

THE FOOD HABITS OF POLYNESIAN PIGEONS AND DOVES: A SYSTEMATIC AND BIOGEOGRAPHIC REVIEW

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Abstract. Pigeons and doves (Aves: Columbidae) are represented in Polynesia by at least 30 species, of which nine are extinct and eight are endangered. Detailed, systematically collected data on diet (frugivory, granivory, omnivory) are lacking for most species of Polynesian columbids. Declines in species richness, taxonomic diversity, geographic distribution, and population size of columbids have occurred in response to human activities over the past 3000 years. We suspect that these declines probably have limited the inter- and intra-island dispersal of seeds from plants eaten by columbids, especially various forest trees. Except for perhaps seven species (*Didunculus strigirostris*, *Ptilinopus perousii*, *P. porphyraceus*, *P. narotongensis*, *P. insularis*, *Ducula pacifica*, *D. larvans*), the largely anecdotal dietary information now available is not sufficient for conservation purposes (e.g., translocation). This situation can be rectified only by conducting new field research, for which we offer recommendations. Accepted 05 January 1999.

Key words: Columbidae, pigeons, doves, islands, Polynesia, frugivory, granivory, tropical forests, extinction, conservation.

INTRODUCTION

Pigeons and doves (Columbiformes: Columbidae) constitute one of the most widespread, conspicuous, and species-rich families of landbirds on tropical Pacific islands, but have suffered much extinction since human settlement of Oceania. The extant populations and species are the residues of millennia of human impact (Steadman 1995, 1997). Since the literature suggests that pigeons and doves are important dispersers of plants, their continued survival may be crucial for maintaining some semblance of a natural functioning of ecosystems in island forests. Little is known, however, about the autecology of these birds.

As a first step in addressing the dearth of knowledge about Polynesian pigeons and doves, we review and synthesize what is known of the food habits of the 21 extant species and discuss this information in the context of anthropogenic extinction and forest ecology on Pacific islands. Finally, we offer recommendations for the study and conservation of Polynesian columbids and their ecosystems.

This paper covers both East Polynesia (Pitcairn, Marquesas, Tuamotu, Society, Austral, and Cook Islands) and West Polynesia (Niue, Tonga, Samoa, Wallis and Futuna, Fiji, Tokelau, and Tuvalu; Fig. 1).

Easter Island, the Hawaiian Islands, and New Zealand are faunally distinct (Steadman 1997) and are excluded. Evidence of indigenous columbids is lacking on Easter Island, although the prehistoric record of landbirds there is limited (Steadman 1995). With an extensive prehistoric record of landbirds from the Hawaiian Islands (Olson & James 1991), the natural absence of columbids there seems well established. New Zealand and its satellite islands, which are temperate rather than tropical, sustain a single native columbid today (*Hemiphaga novaeseelandiae*) and there is no evidence for extinct species of columbids in the extensive fossil record of those islands.

MATERIALS AND METHODS

To present the diet information objectively, we primarily use quotes from published sources, presented in chronological order. We also include our own unpublished observations. While many of the statements quoted below are based on observations or analyses of crop and stomach contents, other statements evidently are not based on original data. Thus, from major works such as Goodwin (1970), duPont (1976), Watling (1982), and Pratt *et al.* (1987), we do not quote statements that seem clearly to be secondary. Notes on captive geese are not included. If no locality is given, the quoted statement was likely intended to pertain throughout the range of

the species. For wide-ranging species we include data from non-Polynesian islands as well. Sequence and nomenclature of species follow Pratt *et al.* (1987) and Steadman (1997). Details of columbid distribution within island groups are found in duPont (1976), Pratt *et al.* (1987), Steadman (1997, 1998) and Steadman & Freifeld (1998). An Appendix lists scientific and common names of all plants mentioned in the text. The Appendix is useful in presenting currently accepted names alongside the many variations on these names that appear in the quotes.

SPECIES ACCOUNTS

Columba vitiensis, White-throated Pigeon

"stomach contained the seeds of the little red pepper so common on shore (chili)" – Fiji (Finsch 1877: 736–737).

"lives exclusively on the capsicums when these are to be had. Otherwise the Pigeon eats the clustered fruit of the Yaga tree (*Dacrydium elatum*), which grows out of the trunk and wood of the larger branches, called 'Fijian figs,' and the fruit of an introduced solanaceous plant. When rice is ripe (March to May) these birds, if their favourite diet is not at hand, invade the paddy fields and eat the crops. In several stomachs I found other fruits and seeds; in one instance many hard black seeds were present, mixed with gravel." – Fiji (Wood 1926: 118).

"hard-seeded fruit. The gizzard is very muscular, as in *C. livia*, not a soft sac as in *Ducula*" – Solomon Islands (Cain & Galbraith 1956: 124).

"Feeding mainly on low scrub-like bushes, its chief food is the fruit of the Solanum weed and chillis." – Fiji (Mercer 1966: 9).

"berries and seeds (wild eggplant – *Solanum torvum* – Swartz, mock tobacco – *Solanum mauritianium* – Scop, etc.)" – New Caledonia (Hannecart & Letocart 1980: 83).

"hard-seeded fruits" – Solomon Islands (Hadden 1981: 56).

"Mainly small fruits and berries, especially those of Prickly Solanum *Solanum torvum*, and wild chillis. May also be found feeding on the ground on seeds and young shoots" – Fiji, Samoa (Watling 1982: 78).

"small fruit, leaf buds and shoots, enrolled fern leaflets, snails and caterpillars, coconut from copra drying racks" – Fiji (Clunie 1984: 38).

"forages in trees for unripe fruits or on the ground for seeds" – New Guinea (Beehler *et al.* 1986: 100).

"wide variety of berries and other small fruits, small nuts, seeds and tender shoots. ... the introduced solanum shrub *Solanum torvum* and especially the introduced chilli bush *Capsicum frutescens*. ... fruit in *Olea paniculata* trees" – Vanuatu (Bregulla 1992: 182).

Gallicolumba erythroptera, East Polynesian Ground-Dove

"seeds more than fruit" (Bruner 1972: 69).

"Trois contenus stomacaux prélevés à Maturéi-Vavao permettent de penser que le régime alimentaire des oiseaux de cette localité ne comprend que des végétaux (graines et débris divers). A Marutea de Sud, les oiseaux se nourrissent de graines de *Tournefortia* et de *Morinda citrifolia* (Seurat 1903)." – Maturéi-Vavao, Marutea, Tuamotu Islands (Lacan & Mougin 1974: 267).

Gallicolumba rubescens, Marquesas Ground-Dove

"insects and seeds" (Bruner 1972: 84).

"Il se nourrissait en petits groupes. On l'a vu manger des graines de *Pisonia* sur Fatuuku." – Fatu Huku (Holyoak 1975: 348).

"Les 2 premiers couples fréquentaient un biotope de falaise avec des peuplements éparpillés de *Pisonia*. Les oiseaux, le plus souvent à terre, se sont toutefois régulièrement perchés dans les arbres dans des positions d'observation ou pour s'y nourrir (sur les inflorescences). Ils semblaient surtout rechercher des graines dans les touffes de la plante grasse." – Fatu Huku (Seitre & Seitre 1991: 25).

Gallicolumba stairi, West Polynesian Ground-Dove

"seeks its food entirely on the ground" – Fiji (Layard 1875a: 438).

"the gizzard contents are generally small seeds. The ventriculus is provided with very thick, muscular walls" – Fiji (Wood 1926: 119).

"feeds on the ground" – Samoa (Ashmole 1963: 14).

"A specimen had its crop filled with seeds up to at least ten millimetres in length, most apparently having been broken by the bird's bill." – Viti Levu, Fiji (Holyoak 1979: 10).

"seeds, fruit, buds and young leaves and shoots taken on the ground or in the substage" (Watling 1982: 80).

"fallen fruits of *Macaranga harveyana*" – Ofu, American Samoa (Amerson *et al.* 1982b: 69).

