

14. ECOLOGY AND SPECIES TURNOVER OF THE BIRDS OF LITTLE CAYMAN

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Introduction

The three Cayman Islands lie in the north-west Caribbean Sea, between Cuba and Jamaica. All are flat, low-lying limestone islands; the largest, Grand Cayman (185 sq. km) is about 117 km west of the two much smaller "lesser" Caymans, Little Cayman (24 sq. km) and Cayman Brac (31 sq. km). Little Cayman is the lowest of the group (maximum elevation 14 m) and is also the least disturbed by man. Human settlement is restricted to the immediate vicinity of the coast, chiefly in the south and west. Almost all the interior of the island is untouched by man, and had not previously been explored biologically. Most recent studies of island ecology and biogeography have been complicated by human disturbance, which introduces an unmeasured but undoubtedly significant factor into an island's ecology. On Little Cayman this effect is very slight, and the history and ecology of its avifauna are therefore of considerable scientific interest.

Previous work

The Cayman Islands were neglected ornithologically between the generally brief visits paid by the early collectors (Bangs 1916, Cory 1889, 1892, English 1916, Lowe 1911, Maynard 1889, Nicoll 1904, Townsend (in Ridgway 1887)) and the recent studies by Johnston and co-workers (Johnston, Blake and Buden 1971, Johnston 1975). All these workers, including the most recent, paid less attention to Little Cayman than to the other two islands. Johnston et.al. (1971) contains a number of unfortunate errors respecting both lesser Caymans, and Johnston (1975) refers chiefly to Grand Cayman and includes data from only 3 days spent on Little Cayman.

Previous workers on Little Cayman have necessarily been restricted to coastal habitats and the small areas of inland scrub woodland that were accessible from the footpaths then existing. In 1974, many narrow footpaths were cut all over the island to delimit plot boundaries, thus

making all the inland habitats accessible for the first time. It was therefore possible in 1975 to make the first thorough ornithological survey of the entire island, over a time period (9 July to 11 August) probably exceeding the total time spent by all previous ornithologists.

This paper is concerned chiefly with the ecology of the birds of Little Cayman, but it is helpful to consider the avifauna of the island first as a part of the Caymans as a group, i.e. in its West Indian context, and second in relation to the other two members of the group. Accordingly, the description of the ecological work that I carried out on the Royal Society and Cayman Islands Government Expedition to Little Cayman, is preceded by a brief analysis of the avifauna, supplementing the previous treatment by Johnston (1975).

The Cayman Island avifauna

(a) Derivation

The Cayman Islands lie more or less equidistant from Cuba and Jamaica, and about half as far again from Central America. These are therefore the most likely sources areas from which the Cayman avifauna has been derived. An analysis of the distribution of the species of land bird (pigeons to passerines) that breed in the Caymans (Tables 22 and 23) shows that their affinities are overwhelmingly West Indian rather than Central American; furthermore, most species occur also in the Greater Antilles, whence the predominant influence is Cuban and, to a much lesser extent, Jamaican. Many Cayman species do also occur in Central America, but all of these also occur in either Cuba or Jamaica (10 of the 14 occur in both) with the sole exception of *Vireo magister* which occurs on Grand Cayman and coastal Central America only. The single Lesser Antillean element in the avifauna is the flycatcher *Elaenia martinica*. The Cayman avifauna as a whole is thus predominantly Greater Antillean in affinities, with Cuba probably playing the major single role as a source area.

(b) Distinctiveness

Only one full species, the thrush *Mimocichla ravidia*, was endemic to the Caymans; it was restricted to Grand Cayman and may well now be extinct. However of the 28 landbird species that breed in the Caymans, no less than 15 species have forms, i.e. subspecies, that are endemic to the Caymans. Three of these — the parrot *Amazona leucocephala*, warbler *Dendroica vitellina* and grackle *Quiscalus niger* — have different forms on Grand Cayman from those on the "lesser" Caymans, making a total of 18 endemic forms (Table 23). The distribution of these forms is set out in Table 24. Clearly Grand Cayman has much the most distinctive avifauna, no less than 54% of its landbirds being endemic to the Caymans and 42% to Grand Cayman alone. The lesser Caymans are less distinctive, only Cayman Brac having an endemic form — the thrush *Mimocichla plumbea* — and the two islands together sharing only 3 endemic forms that are not also found on Grand Cayman (the parrot, warbler and grackle mentioned above). In addition, *Vireo magister* of Grand Cayman (and Central America) is replaced on the lesser Caymans by the very similar

Table 22. The species of land-birds breeding in the Cayman Islands, and their distribution elsewhere

	<u>Central America</u>	<u>Cuba</u>	<u>Jamaica</u>
White-crowned Pigeon <i>Columba leucocephala</i>	(isl)	X	X
Zenaida Dove <i>Zenaida aurita</i>	X	X	X
White-winged Dove <i>Zenaida asiatica</i>	X	X	X
White-bellied Dove <i>Leptotila jamaicensis</i>	(isl)	-	X
Ground Dove <i>Columbina passerina</i>	X	X	X
Cuban Parrot <i>Amazona leucocephala</i>	-	X	-
Mangrove Cuckoo <i>Coccyzus minor</i>	X	X	X
Smooth-billed Ani <i>Crotophaga ani</i>	(isl)	X	X
Barn Owl <i>Tyto alba</i>	X X	X	X
West Indian Nighthawk <i>Chordeiles gundlachii</i>	-	X	X
Flicker <i>Colaptes auratus</i>	-	X	-
W.I. Red-bellied Woodpecker <i>Centurus superciliaris</i>	-	X	-
Grey Kingbird <i>Tyrannus dominicensis</i>	-	X	X
Loggerhead Kingbird <i>Tyrannus caudifasciatus</i>	-	X	X
Stolid Flycatcher <i>Myiarchus stolidus</i>	-	X	X
Caribbean Elaenia <i>Elaenia martinica</i>	(isl)	-	- -
Northern Mockingbird <i>Mimus polyglottos</i>	-	X	X
Red-legged Thrush <i>Mimocichla plumbea</i>	-	X	-
Grand Cayman Thrush <i>Mimocichla ravida*</i>	-	-	-
Thick-billed Vireo <i>Vireo crassirostris</i>	-	-	-
Black-whiskered Vireo <i>Vireo altiloquus</i>	(isl)	X	X
Yucatan Vireo <i>Vireo magister</i>	X	-	-
Yellow Warbler <i>Dendroica petechia</i>	X	X	X
Vitelline Warbler <i>Dendroica vitellina</i>	-	-	-
Bananaquit <i>Coereba flaveola</i>	X	-	X
Stripe-headed Tanager <i>Spindalis zena</i>	(isl)	X	X
Greater Antillean Grackle <i>Quiscalus niger</i>	-	X	X
Jamaican Oriole <i>Icterus leucopteryx*</i>	-	-	X
Yellow-faced Grassquit <i>Tiaris olivacea</i>	X	X	X
Cuban Bullfinch <i>Melopyrrha nigra</i>	-	X	-

(isl) = only on offshore islands, not on mainland.

* = probably extinct.

Table 23. Distributional affinities of the breeding land-birds of the Cayman Islands and Little Cayman.

