SEARCH TACTICS OF INSECTIVOROUS BIRDS FORAGING IN AN AUSTRALIAN EUCALYPT FOREST

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ABSTRACT.—The different ways birds searched for food in an Australian *Eucalyptus* forest led them to detect and capture different kinds of prey. Five major searching modes were identified among 23 common, mostly insectivorous bird species. These were distinguished largely by the rates, distances, and angles moved by birds while foraging and by their prey-capture behavior. Some bird species typically moved slowly, visually examining substrates at relatively long distances, and then took flight to capture prey (e.g. whistlers, flycatchers, muscicapid robins, cuckoos). Others moved at more rapid rates and either gleaned small prey from nearby substrates (e.g. thornbills, treecreepers) or flushed insects that were then pursued (e.g. fantails). Two species (Eastern Shrike-Tit, *Falcunculus frontatus*; White-eared Honeyeater, *Meliphaga leucotis*) were specialized substrate-restricted searchers, seeking invertebrate and carbohydrate foods among the exfoliating bark of *Eucalyptus*.

The search tactics of birds in this south temperate Australian forest were similar to those of birds in a north temperate forest in New Hampshire, USA, previously reported by Robinson and Holmes (1982). The differences in food-searching behavior between these phylogenetically distinct avifaunas (e.g. search flight and prey-attack flight lengths, hop/flight ratios, foraging rates) reflect the effects of unique foliage structures (e.g. spacing of branches, arrangements of leaves) and food resources at each site.

These findings support the hypothesis that habitat structure and food availability provide opportunities and constraints on how birds search for and capture food in forest habitats. These in turn are postulated to affect the success of particular bird species exploiting those habitats and thus influence bird community patterns. *Received 25 October 1985, accepted 25 January 1986.*

THE subject of how and where birds obtain their food has been central to the field of avian ecology (Lack 1954, MacArthur 1958, Watson 1970). While many studies of bird foraging have focused on prey-capture techniques and substrates from which prey are taken (e.g. Morse 1968, Holmes et al. 1979, and others), recent findings have shown that the methods used by birds in searching for food, leading up to prey capture, and the factors that influence these searching patterns may be particularly important for understanding bird diets and ultimately community structure. Robinson and Holmes (1982, 1984) showed that search tactics of foraging birds in a north temperate forest were related to the physical and biotic features of the environment, primarily vegetation structure and prey availability. These in turn were postulated to limit the foraging opportunities available to birds in a given place and, hence, which species of birds could successfully exploit and survive in that environment. Pearson (1975) reached a similar conclusion from analyses of forest structure and bird species diversity in tropical forests.

Although food-searching behavior has been analyzed frequently for species that feed in open country, such as ground-foraging thrushes (Smith 1974a, b; Paszkowski 1982; Moreno 1984) and aerial-feeding flycatchers (Davies 1977), only Morton (1980) and Fitzpatrick (1981) in the Neotropics and Robinson and Holmes (1982, 1984) in the north Temperate Zone have analyzed quantitatively searching patterns of forest birds.

We studied the ways in which insectivorous birds search for and capture prey in a south temperate eucalypt forest in southeastern Australia. We then compared the results with those of Robinson and Holmes (1982), who used the same methods and analytical procedures. The latter study was conducted in a temperate deciduous forest at Hubbard Brook in New Hampshire, USA, where both the flora and avifauna are phylogenetically distinct from those in the Australian study area. Although there is no reason to expect direct niche equivalency between these geographically isolated and independently evolved avifaunas, comparisons of bird foraging patterns in such contrasting environments allow us to identify the habitat features that influence bird search behaviors and diets and thus to understand the factors that help determine bird community structure.