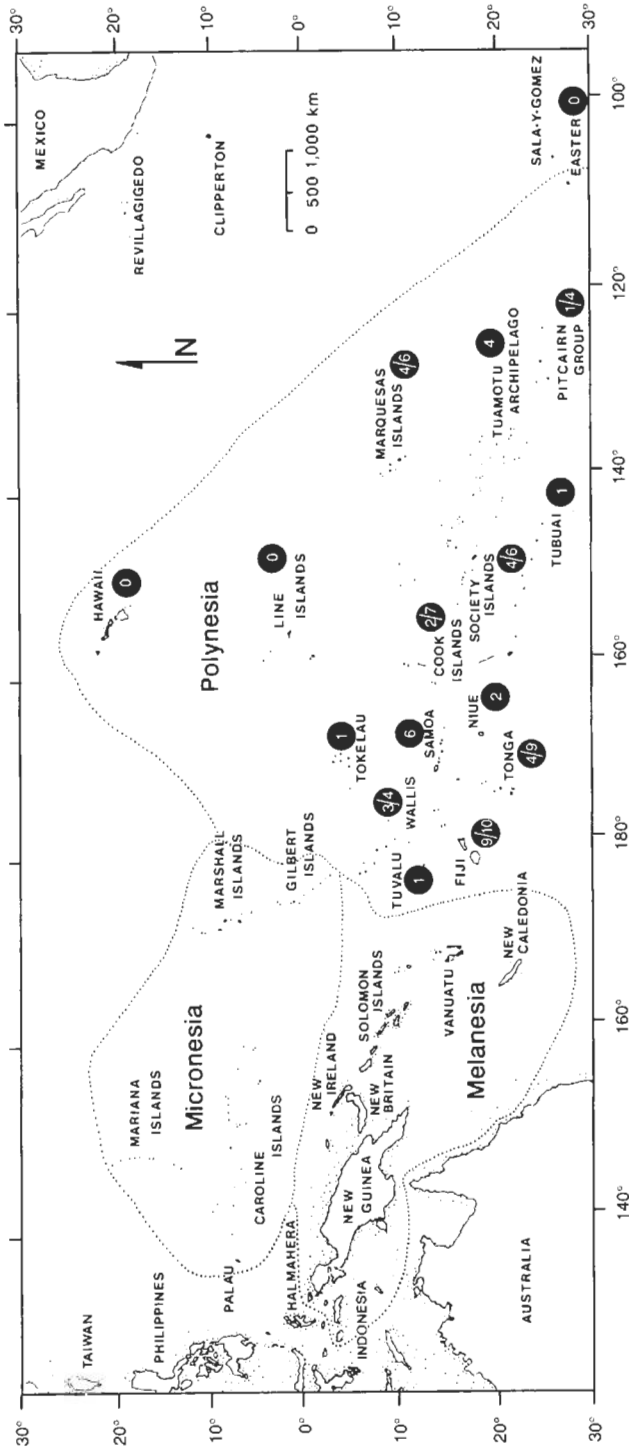


FIG. 1. The Pacific Ocean, showing major island groups. Numbers in black circles represent living (numerator) and living + extinct (denominator) columbid species in each Polynesian island group.

"on forest floor, eating seeds, small fruit, buds, snails and insects ... in small trees in undergrowth on small fruit and caterpillars" – Fiji (Clunie 1984: 42).

"Quatre observations d'oiseaux se nourrissant sur le sol dans des sous-bois de forêts secondarisés" – Alofi, Wallis and Futuna (Guyot & Thibault 1987: 238).

"Although food is mainly taken on the ground (fallen fruits of [*Ficus obliqua*] have been recorded as food items), a few were seen feeding in *Tarenna sambucina*, a common small tree of disturbed habitats, while one was observed feeding in a large [*F. obliqua*]." – Late, Tonga (Rinke 1991: 141).

Didunculus strigirostris, Samoan Tooth-billed Pigeon "berries and wild fruits, their favorite food being the mountain-plantain" (Ramsay 1864: 99).

"plantains, and is partial to the fruit of the soi, a species of Dioscorea, or yam" (Stair 1897: 300).

"feeds on the ground" (Ashmole 1963: 14).

"a ground feeder, being especially fond of the roots of the wild yam, or soi, *Dioscorea bulbifera*" (Muse & Muse 1982: 95).

"particularly on nutmegs *Myristica* sp., and other fruits of *Dysoxylum* sp." (Watling 1982: 84).

Fruits of *Dysoxylum maota*, *D. samoense*, and *D. huittii*; also, fruits of *Rhus taitensis* and *Faradaya powelli* (Beichle 1987).

Seeds of *Dysoxylum* spp. (Beichle 1991).

Ptilinopus perousii, Many-colored Fruit-Dove "favorite food ... is seeds of the Banian; but it will swallow fruits of very large dimensions; I have, in fact, seen hard seeds bigger than nutmegs taken from its crop. ... berries of the Banian tree, the *Loxanthus*, or rat-mistletoe, and the unripe seeds of the mavu tree (*Euphorbia*)" – Fiji (Layard 1875a: 436).

"Its principal habitat is the indigenous banyan (*Ficus prolixa*)" – Western Samoa (Whitmee 1975: 441).

"entirely frugivorous, eating the berries of many trees, especially the small green and yellow fruit of the native 'Ndrau'. I have examined four gizzards of this bird and found in each instance five large and an equal number of small, irregular, conical, gristle-like ridges ... well adapted to the grinding of the rather hard, unyielding pea-like seeds often found in the stomach." – Fiji (Wood 1926: 113–114).

"seems to prefer the fruit of the noso'oi tree [*Cananga odorata*]." – Upolu, Western Samoa (Yaldwyn 1952).

"lives in flocks and feeds in fruiting trees." – Samoa (Ashmole 1963: 14).

"very partial to fruiting fig trees" – Fiji (Morgan & Morgan 1964: 163).

"favourite food of the flock in the Suva Gardens, is the fruit of the weeping fig." – Viti Levu, Fiji (Mercer 1966: 6).

"fruits and berries taken from the branches. The fruits of the banyan *Ficus prolixa* ... other fruits including those of the introduced African Tulip Tree [*Spathodea campanulata*]." (Goodwin 1970: 351).

"only an orange fruit of about 4-mm diameter [*Ficus* sp.]; the small seeds from these fruits were voided intact in the faeces." – Taveuni, Fiji (Holyoak 1979: 9).

"fruit of the ylangylang tree *Cananga odorata*" – Savai'i, Western Samoa (Reed 1980: 155).

"fruits of the banyan trees *Ficus prolixa* and *F. obliqua*" – Tutuila, American Samoa (Amerson *et al.* 1982a: 65, 1982b: 69).

"small fruits and berries, generally in the canopy. Favourite fruits include *Ficus* sp. (especially the Strangling Fig *F. obliqua*), Makasoi (*Cananga odorata*), *Bischofia javanica* and *Dysoxylum* sp." (Watling 1982: 84).

"small fruit – especially wild fig and banyan fruit; also caterpillars and small insects" – Fiji (Clunie 1984: 46).

"The dominant food plant ... is *Ficus obliqua*, and large aggregations of the birds can be found in fruiting banyans, even in villages. Other food items were the fruits of *Ficus tinctoria* and *Santalum yasi*." – Èua, Tonga (Rinke 1987: 30).

"The small feeding groups we found were all in *Ficus* trees, which are believed to be the 'key' to this species' distribution (D. Blockstein, pers. comm.) ... at least four birds ... foraging in a *Ficus* tree ... at least five birds feeding in a large *Ficus* tree" – American Samoa (Engbring & Ramsey 1989: 52, 53).

"fruit-bearing trees, usually members of the fig family" – Western Samoa (Beichle 1991).

"All records are from large [*Ficus obliqua*] extending beyond the forest canopy." – Late, Tonga (Rinke 1991: 142).

"Four pairs of *P. perousii* occupied two large *Ficus obliqua* trees (two pairs observed foraging in each tree, calling once every few minutes; none of the birds ever left these fig trees during an hour of observation." – Lifuka, Tonga (Steadman 1998: 24).

Thirteen observations (2 June–29 Sept 1995) included 10 birds feeding on *Ficus prolixa* fruit and three on *F. obliqua* fruit. Between 1994 and 1996, *P. peroussii* was not observed to feed on any plant other than these two species of figs. – Tutuila, American Samoa (HBF unpub. data).

During six weeks of observations in 1997, *P. peroussii* fed only on *Ficus obliqua* even though other fruits were available. Birds were highly territorial and drove other species from feeding areas. – Lifuka, Tonga (J. Sailer, unpub. data).

Ptilinopus porphyraceus, Purple-capped Fruit-Dove “various wild berries, some even on the low cotton-bushes” – Samoa (Layard 1876: 495–496).

“the fruit of a tall tree; this fruit is about the size of a large olive and is swallowed entire.” – Upolu, Western Samoa (Nicoll 1904: 61).

“fruits of the fig family” (Mayr 1945: 63).

“feeds high in trees, and appears to be particularly fond of figs.” – Samoa (Ashmole 1963: 13).

“fruits and berries, especially wild figs, taken from the branches” (Goodwin 1970: 352).

“fruits of the ylangylang tree (*Cananga odorata*)” – Savai'i, Western Samoa (Reed 1980: 155).

“mainly of berries picked from the branches of fruiting trees. Individuals were seen feeding of berries of *Ficus prolixa* (Niuean name Ovava) and *Ficus scabra* (Masi). One dove collected on 2 September had six large seeds from *Adenanthera pavonina* (Niuean name Pomea) in its crop.” – Niue (Kinsky & Yaldwyn 1981: 31).

“fruits of many kinds of trees, especially *Ficus*.” – American Samoa (Amerson *et al.* 1982b: 69).

“fruits of *Dysoxylum richii* and *Bischofia javanica*” – Fiji, Tonga, Samoa (Watling 1982: 85–86).

“smallish fruit and caterpillars” – Fiji (Clunice 1984: 44).

“observed [in dry, open *Casuarina* forest] in pockets of low *Ficus* sp., *Premna taitensis*, and *Elaeocarpus tonganus* bush. ... in a large fruit-bearing *Ficus obliqua*” – Niuafo'ou, Tonga (Rinke 1986: 84).