Figures in brackets show number of Central American species that are restricted to offshore islands (see Table 21).

	<u>Cayman Islands</u>	<u>Little Cayman</u>
Central America (total)	14 (5)	12 (14)
Cuba (total)	22	14
Jamaica (total)	20	14
All three (total)	10	10
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Cuba + Jamaica (total)	17	14
Central America only	1	0
Cuba only	5	0
Jamaica only	5	0
Cuba + Jamaica only	7	5
Lesser Antilles (+ Central America isl.)	1	1

V. altiloquus, but this form is not a Cayman endemic.

The Cayman avifauna is thus very distinctive at a subspecific level; this is particularly noteworthy in view of the relatively short time for which these low, flat limestone islands can have been available for habitation by landbirds. This argues a rapid rate of evolutionary change on these very small oceanic islands. Later, I show that species turnover is also rapid in the Cayman avifauna, suggesting that if a newly-arrived species is to survive, it must adapt very quickly to the local conditions in order to build up a large enough population to avoid extinction; the high level of endemism, at a subspecific level, is consistent with this suggestion.

One of the most striking features of the Cayman avifauna is the complete absence of hummingbirds. Throughout the West Indies, low islands similar to the Caymans have two species of hummingbird, one large and one small (Lack 1976); the Caymans are the only known exceptions to this. Lack (1976) could suggest no reason for this; ecological unsuitability of the Caymans for hummingbirds is very unlikely to be the cause, since there is no obvious reason why the Caymans should be less suitable for hummingbirds than any of the other low-lying limestone islands of the Caribbean. Lack did not accept that the vagaries of long-distance dispersal could have played any part in the distribution of land-birds in the West Indies, but in this instance it is difficult to avoid this conclusion, as indeed it is in

Table 24. The endemic forms of Cayman Island land-birds, and the islands on which they breed.

Populations probably extinct are bracketed

White-bellied Dove	<i>Leptotila jamaicensis collaris</i> .	G.C.
Cuban Parrot	<i>Amazona leucocephala caymanensis</i> .	G.C.
Cuban Parrot	<i>Amazona leucocephala hesterna</i> .	C.B., (L.C.)
Flicker	<i>Colaptes auratus gundlachii</i> .	G.C.
West Indian Red-bellied Woodpecker	<i>Centurus superciliaris caymanensis</i> .	G.C.
Loggerhead Kingbird	<i>Tyrannus caudifasciatus caymanensis</i> .	G.C., C.B., (L.C.)
Caribbean Elaenia	<i>Elaenia martinica caymanensis</i> .	G.C., C.B., L.C.
Red-legged Thrush	<i>Mimocichla plumbea coryi</i> .	C.B.
Grand Cayman Thrush	<i>Mimocichla ravid</i> .	(G.C.)
Yucatan Vireo	<i>Vireo magister</i> .	(G.C.)
Vitelline Warbler	<i>Dendroica vitellina vitellina</i> .	G.C.
Vitelline Warbler	<i>Dendroica vitellina crawfordi</i> .	C.B., L.C.
Bananaquit	<i>Coereba flaveola</i> .	G.C., C.B., L.C.
Stripe-headed Tanager	<i>Spindalis zena salvini</i> .	G.C.
Greater Antillean Grackle	<i>Quiscalus niger bangsi</i> .	C.B., L.C.
Greater Antillean Grackle	<i>Quiscalus niger caymanensis</i> .	G.C.
Jamaican Oriole	<i>Icterus leucopteryx bairdii</i> .	(G.C.)
Cuban Bullfinch	<i>Melopyrrha nigra taylori</i> .	G.C.

some other cases of bird distribution in the West Indies (Diamond 1973a).

The Little Cayman avifauna

Little Cayman has a depauperate avifauna in comparison to that of the Caymans as a whole, lacking an entire family — woodpeckers (Picidae) — and ten full species that breed, or have recently bred, elsewhere in the archipelago. Whether these species are missing because of ecological deficiencies on Little Cayman, or because of difficulties of dispersal, is difficult to judge. The fact that the Lesser Caymans have 5 forms that are not found in Grand Cayman, where they are replaced by related forms, could be interpreted from either viewpoint; these forms might have arrived in the Caymans from different sources, or they might have evolved differently, after a

single arrival, due to differences in the environments of the lesser Caymans and Grand Cayman. The much higher number of species in Grand Cayman, compared with the lesser Caymans, does suggest that it is richer ecologically (as would be expected from its larger size), since it is a similar distance from possible source areas as are the lesser Caymans.

Probably Little Cayman owes its impoverished landbird fauna chiefly to its ecological poverty; this takes the form not so much of a small variety of habitats as of the small extent and patchy distribution of habitats. Little Cayman probably has at least as many types of habitat as Cayman Brac, for example, but each is so small that it cannot support a distinctive avifauna. The only species that can survive there are therefore those of wide habitat tolerance, and with the ability to recolonise – in most cases probably from Cayman Brac, which is very near – after the local extinctions that seem to be a characteristic feature of the avifauna.

Ecology of the birds of Little Cayman

Objectives and methods

The objectives of the Royal Society and Cayman Islands Government Expedition to Little Cayman were to make as complete as possible a description of the biota of the island, and to make recommendations for its conservation and development. Within this context, the ornithological objectives can be summarised as follows:

- (1) to determine which species occur on Little Cayman, and their status;
- (2) to describe as fully as possible the ecology of each species, particularly in relation to habitat and food;
- (3) to draw attention to any species in need of special conservation measures;
- (4) to identify any habitat in need of special conservation measures because of its importance to birds.

The methods used were first, to define and map the habitats present, in conjunction with other members of the expedition (Stoddart 1979); second, to make systematic bird counts along transects (using cut paths) through each habitat. These counts were carried out before 09:00, i.e. when bird activity was at a maximum, using the methods of Lack (1976) in Jamaica and the Lesser Antilles and Diamond (1973a, unpub.) on St. Lucia, Martinique and Barbuda. This method served for terrestrial birds, but shore and sea birds were assessed differently. Non-systematic observations at coastal lagoons and on the sea shore were thought adequate to assess the status of shore birds and the scarcer seabirds; the large colony of Red-footed Boobies and Magnificent Frigatebirds was studied intensively and is described separately (Diamond 1979).

Results and discussion

(1) The species and their status

The species which have been recorded on Little Cayman are listed in the Systematic List (Appendix 1), which includes all published records to December 1975. The list includes 13 new records, definite breeding records for 13 species, and 21 species that are non-breeding migrants. The list is undoubtedly incomplete as regards North American migrants, but is probably complete for breeding species. Three species previously regarded as breeding residents - *Amazona leucocephala*, *Tyrannus caudifasciatus* and *Vireo crassirostris* - were certainly not breeding in 1975, and indeed of the three species the only record was a single distant view of a parrot. All are best regarded as extinct on Little Cayman, though probably the latter two were always sporadic breeders at best, for which local extinction on Little Cayman, with subsequent recolonisation from Cayman Brac, has been frequent. One waterbird, the Purple Gallinule *Porphyryula martinica*, has probably established itself as a breeding species in the last few years, and the Cattle Egret *Bubulcus ibis* colonised Grand Cayman in 1957 (Johnston et.al. 1971) and probably reached Little Cayman shortly thereafter. The Mockingbird *Mimus polyglottos* colonised sometime before 1966 and now thrives, but only along roads or around human settlements. This is the only one of the six species that have become established or extinct on Little Cayman since records began, in which the change of status can be attributed to man. The others all appear to involve natural species turnover and support the view that such turnover is a common phenomenon on small islands (MacArthur & Wilson 1963, 1967, MacArthur 1972, Diamond 1969, 1971, Diamond and Feare in press), rather than that turnover is rare and chiefly due to human influences (Lack 1976).