STUDY AREA AND METHODS

The study was conducted on the Southern Tablelands of New South Wales (NSW) and adjacent Victoria in southeastern Australia between 1 October and 31 December 1980. Three 10-ha study areas were located approximately 40 km southeast of Bombala, NSW (36°54'S, 149°14'E) near the Bondi State Forest. Detailed descriptions of the vegetation, climate, and bird populations of the Bondi study areas are given by Recher et al. (1983, 1985) and Recher and Holmes (1985). For our purposes here, we treat these three plots as a single habitat, specifically a forest-woodland ecotone grading from a moist, tall, open forest through drier, open forest to woodland at the edge of grazed pastures.

The dominant trees in the moist forest were *Eucalyptus radiata, E. viminalis,* and *E. dalrympleana,* with occasional *E. fastigata* and *E. cypellocarpa.* Canopy height averaged about 22 m, with a few trees reaching 40 m. The subcanopy, shrub, and ground vegetation was well developed and relatively dense.

The areas of drier forest were dominated by *E. radiata, E. viminalis, E. ovata,* and *E. dalrympleana.* Canopy height averaged 16-20 m. The shrub layer was relatively open, due to the grazing of domestic stock and some logging. The dry forest graded into woodland dominated by *E. pauciflora* and *E. stellulata,* which had a lower canopy (8-10 m) than the forest.

We quantified the behavior of foraging birds at Bondi using the methods of Robinson and Holmes (1982). We moved systematically about each study plot, and when a foraging bird was encountered, recorded its actions on a tape recorder. Only adult birds that were clearly foraging were followed, and these were observed for as long as they could be kept in sight. When the bird was lost from view or when it stopped foraging, we moved on until another active forager was located. We alternated study plots and routes between days and at different times of day. The relatively open and evenly dispersed foliage of these eucalypt habitats permitted good visibility at all levels of the vegetation.

We obtained data from 1,136 foraging sequences on 23 bird species; the average length of foraging sequences was 79 s, and the total accumulated observation time was 20,262 s. For the more common species, 20-30 different individuals were observed, while for the less common ones, at least 6 individuals of each were represented in the sample.

Searching movements were divided into (1) flights, in which birds change perches by flying, and (2) hops, in which they shift position without extending their wings. For all flights, we estimated the angles (in increments of 45° from the horizontal) and distances moved (in increments of 0.3 m for distances <1 m, 0.5 m for those between 1 and 2 m, and 1-m units for longer flights). We recorded the frequency of hops but, because most were short moves of <5 cm, distances moved while hopping were not estimated.

We recorded all attempts to capture prey and the substrates on which the prey were located. Because we could not always determine if attempts were successful, any prey-directed action was considered a prey attack. When an attack involved a flight, we estimated the angle flown and the distance moved. Prey attacks were recorded as glean, hawk, snatch (or hover), pounce, probe, or prise. These are defined and described by Holmes et al. (1979) and Recher et al. (1985).

Foraging observations were transcribed from the tapes and timed using a stop watch. We accepted for analysis only sequences >30 s in length, and for each of these we tallied the number of hops, flights, and prey attacks. Dividing these by the length of each sequence, we obtained measures of search and prey-attack rates. These rates were averaged over all sequences for each bird species, following Robinson and Holmes (1982). Correlations were based on values for individual species, not guild averages. Search tactics of Bondi and Hubbard Brook birds were compared, where possible, using Mann-Whitney *U*-tests.

RESULTS AND DISCUSSION

THE BIRD COMMUNITY AND FORAGING GUILDS

We obtained data on the food-searching patterns of 23 species of insectivorous birds [see Table 1 for scientific names and taxonomic (family) affiliations]. These represent the most common, relatively small birds (7-76 g) that feed primarily on insects and other arthropods in eucalypt forests of southeastern Australia (see Loyn 1980; Recher et al. 1980, 1985; Recher and Holmes 1985 for details on the forest avifauna of this region). We included as insectivores the Yellow-faced, White-eared, and White-naped honeyeaters (Meliphagidae), which are often considered nectar feeders (Recher et al. 1985) but which take most of their food from the surface of foliage or from under loose bark (Table 1). Observations on the search behavior of other less common species also were gathered and are referred to below where appropriate.