“observed feeding on the fruits of Sandalwood *Santalum yasi*, *Asparagus plumosus*, *Trema orientalis*, *Ficus obliqua*, *F. scabra*, and *F. tinctoria*, *Micromelum minutum*, *Vavaea amicorum*, *Bischofia simplicifolia*, *Cryptocarya hornei*, *Rhus taitensis*, *Grewia crenata*, and *Solanum verbascifolium*. Most of these plants are small trees, bushes, or vines. ... a sub-canopy feeder (Watling 1982), sometimes descending close to the ground to feed in *Lantana camara* bushes. ... occa-

sionally sighted in large fruiting trees, especially in banyans *Ficus obliqua*” – Eua, Tonga (Rinke 1987: 29–30).

“various fruits, especially *Ficus*.” – American Samoa (Engbring & Ramsey 1989: 54).

“*Ficus prolixa* and *Ficus obliqua*” – Western Samoa (Beichle 1991).

“observed feeding on the fruits of [*Ficus obliqua*], *Ficus tinctoria* or *F. scabra*, *Premna taitensis*, and *Scaevola taccada*.” – Niuafo'ou, Tonga (Rinke 1991: 142).

“congregate in fruiting trees (especially *Ficus* spp.)” – Vava'u, Tonga (Steadman & Freifeld 1998: 618).

Thirty-five observations (2 June–29 Sept 1995) included fruit from the trees *Ficus prolixa* (22 obs.), *Cananga odorata* (6 obs.), *Bischofia javanica* (2 obs.), *F. obliqua* (2 obs.), *Pipturus argenteus* (2 obs.), and *Alphitonia zizyphoides* (1 obs.). – Tutuila, American Samoa (HBF unpub. data).

Ptilinopus rarotongensis, Cook Islands Fruit-Dove “fruit from trees and bushes” – Atiu, Rarotonga (Holyoak 1980: 34).

Fruits of *Elaeocarpus tonganus*, *Ficus prolixa*, *Jasminum didymum*, *Pipturus argenteus*; – Atiu (Franklin & Steadman 1991; Table 1 herein).

Ptilinopus insularis, Henderson Island Fruit-Dove “appeared to be feeding on a berry like a crab-apple with a large stone.” (Bourne & David 1983: 241).

“Stomachs (N = 3) contained fruit pulp and intact fruits (*Nesoluma st-johnianum*, *Ixora fragrans*, and another unidentified species).” (Graves 1992: 36).

Among 19 species found to be eaten, “*Procris pedunculata* (Urticaceae) was the major food ... only in September and October was it absent from the diet. During those two months the fern *Phymatosorus* was the plant most frequently recorded in the diet.” “Other plants frequently eaten (>10 observations through the year) were *Myrsine*, *Xylosma*, *Cyclophyllum*, *Psydrax*, *Ixora*, *Timonius*, *Eugenia*, and *Geniostoma*” (Brooke & Jones 1995: 154).

Ptilinopus purpuratus, Gray-green Fruit-Dove “flowers of the vanilla (*Vanilla planifolia*) ... fruit of the Chili pepper and various seeds, including those of the banyan-tree.” – Tahiti (Wilson 1907: 374, 376).

Guava (Curtiss 1938).

“The main tree preferred are the Motoi, *Cananga odorata*, and the guava, *Psidium guajava*. Other trees

Table 1. Food of the two extant columbids in the Cook Islands, based on specimens collected in Sept–Nov 1987. Data presented as % dry weight (rounded to nearest whole number) of digestive tract contents, followed in parentheses by the number of individuals in which the species of plant was represented. I = introduced species. Modified from Franklin & Steadman (1991).

	<i>Ducula pacifica</i>			<i>Ptilinopus</i>
	Atiu N = 5	Mitiaro N = 7	Mauke N = 15	<i>rarotongensis</i> Atiu (N = 8)
<i>Cyclophyllum</i> (= <i>Canthium</i>) <i>barbatum</i>	--	10 (1)	--	--
Rubiaceae; small tree				
<i>Guettarda speciosa</i>	39 (2)	16 (2)	81 (13)	--
Rubiaceae; tree				
<i>Elaeocarpus tonganus</i>	29 (2)	--	--	74 (5)
Elaeocarpaceae; tree				
<i>Ficus prolixa</i>	--	--	--	13 (2)
Moraceae; tree				
<i>Hernandia moerenhoutiana</i>	13 (2)	--	--	--
Hernandiaceae; tree				
<i>Jasminum didymum</i>	18 (1)	4 (2)	14 (2)	3 (1)
Oleaceae; vine				
<i>Myrsine cheesmanii</i>	--	45 (7)	--	--
Myrsinaceae; small tree				
<i>Pipturus argenteus</i>	--	2 (1)	6 (7)	9 (4)
Urticaceae; small tree				
<i>Ceiba pentandra</i> (I)	--	22 (1)	--	--
Bombacaceae; tree				
Unknown 1	--	--	--	1 (1)
Unknown 2	0.2 (1)	--	--	--

like the banyan, *Ficus indica*, are also used for feeding and roosting." (Bruner 1972: 71).

"differ from *coralensis* in being almost entirely arboreal, eating fewer insects" (Holyoak 1973: 31).

"cats mostly fruit gathered in the forest trees. I often saw it take fruit measuring about 7 mm in diameter, small red berries and figs. Quayle found fruit similar to cherries in the stomach of collected birds [translation]." (Holyoak 1974: 161–162.)

"the smaller varieties of ripened fruit" (Thibault & Rives 1988: 80).

"Observé mangeant les graines de sécropia. ... Malaimé de la population car mange les fleurs de vanille" – Ra'iatea (Seitre & Seitre 1991: 39).

Ptilinopus coralensis, Atoll Fruit-Dove

"insects and grass seeds" (Bruner 1972: 75).

"black berries about 7 mm in diameter from a

low bush, small green flowers of a low tree, and many insects pecked from the foliage of bushes and the ground with a quick darting action." Rangiroa (Holyoak 1973: 30).

"Neuf contenus stomacaux de Ptilope des Tuamotu ont été prélevés à Marutea de Sud et à Matuarei-Vavao. Ils montrent un régime alimentaire strictement végétal: tous ne contiennent en effet que des graines et des débris végétaux divers. Pour Seurat (1903), les oiseaux de Marutea du Sud se nourrissent des graines de *Turnefortia* et de *Morinda citrifolia*." – Marutea, Maturei-Vavao (Lacan & Mougin 1974: 265).

"insects and seeds, and usually forages on the ground" (Pratt *et al.* 1987: 199).

Ptilinopus chalcurus, Makatea Fruit-Dove

"same [as in *P. coralensis*; see above]" (Bruner 1972: 77).

Ptilinopus dupetithouarsii, White-capped Fruit-Dove
 “banyan trees, where the birds were feeding on the berries among the top branches.” – Fatu Hiva. “the banyan tree seemed to be the most important source of food” – Ua Huka, Nuku Hiva (Fisher & Wetmore 1931: 48).

“buds and flowers as well as fruit” (Goodwin 1970: 361).

“remarkably similar to [the food habits of *P. purpuratus*] ... Insects make up the diet of the young, even though the adults do not feed on anything but fruit.” (Bruner 1972: 78,79).

“dans les villages ... il se nourrit des fruits du hilang-hilang.” (Thibault 1973: 312).

“Des groupes de ce Ptilinope viennent souvent manger des fruits dans les arbres, plus rarement dans les buissons et jusqu'à 15 ou 20 oiseaux se rassemblent dans le même arbre. ... Cette espèce passe inaperçue dans les arbres qui ont des feuilles vertes, des feuilles mortes de couleur jaune et des fruits rouges. L'estomac d'une vingtaine d'oiseaux (sujets tués par moi ou spécimens de musée) contenait des fruits de différentes espèces et de couleur rouge, orange, verte, noire ou faune par ordre de fréquence décroissante. Ces fruits mesuraient de 3 à 10 mm de diamètre, y compris les baies. Les fruits des banyans, des poivriers et des petits goyaviers sont fréquemment consommés. Deux fois j'ai vu des Ptilinopes prendre de petits insectes sur des feuilles ... Sur Uapou, j'ai vu cet oiseau manger des grains de café qu'il faisait tomber.” (Holyoak 1975: 346–347).

“il se nourrit des fruits de *Cananga odorata* ou Ylang-Ylang.” (Ehrhardt 1978: 391).

Ptilinopus mercierii, Red-mustached Fruit-Dove
 “the same [as in *P. dupetithouarsii*]” (Bruner 1972: 81).

“On l'a vu manger les fruits d'une plante grimpanche et, en compagnie de *dupetithouarsii*, dans la cime de grandes arbres de fruits. Les sujets collectés avaient des fruits de plantes grimpanches dans l'estomac de des graines intactes dans l'intestin.” (Holyoak 1975: 345).

Ptilinopus buttoni, Rapa Fruit-Dove

“not restricted to fruit alone but it is reported to feed on insects as well.” (Bruner 1972: 82).

“eats quantities of fruit, [although] its long bill may have evolved to facilitate feeding at flowers, which was observed several times in 1974 (J-CT pers. obs.)” (Holyoak & Thibault 1978: 204).