Species turnover on Grand Cayman and Cayman Brac was described by Johnston et.al. (1971). Unfortunately, all but one of the species that they listed as recent colonists, were not: *Phaethon lepturus*, *Sula leucogaster*, *Himantopus himantopus*, *Sterna albifrons*, *Hydranassa tricolor* and *Chordeiles minor* (= *C.gundlachii*) had all been recorded by the early workers. Nevertheless there have been real, documented changes in the avifauna, and these are set out in Table 25, which strongly suggests that species turnover is a regular feature of the avifauna of all three islands.

The numerical status of a species is difficult to estimate from a short visit at one time of year. The systematic list includes my personal assessment of the probable status of each species recorded on Little Cayman; these assessments are based on counts (Table 28) and breeding records (Table 27) for breeding land birds, and general experience in the West Indies, especially the neighbouring island of Jamaica, as well as the general works of Bond (1974) and Lack (1976), for other species. The abundance of island populations is likely to fluctuate considerably between years, and indeed species turnover is only the extreme case of fluctuation in population size.

Table 25. Distribution of Cayman Island endemic land-birds

Figures in brackets show totals before recent extinctions
(see Table 26)

	<u>Total No.</u>		<u>No. Cayman</u>		<u>No. island</u>	
	<u>Breeding Species</u>		<u>endemics</u>		<u>endemics</u>	
Total, Cayman Islands	28	(30)	16	(18)	10	(12)
Grand Cayman	26	(28)	12	(14)	9	(11)
Cayman Brac	20	(21)	7		1	
Little Cayman	18	(21)	6		0	
All three	16		3		-	
Lesser Caymans, total	17	(18)	4		-	
Lesser Caymans, alone	1		3		-	

(2) Habitats, food and ecological segregation

The distribution of habitats, and the transects through them, are shown in Fig. 30. Habitats not included on transects were the beach ridge vegetation and the inland *Sesuvium* marsh which were, respectively, too narrow and too small in area for quantitative sampling.

Bird counts made in each habitat are summarised in Table 28. For comparison, a single count made in the tall forest on the high bluff on Cayman Brac, above Stake Bay, is also included. Table 28 shows that most species occurred in most habitats; exceptions were the two *Dendroica* warblers, the Yellow *D. petechia* occurring only in mangrove and the Vitelline *D. vitellina* in limestone vegetation, the two overlapping only inland dwarf mangrove; the White-crowned Pigeon *Columba leucocephala* which occurred chiefly in mangrove, the only habitat in which it was heard singing; the Ground Dove *Columbina passerina*, not found in mangrove; and the Black-whiskered Vireo *Vireo altiloquus* which was restricted to the vicinity of tall trees, although this is not apparent in Table 28. The two *Dendroica* warblers, though segregated by habitat, also differed in feeding height in a remarkable

Table 26. Extinctions and colonisations in the Cayman Island avifauna

<u>Island</u>	<u>Species extinct</u>	<u>Species colonised</u>	<u>Notes</u>
GRAND CAYMAN	<i>Mimocichla ravidia</i>		Last seen 1938
	<i>Icterus leucopteryx</i>		Last seen 1938
		<i>Bubulcus ibis</i>	1st recorded 1957
		<i>Zenaida asiatica</i>	1st recorded ca.1935
CAYMAN BRAC	<i>Quiscalus niger</i>		absent 1970, 1971 (Johnston et.al.1971), 1971,1975(pers.obs.)
		<i>Bubulcus ibis</i>	Established 1957 or after
		<i>Zenaida asiatica</i>	Established presumably after 1935
		<i>Mimus polyglottos</i>	Date of arrival unknown
		<i>Leptotila jamaicensis</i>	Between 1971 and 1975
LITTLE CAYMAN	? <i>Amazona leucocephala</i>		see text — no good evidence ever bred
	<i>Tyrannus caudifasciatus</i>		see text — perhaps always sporadic
	<i>Vireo crassirostris</i>		Date unknown — see text
		<i>Bubulcus ibis</i>	1957 or after
		<i>Zenaida asiatica</i>	see Cayman Brac
		<i>Mimus polyglottos</i>	1st record ca. 1966
		<i>Porphyryla martinica</i>	post-1971

Table 27. Breeding records of Little Cayman birds, 9 July - 11 August 1975

<u>Species</u>	<u>Date</u>	<u>Description</u>
Common Stilt	24 July	Juvenile, unable to fly.
Common Stilt	25 July	2 fledgelings with 3 adults.
Ground Dove	16 July	Distraction display by empty nest scrape.
Ground Dove	16 July	1 very short-tailed juvenile seen.
West Indies Nighthawk	15 July	1 chick under <i>Tournefortia</i> bush.
West Indies Nighthawk	Late July	1 egg.
Grey Kingbird	16 July	Immature seen (very short-tailed).
Grey Kingbird	17 July	1 adult feeding 1 flying juvenile.
Caribbean Elaenia	13 July	Nest, 4.5 m in 7.6 m <i>Terminalia</i> tree;
Caribbean Elaenia	19 July	Same nest contained at least 2 large young.
Caribbean Elaenia	13 July	Nest, 2 young, 2.4 m in 3.0 m <i>Thrinax</i> tree.
Caribbean Elaenia	3 August	Nest, 5.4 m in 6.0 m <i>Coccoloba</i> tree, robbed (of egg(s)) by Grackle.
Caribbean Elaenia	3 August	Nest, 4.5 m in 4.8 m <i>Bursera</i> tree.
Black-whiskered Vireo	19 July	1 dependent juvenile with 1 adult.
Yellow Warbler	3 August	1 adult carrying nest material.
Yellow Warbler	6 August	2 dependent juveniles netted, Owen Island.
Vitelline Warbler	16 July	1 adult feeding 2 juveniles.
Vitelline Warbler	24 July	1 adult feeding 1 juvenile.
Vitelline Warbler	24 July	2 adults with 2 juveniles begging from them.
Bananaquit	24 July	1 juvenile begging from 1 adult.
Bananaquit	27 July	2 adults copulating.
Bananaquit	3 August	1 nest in <i>Myrcianthes fragrans</i> (Myrtaceae).
Bananaquit	4 August	1 adult carrying nest material.
Bananaquit	?	1 nest in <i>Bumelia glomerata</i> (Sapotaceae).
Greater Antillean	16 July	3/4 juveniles begging from adults.
" Grackle	19 July	2 juveniles begging from 2 adults; 1 adult fed a lizard to one.
"	24 July	1 adult carrying food to 1 juvenile.
"	3 August	1 adult feeding Elaenia egg to juvenile.
Yellow-faced Grassquit	26 July	Male carrying nest material.
Yellow-faced Grassquit	5 August	Male carrying nest material.