The 23 species were divided into foraging guilds (cf. Root 1967) based on their primary methods of prey capture and the substrates to which those prey attacks were directed (boldface entries in Table 1). The groupings of species by guild are given in Table 2.

Searching Patterns

Locomotory patterns.—The movement patterns exhibited by birds searching for prey at Bondi often differed among species, even among those within the same foraging guild (Table 2). For rates of movement while searching, five categories were distinguished among the 23 species: (1) The very fast searchers were birds that changed positions more than 30 times/min, and included 4 ground gleaners, 1 bark gleaner, and 2 foliage gleaners (Table 2). (2) The fast searchers, which consisted of 2 ground gleaners, 1 bark gleaner, 1 loose-bark priser, and 3 foliage gleaners, moved 24–28 times/min (Table 2). (3) The medium-fast searchers moved 15–20 times/min, and included the bark-prising Eastern Shrike-Tit and the aerial-hawking Grey Fantail. (4) The slow searchers changed positions 7–11 times/min. These were the 2 foliage-snatching whistlers. (5) The very slow searchers moved <3.5 times/min; these were the ground-pouncing robins, the Fan-tailed Cuckoo, and the aerial-hawking Satin Flycatcher.

All species but the ground pouncers and Satin Flycatcher had hop/flight (H/F) ratios >1 (Table 2), indicating that hopping is their major mode of movement when searching for prey. The ground pouncers and the flycatcher sat in one place, searched nearby substrates, and flew only occasionally between perches.

Search flight characteristics.—When searching for food in the eucalypt forests, most birds made relatively short flights, primarily horizontally and obliquely upward (Figs. 1 and 2). Hence, they generally stayed within the same strata or patch of vegetation during single foraging bouts. Few discernible differences existed among species or guilds in angles flown. The only exception was the bark-gleaning treecreepers, which flew more often vertically (Recher and Holmes pers. obs.), relating to their use of tree trunks as foraging substrates.

Frequency distributions and average lengths of search flights differed among species and guilds (Figs. 1 and 2). Three major groupings were distinguished: (1) the foliage and ground gleaners, which made many short flights, averaging <0.3 m (Figs. 1 and 2); (2) an intermediate- and variable-distance group consisting of the foliage snatchers and loose-bark prisers, which made flights primarily of 0.5–1.5 m (Fig. 1); and (3) birds that often flew 2 m or more when they changed perches, including the aerial hawkers (Fig. 1) and the ground pouncers (Fig. 2). The mean search flight length (4.7 m) for the latter group is inflated by the inclusion of the Fan-tailed Cuckoo, whose search flights averaged 7.2 m (Fig. 2); the flight lengths of the three other ground pouncers, all muscicapid robins, averaged 3.9 m. Although our sample size for the bark-gleaning treecreepers was small, they do not fit into any of these groups. Treecreepers made few flights, most of which were very short (<0.3 m), often around a tree or up and down the trunk (see Noske 1979, 1985). Treecreepers also made long flights to distant trees, but these trees were considered to be a new foraging "patch" and the flights were not recorded.

Mean lengths of search flights were inversely correlated with average hop rates ($r = -0.77$, $P < 0.001$). Thus, species that hopped frequently made only short flights. Also, the average lengths of search flights and the average rates at which the species changed perches were inversely correlated ($r = -0.80$, $P < 0.001$), indicating that species that flew long distances between perches tended to stay longer on those perches and vice versa. There was no significant correlation between mean bird size (measured as cube root of body mass) and search rate ($r = 0.32$, $P > 0.70$); that is, small species did not change perches more often than large ones. These same relationships were found for foliage-gleaning species at Hubbard Brook (Robinson and Holmes 1982).