Most often eaten from 18 Dec 1989 to 6 Jan 1990 were fruits of *Psidium guajava*, *Coffea arabica*,

Meryta choristantha, *Homalanthus stokesii*, *Corokia collenetti*, *Oparanthus rapensis*, *Apetabia margaretae*, and possibly *Freycinetia arborea*, as well as flowers or nectar of *Metrosideros collina*. (Thibault & Varney 1991: 78).

Ptilinopus layardi, Whistling Fruit-Dove

“berries of a species of banyan” (Layard 1875b: 151).

“stomach contained green fruit with stones. ... Stomach contained a fruit about the size of a cherry, with a large hard stone.” (Finsch 1877: 736).

“berries, or small pea-like fruit, of which many varieties grow wild on the islands. The hard testa is broken and the contents ground by horny tubercles set in the muscular coat of the gizzard.” (Wood 1926: 116).

“common foods include various *Ficus* species, Prickly Solanum *Solanum torvum*, and Koster's Curse *Clidemia hirta*” (Watling 1982: 86, 88).

“smallish fruit, caterpillars and other small insects” (Clunie 1984: 52).

Ptilinopus luteovirens, Golden Fruit-Dove

“capable of swallowing very large seeds, but it also feeds on a small purple berry; and its droppings stain a deep black, like ink, and equally indelible. ... berries of *Araliaceae* trees, and creepers of the genus *Melastoma* (the purple berry, I suppose, I have named)” (Layard 1875a: 436–437).

“some kind of berry” (Wood 1924b: 387).

“small fruits of the size of peas, like those of the Ndrau tree, predominating. This bird is also very fond of the purple berries of *Clidemia hirta*, ... an introduced pest distributed throughout the islands by many birds. The hard seeds eaten by *luteovirens* are readily pulped by hard, coniform, submucous elevations, generally eight in number, scattered over the gizzard.” (Wood 1926: 117).

“fruit” (Mercer 1966: 7).

“fruits of vines” (Holyoak & Thibault 1978: 205).

“Food mainly fruit of trees, vines and bushes, an orange fruit of about 4-mm diameter [*Ficus* sp.] often being taken.” – Viti Levu, Fiji (Holyoak 1979: 9).

“common foods include various *Ficus* species, Prickly Solanum *Solanum torvum*, and Koster's Curse *Clidemia hirta*” (Watling 1982: 86).

“smallish fruit and caterpillars” (Clunie 1984: 48).

Ptilinopus victor, Orange Fruit-Dove

“wild berries” (Layard 1875a: 437).

“many sorts of small and large berries and fruits” (Layard 1876: 152).

"The stomach contents are generally berries of various kinds, the bird being particularly fond of the purplish pea-like fruit of the 'Golegole' (*Abyxia bracteolosa*), a shrub five feet high. The fruit is commonly found unbroken in the oesophagus but macerated or pulpified in the gizzard. The latter condition is reached by means of the horny elevations with which the sub-mucosa is studded. In one adult eleven of these were found – three larger, 3 mm. in diameter, and eight smaller, each about 1 mm. across." (Wood 1926: 115).

"fruits of vines" (Holyoak & Thibault 1978: 205).

"Foods recorded were an orange fruit of 4-mm diameter [*Ficus obliqua*] ... and pale yellow fruit of 7-mm diameter that grew in clusters on twigs and branches of a tree. A male specimen had a soft seed four millimetres in diameter in its stomach, probably from a fruit of which the pulp had been digested. A female was very clearly seen ... eating insects including caterpillars from the caterpillar-eaten leaves in the canopy of a tree" – Taveuni, Fiji (Holyoak 1979: 9).

"Common foods include various *Ficus* species, Prickly Solanum *Solanum torvum*, and Koster's Curse *Clidemia hirta*" (Watling 1982: 86–87).

"smallish fruit, caterpillars, small insects" (Clunie 1984: 50).

Ducula pacifica, Pacific Pigeon

"fruit of the Maota (*Dysoxylum* sp.) and Mosooi (*Cananga odorata*, J.Hook.) ... Tavai (*Rhus taitensis*, var. *taitense*, Guil.) ... nutmegs (*Myristica*, sp.) and the *Faradaya powelli*, Seem." – Western Samoa (Whitmee 1875: 443).

"the fruit of some tree unknown to me. ... Stomach contained a large green fruit." – Fiji (Finsch 1877: 737).

"In their crops were banyan-seeds, and I was told that they feed on the wild plantain and on the banana." – Rarotonga (Wilson 1907: 377).

"fruit of various trees" (Mayr 1945: 64).

"very often seen eating the fruit of the moso'oi tree [*Cananga odorata*]." – Western Samoa (Yaldwyn 1952: 29).

"Stomach contents were always berries or rather big fruits some of which were 30 x 15 mm.

Nestling I: Bones of at least 3 small lizards; 1 dragon-fly (Agrionidae); 1 big locust (Acridiidae); 1 big cicada; 3 rather big beetles (Tenebrionidae and Scarabaeidae); 1 larva of a click beetle (Elateridae); 1 chelicer of a big spider (Avicularioidae).

Nestling II: Bones of 1–2 small lizards; 2 big cicadas; many unidentified remains." – Rennell, Solomon Islands (Bradley & Wolff 1958:99).

"Berries of various trees are the favourite food, common ones eaten being 'uri' *Guettarda speciosa*, 'bero' (*Ficus*), and 'mao' (*Scaevola*). ... ripe breadfruit from the tree" – Tuvalu (Child 1960: 22).

"feeds in large flocks; it may feed in open fields in evening, but when disturbed flies to tops of trees." – Samoa (Ashmole 1963: 14).

"Fresh droppings of one of the Tokelau islet birds contained many seeds of gahu *Scaevola frutescens* ... islanders [said] ... that the berries of this tree and of puapua *Guettarda speciosa* constitute the usual food" – Tokelau (Wodzicki & Laird 1970: 267).

"fruits and berries taken from the branches. The fruits of *Cananga odorata*, *Dysoxylum* sp., *Rhus taitense*, *Faradaya powelli*, and *Myristica* appear to be important foods" (Goodwin 1970: 397).

Myristica sp. – Samoa (Beckon 1980).

"fruit from trees and bushes" – Cook Islands (Holyoak, 1980: 35).

"small fruits and berries picked directly from trees. During late August and September the most important food appears to be the large orange berries of *Dysoxylum forsteri* (Niuean name Moota). Complete and partly digested Moota berries were found in the crops and stomachs of all four birds collected and the hard elongated seeds from these berries were found in the birds' intestines." – Niue (Kinsky & Yaldwyn 1981: 31).

"mainly on the fleshy fruits of large trees. Favoured fruits include those of makaso *Cananga odorata*, *Guettarda*, *Dysoxylum*, *Scaevola*, and *Rhus* sp." – Fiji, Tonga, Samoa (Watling 1982: 81).

"feeding in large forest trees" – American Samoa (Amerson *et al.* 1982b: 69).

"fruits" – Loyalty Islands (Hannecart & Letocart 1983: 50).

"mainly small to medium sized fruit, such as those of the *Ficus* banyans and *tarawau* (*Dysoxylum richii*)." – Fiji (Clunie 1984: 54).

"exclusively of fruit of at least 27 plant species from 0.4 to 6 cm in size, including various species of *Ficus*, *Horsfieldia spicata*, *Dysoxylum caulostachyum*, *Elaeocarpus sphericus*, and numerous drupes" – Rennell, Solomon Islands (Diamond 1984: 152).

"Besides the fruits of *Guettarda speciosa* and *Diospyros samoensis*, the fruit of a small tree called Milo (unidentified) [probably *Thespesia populnea*], common in coconut plantations, was the preferred food

item. These fruits are bright red and about 2.5 cm in diameter.” – Niuafo’ou, Tonga (Rinke 1986: 84).

“Alimentation: nous l’avons observé dans les arbres à fruits suivants: *Syzygium malaccense*, *Elaeocarpus angustifolius* (Wallis); *Syzygium clusiifolium*, *Pometia pinnata* (Alofi). – Wallis and Futuna (Guyot & Thibault 1987: 240).

“fruits of *Guettarda speciosa*. ... observed feeding on the fruits of *Myristica hypargyrea* (16 out of 27 observations), *Grewia crenata*, *Calophyllum neo-ebudicum*, and *Pleiogynium timorensis*. ... very adept in obtaining fruits from the tips of slender branches.” – ‘Eua, Tonga (Rinke 1987: 29).

Fruits of *Guettarda speciosa*, *Jasminum didymum*, *Canthium barbatum*, *Seiba pentandra*, *Elaeocarpus tonganus*, *Hernandia moerenhoutiana*, *Myrsine cheesmani*, *Pipturus argenteus* – Atiu, Ma’uke, Mitiaro, Cook Islands (Franklin & Steadman 1991; see Table 3).

“fruit of *Fagraea berteriana*” – Western Samoa (Beichle 1991).

“fruits of several species of fig trees and other large trees such as *Cananga odorata*, *Guettarda* spp., *Dysoxylum* spp., *Myristica* spp., and *Endospermum* spp. It most probably also takes young still tender leaves of some forest trees and vines.” – Vanuatu (Bregulla 1992: 179–180).