Table 28. Average number of birds per hour recorded in five habitats on Little Cayman

	closed woodland	open scrub	mixed scrub/ woodland	dwarf mangrove	tall mangrove	tall closed woodland, Cayman Brac
No. hours counting	2.0	3.0	3.9	2.3	0.7	0.7
White-crowned Pigeon <i>Columba leucocephala</i>	0	0.7	0	0.4	8.3	9.2
Zenaida Dove <i>Zenaida aurita</i>	5.5	5.6	3.8	0.9	1.4	15.4
White-winged Dove <i>Zenaida asiatica</i>	0	0	0.8	0	0	White-bellied Dove <i>Leptotila</i> <i>jamaicensis</i> 4.6
Ground Dove <i>Columbina passerina</i>	1.0	2.3	2.3	0	0	9.2
Mangrove Cuckoo <i>Coccyzus minor</i>	3.5	0	1.0	0	0	3.1
Grey Kingbird <i>Tyrannus dominicensis</i>	0	1.0	4.9	0.9	1.4	3.1
Caribbean Elaenia <i>Elaenia martinica</i>	24.5	16.3	17.4	3.9	11.1	32.3
Black-whiskered Vireo <i>Vireo altiloquus</i>	2.0	0.7	1.5	0	0	X
Yellow Warbler <i>Dendroica petechia</i>	0	0	0	1.3	6.9	0
Vitelline Warbler <i>Dendroica vitellina</i>	22.0	9.3	20.8	2.2	1.4	16.9
Bananaquit <i>Coereba flaveola</i>	11.5	11.3	5.1	4.8	6.9	1.5
Grackle <i>Quiscalis niger</i>	4.5	6.3	1.3	5.2	8.3	0
						Thick-billed Vireo <i>Vireo crassirostris</i> 9.2
						Yellow-faced Grassquit <i>Tiaris olivacea</i> 4.6
Number of species	8	9	10	8	8	12
Mean no. individuals/ hour	75	54	59	20	46	109

X = present, but not recorded in formal count.

Table 29. Habitats of breeding birds of Little Cayman

Includes probable breeders as well as those for which definite breeding records exist.

SPECIES	HABITAT								
	Exposed reef	Pools and lagoons	Cleared by man	sand beach ridge	Scrub (open)	Scrub woodland (closed)	Dwarf mangrove	Tall mangrove	Sesuvium marsh
Pied-billed Grebe		U							
Red-footed Booby							VC		
Magnificent Frigatebird							U		
Green Heron	FC	FC							FC
Little Blue Heron	FC	FC					FC		
Cattle Egret			FC						
Snowy Egret	FC	FC					FC	FC	
Tricoloured Heron	U	FC							
Yellow-crowned Night Heron		U		U					
West Indian Tree Duck		U							C
Common Guinea Fowl		U				U			
Purple Gallinule		U							U
Common Gallinule		FC							U
American Coot		FC							
Common Stilt		C							U
Willet		U							
Least Tern	U			U					
White-crowned Pigeon					U		U	VC	
Zenaida Dove					VC	VC	U	C	
White-winged Dove					U	U			
Common Ground Dove			C	U	C	U			
Mangrove Cuckoo					U	C			
Smooth-billed Ani			FC						
Barn Owl						U			
West Indian Nighthawk				FC				FC	
Grey Kingbird					C		U	FC	
Caribbean Elaenia			FC		VC	VC	FC	C	
Northern Mockingbird			FC						
Black-whiskered Vireo					U	FC			
Yellow Warbler							FC	C	
Vitelline Warbler					C	VC	FC	U	
Bananaquit			VC	C	VC	VC	FC	FC	
Greater Antillean Grackle			FC	U	FC	FC	FC	FC	
Yellow-faced Grassquit			C						

Notes: U = uncommon, FC = fairly common, C = common, VC = very common, as defined by Johnston (1975).

manner (Fig. 31). The almost complete segregation in feeding height between the two species is due only in part to differences in the height of vegetation in which they occur; this would explain why Yellow Warblers fed higher than Vitelline, since there were more tall mangroves than tall terrestrial trees, but not why almost no Yellow Warbler feeding took place between 2 and 4 metres. The samples are of course very small, but are nonetheless highly significant statistically ($\chi^2 = 28.6$, $p < .001$). Why the species should so segregate, when they already have almost completely different habitats, is very difficult to see; possibly at other seasons one moves more into the other's habitat.

Four species of essentially insectivorous small passerines occur widely, three of them overlapping considerably in habitat, and Table 30 shows that they feed in different ways. The two *Dendroica* warblers have already been discussed; the tyrannid flycatcher *Elaena martinica* took more fruit than the others and also caught more of its insect food by flycatching, whereas the Bananaquit *Coereba flaveola* took a high proportion of nectar. The large tyrannid *Tyrannus dominicensis* might also have been included, but only 13 feeding observations were made, 11 of flycatching at about 6 m above ground and 2 of pouncing onto the ground -- it takes presumably bigger insect prey, and certainly less fruit, than the *Elaenia*. Differences in feeding ecology seem to be rather more important than differences in habitat in maintaining ecological segregation on Little Cayman, probably because of the very limited range of habitats available.

The richest habitat in terms of individuals was closed scrub woodland on marl facies limestone, but slightly more species occurred in the intermediate scrub/scrub woodland area at the western end of the island. The dwarf and coastal mangroves contained about as many species as the limestone habitats, but very many fewer individuals. The tallest forest on Little Cayman, in the centre of the island south of Sparrowhawk Hill, was no different in either species composition or number of individuals from the surrounding woodland, and counts in the two habitats have been combined here. No habitat on Little Cayman approached the tall dense forest on Cayman Brac in numbers of either individuals or species (Table 28).

Not all habitats were counted systematically, but species found in each were recorded and these observations are summarised in Table 28.

(3) Species needing special conservation measures

The Vitelline Warbler *Dendroica vitellina* is the most distinctively Caymanian land-bird breeding on Little Cayman but in 1975 it was widespread and abundant there. It also occurs on both the other islands, where it is common (Johnston 1975). No special measures seem necessary for this or any other land-bird on Little Cayman.

Water-birds may be more threatened, since all stretches of open water are near the coast, where development is most likely. However unless complete drainage or filling, or large-scale pollution, are likely, sufficient area of open water should remain to maintain viable

Table 30. Feeding methods of 4 insectivorous passerines on Little Cayman

Species	n	Feeding method				
		Insects			Other	
		FL	GL	FL-GL	FRUIT	NECTAR
Caribbean Elaenia	40	35	30	12.5	22.5	0
Yellow Warbler	25	12	64	0	0	20
Vitelline Warbler	37	2.7	67.5	27	2.7	0
Bananaquit	25	0	28	0	0	72

Notes: n = number of feeding observations (maximum of 5 taken from one individual). FL = Flycatching; GL = gleaning; FL-GL = flycatcher-gleaning (as defined by Croxall (1977)).