Prey-attack rates.—The rates at which birds attacked prey ranged from 1.7 times/min for ground pouncers to 11.5/min for bark gleaners (Table 2). Prey-attack rates correlated highly with the mean number of perch changes/min ($r = 0.86$, $P < 0.001$); thus, species that moved rapidly made more attempts to catch prey/time. Such species, however, tended to take small prey, while those that foraged more slowly took

TABLE 1. Use of foraging substrates and prey-attack behaviors of the 23 species of common insectivorous forest birds in the eucalypt forests and woodlands near Bondi State Forest.

		Percentage use of substrate/behaviors							
		Foliage		Air	Bark[b]	Loose bark[c]	Ground		
Family and species	Body mass[a] (g)	Glean	Snatch/ hover	Hawk	Glean/ probe	Prise	Pounce	Glean/ probe	(*n*)
Cuculidae									
Fan-tailed Cuckoo (*Cuculus pyrrphanus*)	46.3	1		1	12		**85**[d]	1	(94)
Muscicapidae									
Scarlet Robin (*Petroica multicolor*)	13.0		3	16	13		**66**	2	(460)
Flame Robin (*Petroica phoenicea*)	13.3	6		19	11		**51**	13	(816)
Eastern Yellow Robin (*Eopsaltria australis*)	20.0	5		7	9		**76**	3	(401)
Grey Fantail (*Rhipidura fuliginosa*)	9.3	3	10	**80**	4			3	(2,308)
Satin Flycatcher (*Myiagra cyanoleuca*)	17.5		31	**63**	5		1		(428)
Rufous Whistler (*Pachycephala rufiventris*)	25.8	11	**50**	14	20	3	1	1	(963)
Golden Whistler (*Pachycephala pectoralis*)	25.3	8	**60**	10	17	3		2	(544)
Grey Shrike-Thrush (*Colluricincla harmonica*)	75.6	4	8		24	22	1	**41**	(287)
Eastern Shrike-Tit (*Falcunculus frontatus*)	28.6	3	1		5	**90**		1	(518)
Timaliidae									
Eastern Whipbird (*Psophodes olivaceus*)	62.2	3	2		12	31		**53**	(133)
Maluridae									
Superb Blue Wren (*Malurus cyaneus*)	9.7	7	2	4	2			**85**	(798)
Acanthizidae									
Brown Thornbill (*Acanthiza pusilla*)	6.9	**51**	14	5	18	5		7	(1,820)
Striated Thornbill (*Acanthiza lineata*)	7.1	**68**	13	1	14	4			(2,326)
Yellow-rumped Thornbill (*Acanthiza chrysorrhoa*)	8.8	3		1	1	2		**93**	(376)
Buff-rumped Thornbill (*Acanthiza reguloides*)	7.5	13	2	1	19	6		**59**	(553)
White-browed Scrubwren (*Sericornis frontalis*)	12.8	10	1		6	2		**81**	(704)
Climacteridae									
Red-browed Treecreeper (*Climacteris erythrops*)	23.3				**70**	29		1	(1,211)
White-throated Treecreeper (*Climacteris leucophaea*)	21.8				**92**	7		1	(1,208)
Meliphagidae									
White-eared Honeyeater (*Meliphaga leucotis*)	24.5	17	2		22	**59**			(612)
Yellow-faced Honeyeater (*Meliphaga chrysops*)	17.1	**74**	3		12	10		1	(894)

TABLE 1. Continued.

Family and species	Body mass[a] (g)	Percentage use of substrate/behaviors: Foliage		Air	Bark[b]	Loose bark[c]	Ground		(n)
		Glean	Snatch/hover	Hawk	Glean/probe	Prise	Pounce	Glean/probe	
White-naped Honeyeater (*Melithreptus lunatus*)	14.6	**81**			8	1			(2,792)
Dicaeidae									
Striated Pardalote (*Pardalotus striatus*)	11.9	**84**	9	1	5	1			(805)

[a] Body masses from Recher et al. 1985.
[b] Refers to bark adhering close to tree trunks and branches.
[c] Refers to peeling and hanging strips of bark.
[d] Boldface entries represent the predominant substrate-behavior category for each species.

larger prey (Holmes and Recher unpubl. data). There was no significant correlation between the size of bird species (cube root of body mass) and prey-attack rate ($r = 0.37$, $P > 0.70$).

