs, which are included in the criteria of old-growth.

Although not formally recognized by Oliver and Larson (1996), the presence of cavities can also be used as a criterion of old-growth. The association of cavities with very large trees at Pua 'Ākala is consistent with studies in old-growth forests in Australia (Lindenmayer et al. 1993), similar to Hawai'i in lacking an avian excavator. A similar association of cavities with large trees was detected in an unmanaged stand in Europe for cavities that were not formed by woodpeckers (Wesołowski 1989). Cavities have the potential to be a simple way to identify old-growth forests. The definition of old-growth forest in Hawai'i, in relation to cavities, has the advantage that the growth form of 'ōhi'a is implicit as a variable since large sympodial trees have few cavities. This is important because a forest of primarily sympodial 'ōhi'a trees does not provide the specialized niche requirement of the Hawai'i 'Ākepa.

While the age of the Pua 'Ākala forest is not known, several lines of evidence suggest that 'ōhi'a trees with diameters of >1 m are extremely old. Porter (1973), based on size specific growth studies of 'ōhi'a on younger substrates and primarily lower elevations, estimated that 'ōhi'a trees that were 65 cm in diameter were 300 years old. Trees that are 1 m and larger would be considerably older given the sigmoidal growth curves of trees with increasingly slower growth after the inflection point (Evans 1972). The disproportional use of the largest 'ōhi'a trees by Hawai'i 'Ākepa may involve trees that are surprisingly old. For example, some trees in mountain ash (*Eucalyptus regnans*) forests in Australia may not develop cavities large enough

for vertebrates until they are over 400 years old (Lindenmayer et al. 1991b). Slow growing 'ōhi'a may require a much longer time.

Why do cavities form primarily in larger and older trees? Cavities form as a tree isolates a wound through compartmentalization of wood decayed by microorganisms (Shigo 1984, 1991; Mackowski 1984). Although some microorganisms can gain entry through injuries to sapwood (Adaskaveg and Ogawa 1990), most access is through wounds exposing the heartwood (Carey and Sanderson 1981). Branches large enough to form heartwood may themselves be damaged and decay may then proceed into the heartwood of the trunk. This may be the key reason why older and larger trees are more likely to have cavities. Such trees may be the only ones with branches sufficiently large to have heartwood. An element of chance is also involved because a sufficiently large branch must break to form a cavity. The increasing association of cavities with age or size of trees can represent the greater exposure to rare events of older trees. The rough holes associated with cavities may represent cases where the smaller unit was ripped off the larger unit, along with part or all of the trunk collar (Shigo 1991; Fig. 2). The smooth holes may represent cases where the smaller unit was broken and subsequently rotted off the larger unit, leaving the trunk collar largely intact. The ontogenetic difference between smooth and rough cracks, involving wounded wood on the borders (Shigo 1991; Fig. 2), is less clear.

Under this model, the rarity of cavities among the sympodial trees is based on the relatively small size of the forks. The short main trunk of sympodial trees might have sufficient heartwood for formation of cavities, but each fork may only have the heartwood of a smaller monopodial tree in which cavities are rare or nonexistent. In addition, the short main trunk does not have branches that could break to initiate formation of cavities. A detailed comparison of forks and their branches versus a monopodial tree of the same diameter and its branches might reveal constraints on growth of sympodial trees relevant to cavity formation.

REGENERATION OF OLD-GROWTH 'ŌHI'A-KOA FOREST

The large 'ōhi'a trees used for nesting by 'Ākepa at Pua 'Ākala are old specimens. Their replacement involves regeneration at two different scales of time and size. The first involves the growth of smaller trees, of monopodial growth form, into the size classes in which cavities are likely to develop. The second involves regeneration of monopodial specimens at the seedling stage. There are problems at each scale that may

be involved with human disturbance of the forest.

The large 'ōhi'a (and koa) trees used by the birds for nesting appear to be falling at a faster rate than they are being replaced. The Pua 'Ākala Tract experiences high winds that can exceed 145 km/hr during winter storms. Some trees fall during this time, perhaps more than in pristine forest because exposed trees may now be more vulnerable to wind. Of the 54 nest-site trees, 9 (16.7%) are no longer standing. This mortality has occurred during a 7-year period. At the rate of 0.3 cm growth in diameter per year, the maximum identified by Porter (1973) for trees growing on loamy soil at 1,200 m elevation, a tree would grow about 2 cm during that time (perhaps less at the 1,900 m elevation at Pua 'Ākala and if the growth rate decreases with size). If cavities take a long time to develop after a suitable accident that forms a wound, it is unlikely that there were 9 monopodial trees that had no cavities at the beginning of the study but developed cavities within the seven years to replace the fallen trees. While more effort is required to identify the balance between cavities gained and cavities lost over a given time period, it is clear that a cavity can be lost more quickly due to disturbance than can be gained through growth of trees.