Figures are percentage of observations (n) for each species.

populations of most water-birds. The *Sesuvium* marsh in the east of the island may prove to be an important breeding site for many of these species, especially the Tree Duck *Dendrocygna arborea*, and should be preserved both for its birds and for its intrinsic ecological interest.

The large colony of boobies and frigatebirds is described separately, but is mentioned briefly here as these are the species most in need of conservation measures; this is one of the largest, and surely the most accessible, of all West Indian seabird colonies. Necessary conservation measures include preservation of the mangroves in which both species nest, combined with maximum possible prevention of human and mechanical disturbance near the colony.

(4) Habitats needing special conservation measures

The mangroves comprising the booby and frigatebird colony have been identified (above) as the habitat of the species most in need of protection. No other single habitat is comparable in importance to bird life on Little Cayman. However it must be remembered that all the habitats on Little Cayman extend over small areas, so that destruction or disturbance of one habitat is likely to affect bird populations in others. In Section (2) it was shown that most land-birds occur in most habitats, and probably most individuals use many

of the habitats at one time or another. Hence it is ecologically unrealistic to approach the problem of conserving the avifauna in terms of individual habitats – the whole island needs to be considered as a single unit. It is in the almost completely undisturbed nature of the island as a whole that its chief biological interest lies, no more and no less for the birds than for any other biota. The scientific importance of an island that can be studied in an almost undisturbed state is already great, and will increase as more and more islands become developed. It may be unrealistic to propose that development on Little Cayman be restricted to its present level, but on biological grounds this is the course that must be recommended.

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Appendix 1. Systematic list

Nomenclature follows Lack (1976) for pigeons and passerines, Bond (1974) for remaining families.

Pied-billed Grebe *Podilymbus podiceps*. Regular in small numbers on some of the coastal lagoons, in breeding plumage. Probably a scarce breeding resident.

Brown Pelican *Pelecanus occidentalis*. Johnston *et. al.* (1971) describe this as an occasional visitor to all three islands, but the only definite record given is for Grand Cayman. Probably an occasional visitor.

Red-footed Booby *Sula sula*. The breeding colony of over 7,000 birds in the mangroves north and west of the lagoon behind Blossom Village is one of the largest in the Caribbean, and is described separately (Diamond 1979).

Anhinga *Anhinga anhinga*. 1 record, August 1971 (Johnston *et.al.* 1971).

Magnificent Frigatebird *Fregata magnificens*. Up to 20 pairs bred in the booby colony in 1971 (Diamond, unpub.). In 1975 they were not nesting, but the absence of adult males then suggests a breeding cycle with the same timing as elsewhere in the Caribbean (Diamond 1972, 1973b). Only flying immatures and adult females were seen, the maximum number seen together being 43.

Green Heron *Butorides virescens*. Regular in small numbers in the coastal lagoons and on the reef flats at low tide, and also common in the *Sesuvium* marsh inland. Probably a breeding resident.

Little Blue Heron *Florida caerulea*. Regular in small numbers around coastal lagoons. One immature seen. Probably a scarce breeding resident.

Cattle Egret *Bubulcus ibis*. Up to seven at the airstrip, feeding in short grass, in absence of cattle. Probably a scarce breeding resident, colonised within the last 20 years (Johnston *et.al.* 1971).

Snowy Egret *Egretta thula*. Regular in small numbers, in both coastal lagoons and reef flats at low tide. May breed.

Tricoloured Heron *Hydranassa tricolor*. Regular in coastal lagoons, and the commonest ardeid on the reef flat at low tide. Probably a breeding resident.

Yellow-crowned Night Heron. *Nyctanassa violacea*. Regular in coastal lagoons and on sea shore, especially at dusk. One immature seen; probably a fairly common breeding resident.

Glossy Ibis *Plegadis falcinellus*. One seen at airstrip, 24 July. No other records. Vagrant.

Roseate Flamingo *Phoenicopterus ruber*. 1 record, October 1970 (Johnston *et.al.* 1971). Vagrant.

West Indian Tree Duck *Dendrocygna arborea*. Occasional in coastal lagoons and over dwarf mangrove inland, but main concentration of up to 30 birds in *Sesuvium* marsh, where they fed in *Sesuvium* itself. May breed, probably resident.

Blue-winged Teal *Anas discors*. Recorded in October (Johnston *et.al.* 1971); probably a regular winter visitor.

Osprey *Pandion haliaetus*. Uncommon (Johnston *et.al.* 1971); probably a scarce but regular transient.

Merlin or Pigeon Hawk *Falco columbarius*. 1 record, February 1905 (Lowe 1911). Probably an occasional winter visitor.

Common Guinea Fowl *Numida meleagris*. Seen occasionally at edge of lagoon behind Pirate's Point. Presumably introduced.

Purple Gallinule *Porphyryla martinica*. Only 3 previous records for the Caymans, all from Grand Cayman (Johnston et.al. 1971). Regular, in small numbers, in coastal lagoons and in *Sesuvium* marsh, where a probable juvenile was seen. Probably breeds; evidently a recent colonist.

Common Gallinule *Gallinula chloropus*. Common in coastal lagoons, probably a breeding resident.

American Coot *Fulica americana*. Regular in small numbers in some coastal lagoons, especially at western end of island; probably a breeding resident.

Semipalmated Plover *Charadrius semipalmatus*. Seen regularly on muddy margins of coastal lagoons. Not previously recorded specifically for Little Cayman, though Lowe (1911) described it as "resident in the Caymans". Probably a regular migrant.

Thick-billed Plover *Charadrius wilsonia*. Seen regularly on muddy margins of coastal lagoons. No previous record. Probably a regular migrant.

Black-bellied Plover *Squatorola squatorola*. Seen in ones and twos in coastal lagoons and on sea shore. No previous records. Probably a regular migrant.

Ruddy Turnstone *Arenaria interpres*. Occasional in coastal lagoons. 1 previous record. Probably a regular migrant in small numbers.

Common Stilt *Himantopus himantopus*. A common breeding species of coastal lagoons; also recorded in *Sesuvium* swamp.

Spotted Sandpiper *Actitis macularia*. 2 seen on road, south-west coast, 26 July. Probably a regular winter visitor.

Greater Yellowlegs *Tringa melanoleuca*. Regular in small numbers in coastal lagoons. 1 previous record. Probably a common winter visitor.

Lesser Yellowlegs *Tringa flavipes*. Same status as *T. melanoleuca*; often seen together. No previous record.

Willet *Cataprophorus semipalmatus*. Coastal lagoons; probably less than 20 birds in all. May breed, but no good evidence.

Least Sandpiper *Calidris minutilla*. Small numbers arrived with the following species on 24 July, in coastal lagoons. No previous record. Probably a regular migrant.

Semi-palmated Sandpiper *Calidris pusilla*. See preceding species. No previous record. Probably a regular visitor.

Sanderling *Crocethia alba*. 1 seen on south coast. No previous record. Probably a regular visitor.

American Dowitcher *Limnodromus griseus*. 2 seen with a single *L. scolopaceus* in the pool behind Pirate's Point, 12 to 14 July. No previous record. Probably a scarce migrant.

Long-billed Dowitcher *Limnodromus scolopaceus*. See preceding species. No previous record; probably a vagrant.