Characteristics of prey-attack flights.—The distances and angles of flights used by birds in attacking prey provide further insight into their search behavior. Flight lengths indicate the distance over which the birds sight prey (see Robinson and Holmes 1982), while the angles of flights indicate directions from which prey are detected.

The distances and angles of prey-attack flights that terminated in snatching, hovering, or pouncing are summarized in Fig. 3 for species that frequently employed these foraging maneuvers (see Table 1). The angles for prey-attack flights of foliage gleaners, foliage snatchers, and aerial hawkers were strongly oriented horizontally or obliquely upwards. The prey-attack flights of species in these guilds were directed primarily at snatching prey. An exception was the Striated Thornbill, which snatched and hovered about equally (6 and 7% of all prey attacks, respectively; Recher et al. 1985). In contrast, ground pouncers directed 83% of their prey attacks obliquely downward (Fig. 3). Almost all of these were pounces onto the ground, or, less frequently, onto tree trunks. The few attacks directed horizontally or upward (Fig. 3) represented snatches, which comprised <10–15% of prey attacks (Recher et al. 1985). The distances flown to snatch or pounce on prey varied considerably among species (Fig. 3). The shortest strikes were made by foliage gleaners, with progressively longer ones by foliage snatchers, aerial hawkers, and ground pouncers (Fig. 3).

When hawking insects, the foliage-gleaning thornbills made short flights (mean = 0.3 m) directed horizontally or obliquely upwards (Fig. 4). In contrast, the whistlers hawked insects at an average distance of 1.1 m and moved horizontally or obliquely downward (Fig. 4). The hawking flights of Grey Fantails and Satin Flycatchers, the two species that foraged predominately in this manner, averaged 1.6 m and, like the thornbills, were angled mostly horizontally and obliquely upward (Fig. 4). The hawking flights of Flame and Scarlet robins were long, averaging 3 m, and were mainly directed horizontally and obliquely downward (Fig. 4).

Average lengths of flights that terminated in attacks on sitting prey (i.e. hovers, snatches, and pounces) were correlated highly with the average distance moved between perches while searching for prey ($r = 0.95$, $P < 0.001$; data from Fig. 3). The lengths of hawking flights and distances moved between perches also were correlated significantly ($r = 0.98$, $P < 0.001$; data from Fig. 4). Thus, birds that flew short distances between perches attacked prey that were nearby, while those that flew long distances saw and attacked prey that were farther away. Thus, these forest birds moved just far enough when they changed perches to take them into a new, previously unsearched area. The same relationship was found for foliage-searching

TABLE 2. Searching and prey-attack rates ($\bar{x} \pm$ SE) of foraging insectivorous birds near Bondi State Forest.