Thirty-four observations (2 June–29 Sept 1995) included fruits from the trees *Ficus prolixa* (15 obs.), *F. obliqua* (5 obs.), *Dysoxylum maota* (4 obs.), *Dysoxylum* sp. (2 obs.), *Cananga odorata* (2 obs.), *Canarium vitiense* (2 obs.), *Myristica fatua* (1 obs.), *Planchonella samoensis* (1 obs.), and *D. samoense* (1 obs.). One bird also ate lichen stripped from the bark of *C. vitiensis*. – Tutuila, American Samoa (HBF unpub. data).

Ducula latrans, Peale’s Pigeon

“To give some idea of the gastronomic powers of these large Pigeons, I annex the size of two seeds found in the crop of one, axis 4”, circum. 3”6”; axis 5”, circum. 3”. This was only the hard woody part, the pulp had been digested! [Layard’s italics] ... feeds largely on the wild nutmeg, the large drupe-like seeds of some Laurinaceous forest trees, and the fruits of both the *Kaufia Pakus*” (Layard 1875a: 438).

“fruit of some tree unknown to me” (Murray 1877: 737).

“A complete fruit of *Onocarpus vitiensis*” (Garrod 1878: 738).

“dissected twenty-one specimens ... mostly from Viti Levu ... In 16 instances the stomach or other part

of the digestive tract contained one variety of the wild nutmeg. Indeed where nutmegs were obtainable this Fruit Pigeon appeared to live on them exclusively; it seemed that other fruits were swallowed only when there were no nutmeg-bearing trees in the neighborhood. ...

“July 18, 1923. In the gizzards of eight specimens ... were 13 wild nutmegs (*Myristica castanaefolia*) and a drupe that resembled the fruit of a small cherry. Two stomachs were empty, one held a single nutmeg with no traces of the pericarp; five held two nutmegs, one quite large; another had two of the largest nutmegs as well as a second drupe of the species aforementioned and unknown to me. ...

“August 12, 1923. Took from the gizzard of a Nutmeg Pigeon at Vunisea, Kandavu, a large quantity of softened and disintegrated mace, and with this inspissated arillus a wild nutmeg 32 mm. long and 29 mm. wide.

“There are at least four species of the genus *Myristica* growing wild in Fiji, all of which furnish food to the ‘Soqi’ or Nutmeg Pigeon. The commonest of these is *M. castanaefolia*, found in all the larger islands as a handsome tree 60–80 feet high. The mature fruit is as large as a full-sized butternut which it resembles, both as to testa and pericarp. Some writers assert that settlers in Fiji use the kernel of one species as a substitute for the nutmeg of commerce – *M. moschata*. It has the shape and size of the latter, and the color of the aril or ‘mace’ is similar, but its aromatic properties are not well developed. The present writer investigated this matter and found that the wild Fijian nutmeg, exhibiting as it does only a suspicion of the characteristic, spicy odor and taste, is rarely used as a condiment either by Europeans, Indians or aboriginals. Moreover, several attempts to export the most promising of the species failed as a business speculation. *Globicera [D. latrans]* has also a liking for the small fruit of the Banyan Fig (*Ficus bengalensis*) of which it eats sparingly and when nutmegs are not available. The writer has found the remains of these in the gizzard of three specimens.

“H.B. Guppy (Observations of a Naturalist, p. 403, 1906) notes that species of two other floral genera – *Canarium* and *Elaeocarpus* – furnish food for Fruit Pigeons. Of *E. graeffei*, he found the stone in this pericarpal fruit measure 3–5 cm. Of *Canarium*, with its large drupe, the ‘pit’ was 2 cm. in length. The distribution of this tree in Fiji is mostly by Fruit Pigeons, in whose crop Guppy found fruits measuring 25 x 28 mm.

"Seeman also mentions the drupes of *Couthovia corynocarpa* as part of the diet of the Fruit Pigeons of Fiji." (Wood 1924a: 434–436).

"its peculiar digestive apparatus ... arranged for the removal and grinding of the arillus or 'mace' of wild nutmeg, upon which this species always feeds when the fruit is accessible.

"There are three or four varieties of *Myristicae* [sic] in the Fiji group, and the trees are mostly distributed by this species. The Nutmeg Pigeon also eats (or rather swallows) fruits of the same character as the nutmegs, rejecting the 'nut', which passes through unchanged, and digesting the outer covering, which is reduced to pulp by the 'grater' planted in the submucosa of the gizzard." (Wood 1926: 117–118).

"many types of berries and fruits, but especially the fruit of the Kauvula (*Endospermum macrophyllum*) and the Makasoi (*Cananga odorata*)." (Mercer 1966: 8).

"Diet consists of fruit, the following kinds being seen eaten or found in crops of shot birds: 12-mm diameter round fruit, 25-mm long yellow-green fruit, 20-mm diameter black fruit. Judged by the size of the gape of specimens, this bird can probably swallow fruit of up to about 40-mm diameter." – Viti Levu, Fiji (Holyoak 1979: 9).

"*Myristica* sp." (Beckon 1980).

"large fleshy fruits especially those of Makasoi *Cananga odorata*, *Dysoxylum richii*, *Endospermum macrophyllum*, and nutmegs *Myristica* sp." (Watling 1982: 83).

"mainly large-stoned fruits, many of them thumb-sized" (Clunie 1984: 56).

Ducula auroae, Polynesian Pigeon

"In the crops of two examples which I procured on June 2nd in the district of Hitiaa was a large quantity of seeds of the lié vine (*Freycinetia arborea*), but I was told that their chief food was the fei or wild plantain, though they also eat the seeds of the banyan-tree." – Tahiti (Wilson 1907: 376).

"seeds of a vine, *Freycinetia arborea*, seeds of wild figs and wild plantains. Most probably it is the fruits of all these plants that are taken, their pulp digested and their seed passing undigested through the bird as with other *Ducula* species." (Goodwin 1970: 399).

"guava and 'autera'a' [*Terminalia catappa*] along with other fruits as they came into season." – Tahiti (Bruner 1972: 66).

"fruit of *Psidium guajava* ... Quayle found red figs and other fruits as well as numerous seeds in the

crop of the birds he collected [translation]." – Tahiti (Holyoak 1974: 162–163).

"only fleshy fruit ripening in the trees" – Tahiti (Thibault & Rives 1988: 82).

Ducula galeata, Nuku Hiva Pigeon

"almost exclusively of large yellow guava's, *Psidium guajava*, and the fruit of the 'autera'a' tree, *Terminalia catappa*." (Bruner 1972: 64).

"C'est un oiseau arboricole qui se nourrit surtout, sinon entièrement, de fruits assez gros, cueillis sur les buissons et les arbres. Je l'ai souvent vu dans des goyaviers mesurant de 5 à 12 m de haut et il ne mangeait que les fruits mûrs, jaunes, ignorant ceux qui étaient encore verts. Il saisissait le fruit dans son bec et le détachait en le tournant, puis l'avalait en entier. Un sujet tué par un habitant avait des goyaves de 3 cm de diamètre dans le jabot, des morceaux de fruits dans l'estomac et des graines intactes dans l'intestin. Son gosier était très extensible et son jabot très vaste. Cet oiseau peut probablement avaler d'un coup des fruits mesurant 4,5 à 5 cm de diamètre. Dans l'arbre où il s'alimente, il saute sur les branches ou s'y déplace latéralement, vole de l'une à l'autre et bat fréquemment des ailes pour garder son équilibre sur les rameaux qu'il courbe. Quayle nota qu'il mange surtout des goyaves mais il le vit aussi prendre des feis (petites bananes)." (Holyoak 1975: 342).

"Sa nourriture consiste presque exclusivement en fruits de badamier, *Terminalia catappa* L. et de goyavier *Psidium guajava* L." (Ehrhardt 1978: 392).

DISCUSSION

General patterns. Perhaps the most important point to take from the species accounts is that few detailed or quantitative data exist on columbid diets in Polynesia. Taxonomic and geographic coverages are very uneven. Quantitative studies include the outstanding work by Brooke & Jones (1995) on the year-round diet of *Ptilinopus insularis* on Henderson Island, and seasonally limited analyses by Wood (1924a) on *Ducula latrans* in Fiji, by Franklin & Steadman (1991) on *D. pacifica* and *P. rarotongensis* in the Cook Islands, and by HBF on *D. pacifica*, *P. perousii*, and *P. porphyrae* in American Samoa. The other observations are opportunistic rather than collected in a rigorous or standardized manner. While useful, such anecdotes must be interpreted with caution. For example, feeding observations made in gardens and other disturbed vegetation may give the impression

Table 2. The modern (M) and prehistoric (P) distribution of columbids in Polynesia. Island groups: Au = Austral; Co = Cook; Fi = Fiji; Ma = Marquesas; Ni = Niue; Pi = Pitcairn; Sa = Samoa; So = Society; Tk = Tokelau; To = Tonga; Tu = Tuamotu; Tv = Tuvalu; WF = Wallis and Futuna. E, extinct species; r, rare species. Feeding guilds: CF, canopy/subcanopy frugivore/granivore; MF, mid-level/understory frugivore/granivore; GF, ground frugivore/granivore. Modified from Steadman (1997).