Laughing Gull *Larus atricilla*. 1 seen by Dr M.V. Hounsome. 1 previous record; probably an occasional visitor.

Gull-billed Tern *Geochelidon nilotica*. 2 adults, over west end of booby colony, 26 July. No previous record. Probably a vagrant.

Least Tern *Sterna albifrons*. One or two seen regularly along the south coast, including the lagoons. 1 dependent juvenile begging from 2 adults, 22 July, is not conclusive evidence of breeding because it might have flown from Cayman Brac. Probably a small resident breeding population.

Royal Tern *Thalasseus maximus*. 1 seen with 6 Least Terns, Owen Island, 25 July (Dr G. Potts). 1 previous record, October 1956 (Johnston et.al. 1971). Probably an occasional visitor.

White-crowned Pigeon *Columba leucocephala*. Commonest in mangrove, especially the tall coastal *Rhizophora*, the only place where song was heard. Substantial evening passage over East Point to Cayman Brac. Probably breeds, but most may do so on Cayman Brac.

Zenaida Dove *Zenaida aurita*. Common in all the limestone habitats, scarce in mangrove. Several times seen feeding on ground, occasionally apparently on *Bursera* fruits. Probably a breeding resident.

White-winged Dove *Zenaida asiatica*. Recorded only in the intermediate scrub/scrub woodland at west end, and scarce even there. Probably a breeding resident.

Common Ground Dove *Columbina passerina*. A fairly common breeding resident, found in all terrestrial habitats but not mangrove.

Cuban Parrot *Amazona leucocephala*. Only 1 record during the expedition, of a bird flying over the centre of the island, 27 July. May once have bred in large trees in the tall central forest, but probably not since the hurricane of 1935 destroyed the largest trees there, leaving no suitable nest sites.

Mangrove Cuckoo *Coccyzus minor*. Heard commonly in more closed limestone habitats. Not found in mangrove. Probably a breeding resident. Twice seen mobbed by small passerines, once by *Elaenia martinica* and once by *Quiscalus niger*.

Yellow-billed Cuckoo *Coccyzus americanus*. 2 records, August and October (Johnston et.al. 1971); probably a vagrant.

Smooth-billed Ani *Crotophaga ani*. A common breeding resident, restricted to beach-hedge vegetation and disturbed areas around houses and the airfield, where commonly seen in groups of up to 10, including immatures.

Barn Owl *Tyto alba*. Heard in tall central forest at night, by Dr M.V. Hounsome. Apparently very scarce on all these islands (Johnston *et.al.* 1971), but probably breeds.

Common or West Indies Nighthawk *Chordeiles gundlachii*. Apparently restricted to the coast, where 2 nests were found. Commonly seen feeding at dusk over the coast. A scarce breeding resident.

(Family Picidae. Woodpecker sp. Dr M.V. Hounsome heard a woodpecker drumming on 26 July but was unable to see the bird. There is no previous record of any woodpecker from either of the lesser Caymans, although two species breed on Grand Cayman.)

Yellow-bellied Sapsucker *Sphyrapicus varius*. "Uncommon winter visitor" (Johnston *et.al.* 1971); the characteristic holes made by this species were conspicuous in palm *Cocos nucifera* trunks on the coast.

Grey Kingbird *Tyrannus dominicensis*. Described by Johnston *et.al.* (1971) as a summer resident on all three islands. Commonest in the more open habitats of Little Cayman, absent from tall closed woodland (including mangrove); its habitats are very similar to those on Jamaica (Lack 1976). Only 13 feeding observations were made, 11 of flycatching at about 6 m, 2 of pouncing to the ground. Probably a summer visitor, as elsewhere in the north and western Caribbean (Bond 1974, Lack 1976).

Loggerhead Kingbird *Tyrannus caudifasciatus*. Described by Johnston *et.al.* (1971) as a "fairly common resident" on all the Caymans. I did not find it and queried its presence with Johnston who (in litt. 1975) confirmed that he saw only 1 on Little Cayman. Brown collected several on Little Cayman in 1911 (Bangs 1916), but neither Nicoll (1904) nor Lowe (1911) recorded it there in 1904. This species seems therefore to have been at best a sporadic inhabitant of Little Cayman.

Caribbean Elaenia *Elaenia martinica*. A very common breeding resident, the most conspicuous and widespread landbird on Little Cayman, especially in closed forest. The only positively identified food was the red berry of *Guapira discolor* (Nyctaginaceae), which was fruiting abundantly and was commonly taken by Elaenias.

Caribbean Martin *Progne dominicensis*. 1 recorded by expedition; no previous records. Probably an occasional visitor to all three islands.

Barn Swallow *Hirundo rustica*. Seen on about ten days during the expedition. 1 previous record, but probably a regular passage migrant.

Northern Mockingbird *Mimus polyglottos*. First recorded in 1966 (Johnston *et.al.* 1971), now established in the coastal areas inhabited or cleared by man, including the end of the road at Calabash Spot where one was heard singing.

Blue-gray Gnatcatcher *Polioptila caerulea*. 1 record (Cory 1889). Probably a vagrant.

Cedar Waxwing *Bombycilla cedrorum*. 1 record, April 1888 (Johnston *et.al.* 1971); vagrant.

Thick-billed Vireo *Vireo crassirostris*. Previously reported as a common breeding resident, and certainly collected by the early workers. Johnston (*in.litt.* 1975) did not see it in 1971, and nor did we in 1975 though it was common on Cayman Brac then. This species, like *Amazona leucocephala* and *Tyrannus caudifasciatus*, has evidently become extinct on Little Cayman since the early part of the century.

Black-whiskered Vireo *Vireo altiloquus*. A scarce but widespread bird on Little Cayman, probably breeding, and apparently confined to the vicinity of tall trees (ca. 8 m and over).

Black-and-White Warbler *Mniotilta varia*. 1 record (Lowe 1911), but probably a regular winter visitor.

Prothonotary Warbler *Protonotaria citrea*. 1 record, August 1961 (Johnston *et.al.* 1971); probably a vagrant.

Yellow Warbler *Dendroica petechia*. Common breeding resident, confined almost entirely to mangrove. Elsewhere in the West Indies, shows complex interactions with other *Dendroica* species, in some places being confined to coastal habitats by a sympatric congener in the forest inland (e.g. *D.adelaidae* on St. Lucia), moving into rain forest where no congener is present (e.g. Martinique), elsewhere coexisting with a congener in habitats similar to those on Little Cayman (e.g. *D.adelaidae* on Barbuda (*pers.obs.*)) — Diamond (1973a, Lack 1976). The Barbuda situation is most similar ecologically to that on Little Cayman, yet there *D.petechia* overlaps considerably in habitat with a congener, whereas on Little Cayman the two *Dendroica* species are strictly separated by habitat, at least in the summer — this situation would warrant further study.

Black-throated Blue Warbler *Dendroica caerulescens*. 1 record (Cory 1889); probably a scarce winter visitor.

Yellow-throated Warbler *Dendroica dominica*. Seen in mangroves 26 July and 2 August. 2 previous records. Probably a scarce passage migrant or winter visitor.