A related concern is that existing cavities become unsuitable even though the tree is still standing. This has happened at least three times where we could observe deterioration of the cavity over time. Thus the balance between cavities gained and cavities lost must include loss of cavities within trees still standing as well as fallen trees.

Replacement of large old trees with cavities ultimately requires regeneration of trees of appropriate growth form. 'Ōhi'a has pseudodichotomous branching (Porter 1973), meaning that forking occurs when the apical meristem aborts or is injured, thereby releasing dominance over the lateral buds which then develop into shoots that represent the two forks (Bell 1991). The height of first forking probably reflects the actual height of the event since no trees, among thousands inspected, have been found with an intermediate form of one fork lost and one present below the first intact forking. The form would be evident by the remaining fork forming an angle to the trunk below it. Growth form appears to be set early in the growth of a seedling. Thus the different proportions of monopodial and sympodial trees in larger and smaller size classes found in this study suggest that environmental conditions for growth were different for the trees when they were seedlings.

Direct and indirect effects of cattle ranching

have consequences for regeneration of trees. The effect most recognized is mortality of seedlings through herbivory (Stone 1985). However, there are two consequences related to growth form that do not involve mortality. One of these is herbivory that involves removing the apical bud of seedlings. This action releases dominance over the lateral buds, thereby promoting sympodial growth form. There are large numbers of 'ōhi'a seedlings on nursery logs within or at the margins of pastures with a dbh of 0.5 to 2 cm and repeated forking beginning at a height of 10 cm or less. While these seedlings are now the most conspicuous indicator of regeneration, the results of my study indicate that these are unlikely to develop cavities when they reach large size.

The second consequence of cattle ranching, without seedling mortality, is that seedlings are regenerating now in the presence of more light. A significant role of gap dynamics for regeneration within an otherwise intact forest has been identified (Cooray and Mueller-Dombois 1981, Burton and Mueller-Dombois 1984). However, the size of gaps associated with human clearing of forest for cattle ranching, and the destruction of the understory by herbivory, have jointly resulted in seedlings exposed to more light than expected in natural gaps caused by tree falls. Even though cattle have been eliminated at Pua 'Ākala for 10 years, there is a continuing edge effect between pasture and forest and lesser midstory within forests. Light is considered one of the important variables that influences apical dominance over lateral buds at the same level (Brown et al. 1967; Kozłowski and Pallardy

1997a,b). My observations of young 'ōhi'a seedlings indicate that over 90% have forked by the time they reach a height of 0.25 m. It is difficult to identify among existing seedlings those that may become the monopodial giants whose height of first forking can occur as high as 20 m.

Based on this study, regeneration of old-growth 'ōhi'a-koa forests involves growth form as well as presence and size of trees. One of the great challenges to managing restoration and regeneration in disturbed areas is how to mimic the conditions that have produced the monopodial giants in the past. The future of the endangered Hawai'i 'Ākepa depends on implementation of appropriate management of regeneration over wide areas at upper elevations. Provision of artificial cavities may be an appropriate stop-gap management technique. At least five different pairs of birds have used such cavities at Pua 'Ākala and nested successfully. Artificial cavities may be essential if the birds are to persist at high density despite loss of cavity trees and slow regeneration of new ones.

ACKNOWLEDGMENTS

I dedicate this paper to Doug Ackerman, architect of Hakalau Forest Biological Field Station of the University of Hawai'i, with whom I have worked closely for several years. Our mutual interests in wood extend from strength and beauty for construction and finish work to conservation of forests and the animals that depend on trees. I thank J. Lepson for finding most of the 'Ākepa nests, and for helping me document the characteristics of trees used by the birds. P. Hart, S. Fretz, J. Rohrer, M. Burt, and J. Bennett helped gather data in both the inventory and sampling areas. Thanks also to S. Monden for most of the artwork, and to J. Lepson, S. Conant, and J. M. Scott for helpful comments.