															Totals			Feeding
	Pi	Ma	Tu	So	Au	Co	Ni	To	Sa	WF	Fi	Tk	Tv	M	P	M+P	Guild	
<i>Columba vitiensis</i>	-	-	-	-	-	-	-	-	M	-	MP	-	-	2	-	2	CF/MF/GF	
E <i>Macropygia beana</i>	-	P	-	-	-	-	-	-	-	-	-	-	-	-	1	1	MF	
E <i>Macropygia arevarevaauupa</i>	-	-	-	P	-	-	-	-	-	-	-	-	-	-	1	1	MF	
E <i>Caloenas canacorum</i>	-	-	-	-	-	-	-	P	-	-	-	-	-	-	1	1	MF/GF	
E <i>Gallicolumba nui</i>	-	P	-	P	-	P	-	-	-	-	-	-	-	-	3	3	GF	
E <i>Gallicolumba new sp.</i>	P	-	-	-	-	P	-	-	-	-	-	-	-	-	2	2	GF	
r <i>Gallicolumba erythroptera</i>	-	-	M	MP	-	P	-	-	-	-	-	-	-	2	2	3	GF	
r <i>Gallicolumba rubescens</i>	-	MP	-	-	-	-	-	-	-	-	-	-	-	1	1	1	GF	
r <i>Gallicolumba stairi</i>	-	-	-	-	-	-	-	MP	MP	M	M	-	-	4	2	4	GF	
r <i>Didunculus strigirostris</i>	-	-	-	-	-	-	-	-	M	-	-	-	-	1	-	1	CF/MF/GF	
E <i>Didunculus new sp.</i>	-	-	-	-	-	-	-	P	-	-	-	-	-	-	1	1	CF/MF/GF	
<i>Ptilinopus perousii</i>	-	-	-	-	-	-	-	MP	M	-	M	-	-	3	1	3	CF	
<i>Ptilinopus porphyraceus</i>	-	-	-	-	-	-	M	MP	M	M	M	-	-	5	1	5	CF	
r <i>Ptilinopus narotongensis</i>	-	-	-	-	-	MP	-	-	-	-	-	-	-	1	1	1	CF	
<i>Ptilinopus insularis</i>	MP	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	CF	
<i>Ptilinopus purpuratus</i>	-	-	-	MP	-	-	-	-	-	-	-	-	-	1	1	1	CF	
<i>Ptilinopus condensis</i>	-	-	M	-	-	-	-	-	-	-	-	-	-	1	-	1	MF/GF	
<i>Ptilinopus chalcurus</i>	-	-	M	-	-	-	-	-	-	-	-	-	-	1	-	1	CF	
<i>Ptilinopus dupetithouarsii</i>	-	MP	-	-	-	-	-	-	-	-	-	-	-	1	1	1	CF	
E <i>Ptilinopus mercierii</i>	-	MP	-	-	-	-	-	-	-	-	-	-	-	1	1	1	CF	
r <i>Ptilinopus buttoni</i>	-	-	-	-	M	-	-	-	-	-	-	-	-	1	-	1	CF	
<i>Ptilinopus layardi</i>	-	-	-	-	-	-	-	-	-	-	M	-	-	1	-	1	CF/MF	
<i>Ptilinopus luteovirens</i>	-	-	-	-	-	-	-	-	-	-	M	-	-	1	-	1	CF/MF	
<i>Ptilinopus victor</i>	-	-	-	-	-	-	-	-	-	-	M	-	-	1	-	1	CF/MF	
<i>Ducula pacifica</i>	-	-	-	-	-	M	M	MP	M	M	M	M	M	8	1	8	CF	
<i>Ducula latrans</i>	-	-	-	-	-	-	-	P	-	-	MP	-	-	1	2	2	CF	
r <i>Ducula auroae</i>	P	-	M	MP	-	P	-	-	-	-	-	-	-	2	3	4	CF	
r <i>Ducula galeata</i>	P	MP	-	MP	-	P	-	-	-	-	-	-	-	2	4	4	CF	
E <i>Ducula david</i>	-	-	-	-	-	-	-	P	-	P	P?	-	-	-	3	3	CF	
E <i>Ducula new sp.</i>	-	-	-	-	-	-	-	P	-	-	-	-	-	-	1	1	CF	
Total (M)	1	4	4	4	1	2	2	4	6	3	9	1	1	42	35	61		
Total (P)	4	6	0	6	0	6	0	9	1	1	2	0	0					
Total (M+P)	4	6	4	6	1	7	2	9	6	4	10	1	1					
Number of islands with prehistoric columbid bones	1	4	0	1	0	2	0	3	1	1	1	0	0					

Table 3. The modern (M) and prehistoric (P) distribution of columbid genera in Polynesia, based on data in Table 2. Abbreviations of island groups: Au = Austral; Co = Cook; Fi = Fiji; Ma = Marquesas; Ni = Niue; Pi = Pitcairn; Sa = Samoa; So = Society; Tk = Tokelau; To = Tonga; Tu = Tuamotu; Tv = Tuvalu; WF = Wallis and Futuna.

	Pi	Ma	Tu	So	Au	Co	Ni	To	Sa	WF	Fi	Tk	Tv	Totals			Feeding Guild
														M	P	M+P	
<i>Columba</i>	-	-	-	-	-	-	-	-	M	-	MP	-	-	2	1	2	CF/MF/GF
<i>Macropygia</i>	-	P	-	P	-	-	-	-	-	-	-	-	-	-	2	2	MF
<i>Caloenas</i>	-	-	-	-	-	-	-	P	-	-	-	-	-	-	1	1	MF/GF
<i>Gallinolumba</i>	P	MP	M	MP	-	P	-	MP	MP	M	M	-	-	7	6	9	GF
<i>Didunculus</i>	-	-	-	-	-	-	-	P	M	-	-	-	-	1	1	2	CF/MF/GF
<i>Ptilinopus</i>	MP	MP	M	MP	M	MP	M	MP	M	M	M	-	-	11	5	11	CF/MF/GF
<i>Ducula</i>	P	MP	M	MP	-	MP	M	MP	M	MP	MP	M	M	11	7	12	CF
Total (M)	1	3	3	3	1	2	2	3	5	3	4	1	1	32	22	39	
Total (P)	3	4	0	4	0	3	0	5	1	1	2	0	0				
Total (M+P)	3	4	3	4	1	3	2	5	5	3	4	1	1				
Number of islands with prehistoric columbid bones	1	4	0	1	0	2	0	3	1	1	2	0	0				

that a species favors fruits of introduced or forest-edge species such as *Cananga odorata* or *Macaranga harveyana*, overlooking the foraging that occurs inside native forests.

In spite of this caveat, some general patterns are evident:

1. Most columbids favor native fruits and seeds. Of the 101 species of plants in our accounts, 84 are native trees, shrubs, or vines (see Appendix). Columbid populations are maintained principally by native forest.
2. Some species do feed on introduced plants. Prime examples are from Fiji, where *Columba vitiensis* feeds on *Solanum* and *Capsicum*, and *Ptilinopus layardi*, *P. luteovirens*, and *P. victor* feed on *Solanum* and *Clidemia*. Populations of these non-native plants are thus probably maintained and spread, in part, by native birds.
3. Fleshy fruits, important in avian diets worldwide (Willson *et al.* 1989), are a major part of the diet of Polynesian columbids. The fleshy fruits of *Ficus* are of great importance. At least one species, *Ptilinopus perousii*, is a fig specialist. Eight other Polynesian species of *Ptilinopus* are known to feed on figs. Of the four remaining species, only one, *P. insularis*, occurs on an island (Henderson) where *Ficus* is absent. Ironically, this is where the most detailed dietary study of any Polynesian columbid has taken place

(Brooke & Jones 1995). Feeding on *Ficus* fruits has not been observed in *P. coralensis*, *P. chalcurus*, or *P. huttoni*, which inhabit remote parts of East Polynesia where only one species of fig (*F. prolixa*) occurs (Corner 1963). None of these fruit-doves, however, is well studied.

Figs provide high levels of calcium, which birds need for growth and egg production (O'Brien *et al.* 1998). Figs play a crucial dietary role for frugivorous birds and mammals at Manú in Amazonian Perú (Terborgh 1986). In West African forests, figs seem to be less important (Gauthier-Hion & Michaloud 1989). In Malaysia, where the biota is more closely related to that of Polynesia, figs once again are important, especially for seven species of columbids in the genera *Trepon*, *Ptilinopus*, *Ducula*, and *Chalcochaps* (Lambert 1989, 1991). New Guinea sustains more species of *Ficus* than anywhere else in the world, although Malaysia and large Indonesian islands are nearly as rich (Corner 1963, 1967). New Guinea also holds more genera and species of columbids than any other island or country (Beehler *et al.* 1986), with as many as 26 species occupying a single forest locality (Bell 1982).

4. From a standpoint of avian feeding guilds (Tables 2, 3), columbids exploit all structural layers of Polynesian forests. *Columba*, *Caloenas*, and *Didunculus* forage at variable heights. Among the more wide-

spread genera, *Ducula* tends to be a canopy feeder, *Ptilinopus* prefers the canopy and sub-canopy (but feeds low, even on the ground, in atolls), and *Gallinucula* feeds on the ground or in the understory. Diversity in columbid feeding guilds was greater on any given island or island group before the onset of anthropogenic extinction (see below).