Blackpoll Warbler *Dendroica striata*. 1 record, August 1961 (Johnston *et.al.* 1971). Probably a vagrant.

Prairie Warbler *Dendroica discolor*. Recorded by Cory (1889) and Johnston *et.al.* (1971). Probably a regular winter visitor.

Vitelline Warbler *Dendroica vitellina*. This species is endemic to the Cayman and Swan Islands. Common throughout Little Cayman, except in mangrove. Breeding success was high in 1975; of the individuals whose age could be told in the field, 22 were adult and 17 juvenile, a proportion of 1.6 young per pair which is much higher than is usual in tropical passerines (c.f. 0.34 in Sarawak (Fogden 1972), 0.90 in Jamaica (Diamond 1974)). The juvenile plumage is sufficiently similar to the adult *Vireo crassirostris* to cause some initial confusion in the field, and is not described in the literature — olive grey above, pale eye-ring and superciliary, pale buff beneath. The ecological relationship between this species and the Yellow Warbler is described under *D. petechia* and in section 2 of the Results.

Palm Warbler *Dendroica palmarum*. 1 record (Cory 1889); probably a common winter visitor.

Ovenbird *Seiurus aurocapillus*. 1 record (Lowe 1911); probably a regular winter visitor.

Louisiana Waterthrush *Seiurus motacilla*. 1 netted and ringed, 30 July. No previous record, but probably a regular winter visitor.

Common Yellowthroat *Geothlypis trichas*. 1 record (Cory 1889), but probably a common winter visitor.

American Redstart *Setophaga ruticilla*. 1 record (Johnston *et.al.* 1971), but probably a regular winter visitor.

Bananaquit *Coereba flaveola*. A common and widespread breeding resident, in all habitats.

Greater Antillean Grackle *Quiscalus niger*. A common breeding resident, occurring in all habitats. Once seen taking an egg from a nest of *Elaenia martinica*.

Bobolink *Dolichonyx oryzivorus*. 1 record (Cory 1889); probably a regular spring passage migrant.

Yellow-faced Grassquit *Tiaris olivacea*. A common breeding resident, but confined to more open and disturbed coastal areas and roadsides.

Appendix 2. Ring number, weight, moult and breeding condition of land-birds ringed on Little Cayman, July - August 1975.

Ring	Species	Date	Age/Sex	Weight,g	Moult	Brood patch
Y 1	<i>Elaenia martinica</i>	19 July	F.G.	20.0	Early	-
Y 2	<i>Vireo altiloquus</i>	19 July	F.G.	20.25	Early	-
Y 3	<i>Coereba flaveola</i>	19 July	Ad.	10.75	Late	Present
Y 4	<i>Coereba flaveola</i>	19 July	Ad.	10.75	Late	-
Y 5	<i>Elaenia martinica</i>	19 July	F.G.	21.5	Early	-
Y 6	<i>Elaenia martinica</i>	19 July	F.G.	22.25	-	-
Y 7	<i>Elaenia martinica</i>	19 July	F.G.	22.75	Early	-
Y 8	<i>Elaenia martinica</i>	19 July	F.G.	20.0	Early	-
Y 9	<i>Coereba flaveola</i>	19 July	Ad.	12.25	Late	-
Y 10	<i>Coereba flaveola</i>	19 July	Juv.	-	Mid	-
Y 11	<i>Coereba flaveola</i>	19 July	Juv.	11.5	-	-
Y 12	<i>Coereba flaveola</i>	19 July	Juv.	8.75	-	-
B 1	<i>Columbina passerina</i>	19 July	F.G.	35.0	-	-
B 22	<i>Columbina passerina</i>	20 July	Imm	25.75	-	-
Y 13	<i>Elaenia martinica</i>	20 July	Ad.	27.0	Early	Present
Y 14	<i>Coereba flaveola</i>	20 July	Imm	9.75	-	-
Y 15	<i>Coereba flaveola</i>	20 July	Imm/Ad.	10.25	Late	-
Y 16	<i>Coereba flaveola</i>	20 July	Ad.	10.75	Late	-
Y 17	<i>Elaenia martinica</i>	20 July	F.G.	19.25	Early	-
Y 18	<i>Elaenia martinica</i>	20 July	F.G.	21.0	-	-
Y 19	<i>Coereba flaveola</i>	20 July	Ad.	10.5	Mid	-
B 3	<i>Columbina passerina</i>	20 July	Imm	24.5	-	-
B 4	<i>Columbina passerina</i>	20 July	Ad.	39.0	Mid	-
B 5	<i>Tyrannus dominicensis</i>	29 July	Ad.	-	-	-
Y 20	<i>Elaenia martinica</i>	29 July	Ad.	23.5	-	Present
Y 21	<i>Coereba flaveola</i>	30 July	Ad.	10.75	Complete	-
Y 22	<i>Elaenia martinica</i>	30 July	F.G.	20.5	-	-
Y 23	<i>Seiurus motacilla</i>	30 July	F.G.	18.0	Complete	-
Y 24	<i>Elaenia martinica</i>	30 July	F.G.	21.0	-	-
Y 25	<i>Coereba flaveola</i>	30 July	Juv.	9.0	-	-
Y 26	<i>Coereba flaveola</i>	30 July	Ad.	9.0	Late	-
-	<i>Elaenia martinica</i>	6 August	F.G.	19.5	Early	-
-	<i>Dendroica petechia</i>	6 August	Ad.M.	11.25	Early	-
-	<i>Dendroica petechia</i>	6 August	Juv.F.	11.0	-	-
-	<i>Dendroica petechia</i>	6 August	Juv.M.	11.5	-	-

Notes: Rings were plastic, coloured, Y = yellow, B = blue. All netted at Pirate's Point except those on 6 August, netted on Owen Island.

F.G. = full grown; Ad. = adult; Juv. = juvenile; Imm. = immature; Imm/Ad. = moulting from Imm. to Ad. plumage; M = male; F = female.

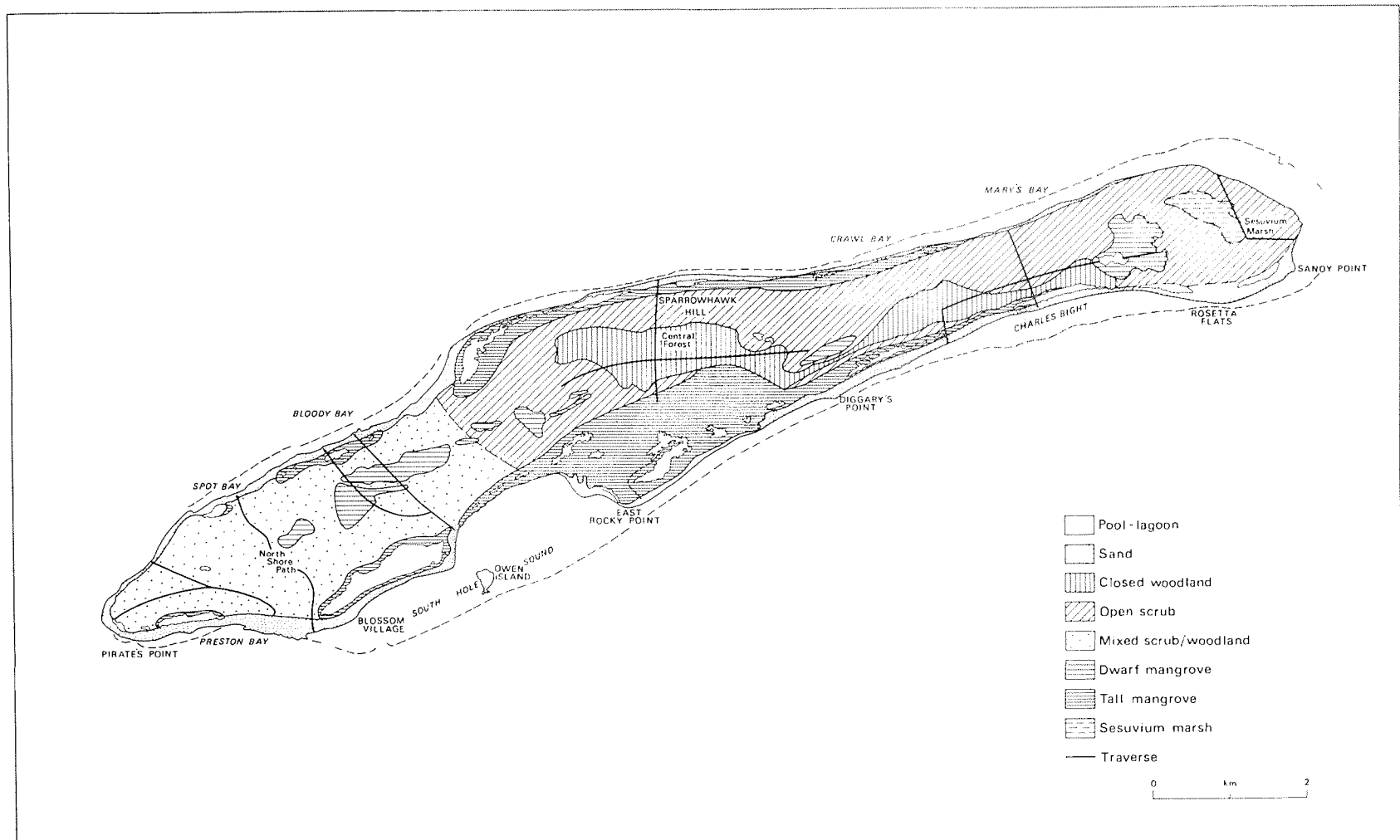
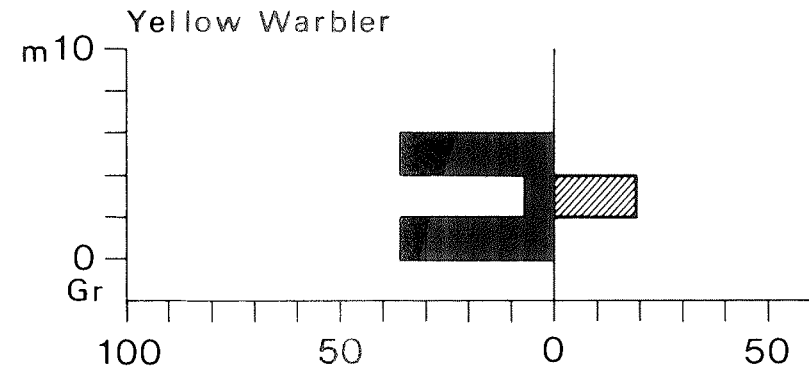
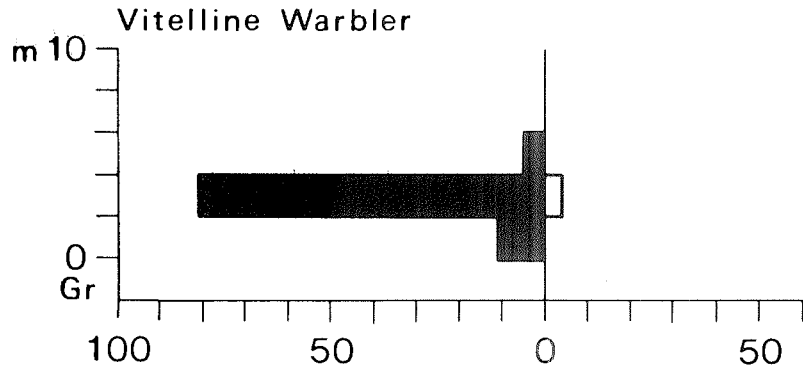
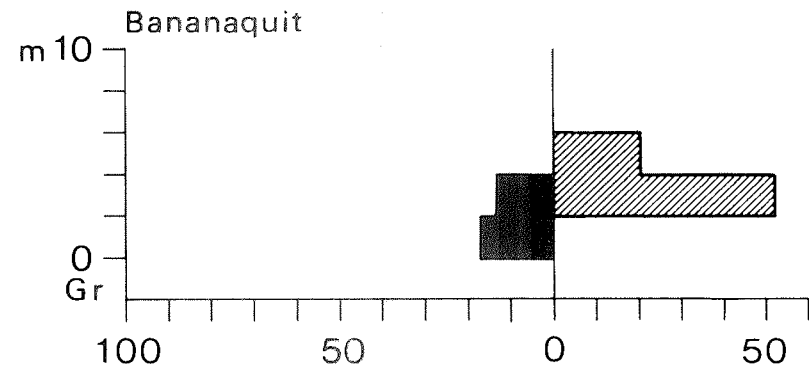
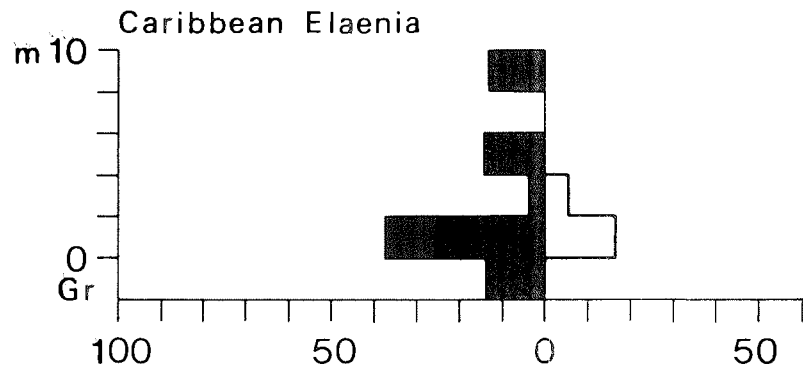


Figure 30. Map showing location of the main habitats on Little Cayman, place names, and cut paths used as transects



Feeding on insects
 Feeding on fruit
 Feeding on nectar

Figure 31. Feeding heights of four insectivorous passerines on Little Cayman: (a) Caribbean Elaenia; (b) Bananaquit; (c) Vitelline Warbler; (d) Yellow Warbler. Ordinate: height in intervals of 2 m (Gr = ground). Abscissa: percentage of feeding observations in each height class. White areas (right of 0%): feeds on fruit (Elaenia, Vitelline Warbler) or nectar (Bananaquit, Yellow Warbler). Black areas (left of 0%): feeds on insects. For sample sizes, see Table 29