Generic-level synthesis. The cuckoo-doves (*Macropygia*) occur today from Southeast Asia east to Vanuatu. The extinct *M. beana* (Marquesas) and *M. arevarevauupa* (Society Islands) represent an East Polynesian radiation of relatively large species (Steadman 1992). Bones of *Macropygia* have not yet been found in any island groups between Vanuatu and the Society Islands. In Vanuatu, *M. mackinlayi mackinlayi* (see Amadon 1943:16-17) feeds "on a wide variety of small berries, fruits and seeds usually beneath the canopy in small trees, shrubs and vines" (Bregulla 1992:184). We assume that the extinct East Polynesian forms of *Macropygia* also occupied the mid-level/understory of forests and consumed many types of fruits and seeds.

The single living species of *Caloenas*, the Nicobar Pigeon *C. nicobarica*, does not occur today east of the Solomon Islands and Palau, where it forages at varying heights but primarily on fallen fruits and seeds on the ground (Hadden 1981, Engbring 1988). The larger, extinct *C. canacorum* is from New Caledonia (Balouet & Olson 1989) and Tonga (Steadman 1989). Its foraging habits probably resembled those of its living congener.

Most Polynesian islands lack species of *Gallicolumba* today. Those islands with ground-doves never have more than one species. Bones indicate that one or two species of *Gallicolumba* once inhabited most or all islands. Mangaia (Cook Islands) even had three species of *Gallicolumba*, a situation without parallel east of New Guinea. The smallest Polynesian species of ground-dove is *G. rubescens*, now confined to the small, uninhabited Marquesan islands of Hatutu and Fatu Huku. This species and *G. erythroptera* are among the least studied of Polynesian columbids. *Gallicolumba* has a relatively thicker bill than frugivorous columbids. This, combined with the scant dietary data, suggests a granivorous and insectivorous rather than frugivorous diet. Confirmation of this awaits detailed feeding observations, stomach-content analyses, and dissections of the digestive tract.

The living Tooth-billed Pigeon *Didunculus strigirostris* inhabits Western Samoa (Beichle 1987, 1991).

An extinct, larger species of *Didunculus* has been found in prehistoric sites in Tonga (Steadman 1993, 1995, pers. obs.). Today, *D. strigirostris* feeds primarily in trees on the pea-sized seeds of *Dysoxylum*, obtained by using its unusual bill to saw through the tough, fibrous pericarp (Beichle 1987).

Fruit-doves (*Ptilinopus*) are widespread in Polynesia (Table 2). Their current absence on Tokelau and Tuvalu suggests human impact. The survival of *P. coralensis* in the Tuamotus and former occurrence of *P. porphyraceus* in the Marshall Islands (Peters & Griscom 1928) demonstrate that *Ptilinopus* can inhabit atolls as well as high islands. In East Polynesia, two sympatric species of *Ptilinopus* occur only in the Marquesas. *Ptilinopus peroussii* and *P. porphyraceus* are sympatric through much of Tonga, Samoa, and eastern Fiji. A species in the *layardi-luteovirens-victor* species group replaces *P. porphyraceus* on islands in western Fiji. Fruit-doves have a large gape for their size, facilitating consumption of whole soft fruits. The relatively large *P. insularis* consumes fruits up to 18 mm in diameter (Brooke & Jones 1995). *Ficus* has been recorded in the diets of nine of the 13 Polynesian species of *Ptilinopus*. Figs are a regular part of the diet at least as far east as the Cook Islands, where two native species (*F. prolixa* and *F. tinctoria*) occur (Whistler 1990, Franklin & Steadman 1991, Merlin 1991). In Polynesia, the most species of *Ptilinopus* (5) live in Fiji, which is also richest in *Ficus* (14 species, 8 endemic). *Ptilinopus* spp. have been observed to feed on 44 other plant genera in Polynesia, representing 30 families.

A species of fruit-pigeon or imperial-pigeon (*Ducula*) occurs in most island groups (Table 2), although the current absence of *Ducula* on most individual East Polynesian islands is unnatural. In fact, two species (*D. galeata*, today confined to Nuku Hiva, Marquesas, and *D. aurorae*, now only on Tahiti and Makatea) were once widespread and often sympatric. In West Polynesia, where *D. pacifica* and *D. latrans* are allopatric today, two extinct species occurred prehistorically, the large *D. david* and an even larger, undescribed species (Balouet & Olson 1987, Steadman 1989, 1993). Three and four species of *Ducula* occurred on individual islands in the Cook Islands and Tonga, although the contemporaneity of *D. pacifica* with the other species is uncertain. The diet of *Ducula* is diverse (and even can include invertebrates and small vertebrates fed to nestlings). Usually, however,

the diet is dominated by large-fruited (*Myristica*, *Guettarda*, *Canarium*) and smaller-fruited (*Cananga*, *Dysoxylum*, *Elaeocarpus tonganus*, *Ficus*) native species and the introduced *Cananga*. All species of *Ducula* have large gapes for their size, allowing them to swallow whole, large fruits.

Island ecology and the loss of frugivores. Columbids are seed dispersers of forest trees from Malaysia (Lambert 1989), New Guinea (Terborgh & Diamond 1970, Frith *et al.* 1976, Coates 1985, Pratt & Stiles 1985), Australia (Crome 1975a, 1975b, Innis 1989), the Solomon Islands (Hadden 1981), and Vanuatu (Bregulla 1992) out to the remote islands of East Polynesia (Franklin & Steadman 1991). The precise roles that oceanic columbids play in plant dispersal, however, are not well studied. The species of *Ducula* and *Ptilinopus* are regarded as excellent seed dispersers because the cornified ridges and nodules in their thin-walled gizzards remove fruit pulp but allow seeds to pass through intact (Cadow 1933). While the muscular, grit-filled gizzards of most other genera would classify them as seed predators rather than seed dispersers, the dichotomy between seed predators and dispersers is not absolute (Lambert 1989, Green 1993). All South Pacific columbids probably disperse seeds to some extent.

Modern columbid faunas have been depleted across Polynesia by human activities (reviewed in Steadman 1997; see "M" vs. "P" in Tables 2 and 3 herein). For example, in the last 1000 years, Huahine (Society Islands) and Ua Huka (Marquesas) have each lost five of six columbid species, and Mangaia has lost all six of its species. These losses probably have had profound ecological consequences for Polynesian forests by reducing overall frugivore diversity, altering the range of body size in extant frugivores, and possibly destroying coevolved relationships between particular species of columbids and food plants.

Eastward from New Guinea, species richness in mammals decreases at a faster rate than in birds, which are the dominant frugivores east of the Solomon Islands. Fruit bats or flying foxes (Pteropodidae) are important frugivores on West Polynesian islands (Cox *et al.* 1991), although their role in seed dispersal has not been studied in great detail (Rainey *et al.* 1995, Banack 1996). Pteropodids are represented by four species in Fiji, three in Tonga, two in Samoa, and one at their eastern limit in the Cook Islands (Koopman & Steadman 1995).

Columbid diversity also decreases from west to east (Fig. 1). Over the last three millennia, however, the extinction of so many populations and species has exaggerated their taxonomic attenuation across Polynesia and reduced the number of potential seed dispersers within and between islands. Because species richness in plants decreases at a lesser rate (Guppy 1906), the ratio of plant species to extant disperser species increases from west to east. In more remote island groups, such as the Cooks or Marquesas, each extant frugivore potentially plays a more critical part in forest ecology.

In addition to reduced species richness, the body sizes of extinct/extirpated columbids average larger than in surviving species. This trend may affect forest composition by limiting the size of fruits that can be eaten and dispersed today. For example, the two extinct species of *Ducula* from Tonga were larger than any extant Polynesian columbids and therefore capable of consuming and dispersing much larger fruits, such as the Samoan endemics *Elaeocarpus ulianus* or *Palaquium stehlinii*, than any extant birds. Also larger than living congeners were the extinct Tongan species of *Caloenas* and *Didunculus*, and the extinct East Polynesian species of *Gallilcolumba* and *Macropygia*.

The anthropogenic extinction of columbids probably has led to long-term changes in Polynesian forests, yet the nature of these effects will remain mostly speculative until we improve the quality of information on columbid foraging habits and the history and dynamics of vegetation change. Also, the population status and possible endangerment of plant species are not well known in our study region. An exception is Mangaia, where the loss of columbids can be related to prehistoric deforestation and invasions by exotic plants that have altered native plant communities and erased populations of some trees, such as *Weinmannia* and *Coprosma* (Ellison 1994).

In Tonga, only four of the nine species of columbids that once occurred still exist (Table 2). Long-term forest surveys, such as those initiated in Tonga by Drake *et al.* (1996) and Franklin *et al.* (1999), should help to elucidate correlations in distribution between species of trees and living columbids, the latter having also been surveyed (Steadman & Freifeld 1998). Great potential also exists for genetic and paleobotanical research to clarify the history of vegetation change on islands and to generate hypotheses about the links between forest ecology and columbid extinctions.

RESEARCH AND CONSERVATION PRIORITIES

Although the modern distribution of pigeons and doves is known for most island groups in Polynesia, the population size of most species is poorly estimated. Aside from surveys, the following research would add greatly to our understanding of the ecology and conservation biology of Polynesian columbids.

1. Rigorous foraging and diet studies in both mature and successional forests to determine the relative contributions of each species of columbid to the dispersal of plants. Such studies should involve both observations and analyses of gut contents.
2. Vegetation surveys to determine how the composition of plant communities is related to the distribution and abundance of columbids or other frugivores.
3. Filling the major geographic gaps in the avian extinction record, especially in Tubuai, Niue, Samoa, Fiji, and atoll-dominated groups such as the Tuamotus, Tokelau, and Tuvalu.
4. Estimates of how the loss of dispersers has affected Polynesian forests by reconstructing vegetation change (palynology and plant macrofossil records) and studying the genetic variability between and within populations of vertebrate-dispersed plants.

The surviving populations of Polynesian pigeons and doves deserve sound conservation programs, for the sake of the birds as well as the co-dependent forests. As noted by Franklin & Steadman (1991), Siette & Siette (1991, 1992), and Graves (1992), translocations should be attempted to preserve certain columbid populations. On Mangaia, for example, a fair amount of indigenous forest remains on the rugged limestone terrain (Merlin 1991) in spite of 2500 years of human impact (Ellison 1994, Kirch et al. 1995). The six species of columbids that used to live on Mangaia include *Ptilinopus rarotongensis* and *Ducula pacifica*, two frugivores that could inhabit Mangaia's *Ficus*- and *Elaeocarpus*-rich forests once again if they were protected initially from hunting. The case for translocating *P. rarotongensis* is compelling since it survives now only on two other islands.

Humans have been influencing South Pacific columbids in negative ways for thousands of years. We see little logic in adopting a hands-off policy now, when we have at least some potential for exerting a positive influence.

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APPENDIX. Classification and nomenclature of plants mentioned in the text. Current names are given; other names used in text are in parentheses. The left columns represent generally accepted scientific nomenclature. I = introduced (non-native) species.

Scientific Name	Other names mentioned in text
PTERIDOPHYTA	
Polypodiaceae	
<i>Phymatosorus scolopendria</i>	
DICOTYLEDONAE	
Anacardiaceae	
<i>Semecarpus</i> (= <i>Onocarpus</i>) <i>vitiensis</i>	
<i>Pleiogynium timorense</i>	
<i>Rhus taitensis</i>	
Annonaceae	
<i>Cananga odorata</i> (I)	makaso, moso'oi, motoi, ylang-ylang
Apocynaceae	
<i>Alyxia bracteolosa</i>	golegole
Araliaceae	
<i>Meryta choristantha</i>	
Asteraceae	
<i>Oparanthus rapensis</i>	
Bignoniaceae	
<i>Spathodea campanulata</i> (I)	African tulip tree
Bombacaceae	
<i>Ceiba pentandra</i> (I)	
Boraginaceae	
<i>Tournefortia argentea</i>	

Scientific Name	Other names mentioned in text
Burseraceae	
<i>Canarium vitiensis</i>	
<i>Canarium</i> sp.	
Casuarinaceae	
<i>Casuarina equisetifolia</i>	
Clusiaceae	
<i>Calophyllum neo-ebudicum</i>	
Combretaceae	
<i>Terminalia catappa</i>	autera'a, badamier
Ebenaceae	
<i>Diospyros samoensis</i>	
Elaeocarpaceae	
<i>Elaeocarpus graeffei</i>	
<i>Elaeocarpus sphericus</i>	
<i>Elaeocarpus tonganus</i>	
<i>Elaeocarpus ulianus</i>	
Escalloniaceae	
<i>Corokia collenetti</i>	
Euphorbiaceae	
<i>Bischofia javanica</i>	
<i>Bischofia simplicifolia</i>	
<i>Endospermum macrophyllum</i>	kauvula
<i>Endospermum</i> spp.	
<i>Euphorbia</i> sp.	mavu
<i>Homalanthus stokesii</i>	
<i>Macaranga harveyana</i>	
Flacourtiaceae	
<i>Xylosma suaveolens</i>	
Gentianaceae	
<i>Couthovia</i> (= <i>Coutoubea</i> ?) <i>corynocarpa</i>	
Goodeniaceae	
<i>Scaevola frutescens</i>	gahu, mao
Hernandiaceae	
<i>Hernandia moerenhoutiana</i>	
Lauraceae	
<i>Cryptocarya hornei</i>	
Loranthaceae	
<i>Amyema</i> or <i>Descainina</i> (= <i>Loranthus</i>) sp.	rat-mistletoe
Lobeliaceae	
<i>Apetahia margaretae</i>	
Loganaceae	
<i>Fagraea berteriana</i>	
Malvaceae	
<i>Thespesia populnea</i>	milo
<i>Gossypium</i> ?	cotton-bushes [<i>Ptilinopus perousii</i>]
Melastomataceae	
<i>Clidemia hirta</i> (L)	Koster's curse
<i>Melastoma</i> sp. (L?)	

Scientific Name	Other names mentioned in text
Meliaceae	
<i>Dysoxylum caulostachyum</i>	
<i>Dysoxylum forsteri</i>	moota
<i>Dysoxylum huntii</i>	
<i>Dysoxylum maota</i>	
<i>Dysoxylum richii</i>	tarawau
<i>Dysoxylum samoense</i>	
<i>Vavaea amicorum</i>	
Mimosaceae	
<i>Adenanthera pavonica</i> (1)	pomea
Moraceae	
<i>Artocarpus altilis</i> (1)	breadfruit
<i>Ficus bengalensis</i>	
<i>Ficus indica</i>	
<i>Ficus obliqua</i>	strangling fig
<i>Ficus prolixa</i>	bero, ovava
<i>Ficus scabra</i>	masi
<i>Ficus tinctoria</i>	
± any species of <i>Ficus</i>	banian, banyan, fig, wild fig
Myristicaceae	
<i>Horsfieldia spicata</i>	
<i>Myristica castaneifolia</i>	
<i>Myristica fatua</i>	
<i>Myristica hypargyrea</i>	
<i>Myristica moschata</i>	
any species of <i>Myristica</i>	nutmeg
Myrsinaceae	
<i>Myrsine cheesmanii</i>	
<i>Myrsine hosake</i>	
Myrtaceae	
<i>Metrosideros collina</i>	
<i>Psidium guajava</i> (1)	goyavier, guava
Nyctaginaceae	
<i>Pisonia</i> sp.	
Oleaceae	
<i>Jasminum didymum</i>	
<i>Olea paniculata</i> [likely misidentified]	
Podocarpaceae	
<i>Dacrydium elatum</i>	Fijian fig, yaga
Rhamnaceae	
<i>Alphitonia zizyphoides</i>	
Rubiaceae	
<i>Cyclophyllum</i> (= <i>Canthium</i>) <i>barbatum</i>	
<i>Coffea arabica</i> (1)	café
<i>Eugenia reinwardtiana</i> (= <i>rariflora</i>)	
<i>Geniostoma hendersonense</i>	
<i>Guettarda speciosa</i>	puapua, uri
<i>Ixora fragrans</i>	

Scientific Name	Other names mentioned in text
<i>Morinda citrifolia</i>	
<i>Psydrax odoratum</i>	
<i>Tarenga sambucina</i>	
<i>Timonius polygamus</i>	
Rutaceae	
<i>Micromelum minutum</i>	
Santalaceae	
<i>Santalum yasi</i>	sandalwood
Sapotaceae	
<i>Nesoluma st-johnianum</i>	
<i>Palaquium steblinii</i>	
Solanaceae	
<i>Capsicum frutescens</i> (I)	capsicum, chili, chilli, little red pepper, wild chilli
<i>Solanum mauritianum</i> (I)	mock tobacco
<i>Solanum torvum</i> (I)	prickly solanum, salanum weed, wild eggplant
<i>Solanum verbascifolium</i> (I?)	
Tiliaceae	
<i>Grewia crenata</i>	
Ulmaceae	
<i>Trema cannabina</i> (= <i>orientalis</i>)	
Urticaceae	
<i>Pipturus argenteus</i>	
<i>Procris pedunculata</i>	
Verbenaceae	
<i>Faradaya powellii</i>	fei, mountain-plantain, petite banane, plantain
<i>Lantana camara</i> (I)	
<i>Premna serratifolia</i> (= <i>taitensis</i>)	
MONOCOTYLEDONAE	
Arecaceae	
<i>Cocos nucifera</i>	coconut
Dioscoreaceae	
<i>Dioscorea bulbifera</i>	soi, yam
Liliaceae	
<i>Asparagus cetaceus</i> (= <i>plumosus</i>) (I)	
Musaceae	
<i>Musa</i> sp.	banana
Orchidaceae	
<i>Vanilla planifolia</i> (I)	vanilla, vanille
Pandanaceae	
<i>Freycinetia arborea</i>	iié
Poaceae	
<i>Oryza</i> sp. (I)	rice
genus unknown	grass
[Family/scientific name unknown]	kaufia paku ndrau [<i>Ptilinopus perousii</i>]