	n (S)[a]	Hops/min (H)	Flights/min (F)	Perch changes/min (H + F)	H/F ratio	Prey attacks/min
Foliage gleaners						
Brown Thornbill	105 (5,560)	30.5 ± 1.0	5.0 ± 0.3	35.5	6.1	9.9 ± 0.4
Striated Thornbill	149 (7,036)	29.1 ± 0.8	6.4 ± 0.3	35.5	4.5	13.2 ± 0.4
Striated Pardalote	29 (1,693)	23.7 ± 1.5	4.5 ± 0.7	28.2	5.3	7.3 ± 0.6
Yellow-faced Honeyeater	38 (2,179)	22.1 ± 1.3	5.8 ± 0.4	27.9	3.8	10.6 ± 0.7
White-naped Honeyeater	31 (1,911)	22.8 ± 1.4	4.2 ± 0.5	27.0	5.4	12.6 ± 1.0
Mean		25.1	5.2	30.3	5.0	11.0
Foliage snatchers						
Rufous Whistler	107 (13,122)	6.1 ± 0.4	3.9 ± 0.2	10.0	1.6	1.5 ± 0.1
Golden Whistler	39 (4,102)	5.9 ± 0.7	4.7 ± 0.3	10.6	1.3	2.3 ± 0.3
Mean		6.0	4.3	10.3	1.5	1.9
Aerial hawkers						
Grey Fantail	110 (7,298)	10.0 ± 0.9	5.4 ± 0.3	15.4	1.9	6.1 ± 0.2
Satin Flycatcher	52 (6,675)	0.4 ± 0.1	2.4 ± 0.2	2.8	0.2	2.3 ± 0.1
Mean		5.2	3.9	11.1	1.1	4.2
Bark gleaners						
Red-browed Treecreeper	19 (1,102)	26.2 ± 2.1	1.0 ± 0.2	27.2	26.0	8.9 ± 2.0
White-throated Treecreeper	23 (1,273)	39.7 ± 3.4	0.2 ± 0.1	39.9	198.2	14.1 ± 1.8
Mean		33.0	0.6	33.6	112.1	11.5
Loose-bark prisers						
Eastern Shrike-Tit	23 (1,775)	16.2 ± 1.2	3.1 ± 0.4	19.3	5.2	5.6 ± 0.5
White-eared Honeyeater	31 (1,911)	22.8 ± 1.4	4.2 ± 0.5	27.0	5.4	12.6 ± 1.0
Mean		19.5	3.7	23.2	5.3	9.1
Ground pouncers						
Fan-tailed Cuckoo	14 (4,459)	0.03 ± 0.02	0.8 ± 0.2	0.8	0.04	0.5 ± 0.1
Flame Robin	32 (3,765)	0.9 ± 0.3	2.6 ± 0.3	3.5	0.3	2.6 ± 0.2
Scarlet Robin	37 (4,919)	0.1 ± 0.07	1.5 ± 0.2	1.6	0.1	2.1 ± 0.2
Eastern Yellow Robin	44 (4,725)	0.4 ± 0.1	2.4 ± 0.3	2.8	0.2	1.6 ± 0.1
Mean		0.4	1.8	2.2	0.2	1.7
Ground gleaners/probers						
Grey Shrike-Thrush	33 (3,162)	23.8 ± 2.5	2.2 ± 0.3	26.0	10.8	5.8 ± 0.3
Eastern Whipbird	22 (1,644)	21.2 ± 1.8	3.0 ± 0.3	24.2	7.1	5.8 ± 0.6
Superb Blue Wren	37 (1,945)	39.5 ± 2.5	4.2 ± 0.4	43.7	9.4	8.3 ± 0.8
White-browed Scrubwren	36 (1,621)	35.0 ± 1.6	4.0 ± 0.5	39.0	8.8	13.7 ± 0.9
Yellow-tailed Thornbill	31 (1,608)	45.4 ± 1.9	0.5 ± 0.2	45.9	90.8	9.7 ± 0.8
Buff-rumped Thornbill	30 (1,615)	30.9 ± 2.3	3.6 ± 0.6	34.5	8.6	11.3 ± 0.6
Mean		32.6	2.9	35.5	22.6	9.1

[a] n = number of foraging sequences (S = cumulative number of seconds).

insectivorous birds at Hubbard Brook (Robinson and Holmes 1982) and for neotropical tyrannid flycatchers (Fitzpatrick 1981).

SEARCHING MODES AND DIETS: BONDI VS. HUBBARD BROOK

The search behavior of insectivorous birds at Bondi can be summarized by combining species with similar search patterns into 5 major searching modes. Each mode is characterized by a set of searching tactics and prey-attack methods that result in the perception and capture of different types of prey (Table 3). The information on diets of these Australian species are largely qualitative, deriving from our observations at Bondi and from the literature (particularly Lea and Gray 1936). These search-

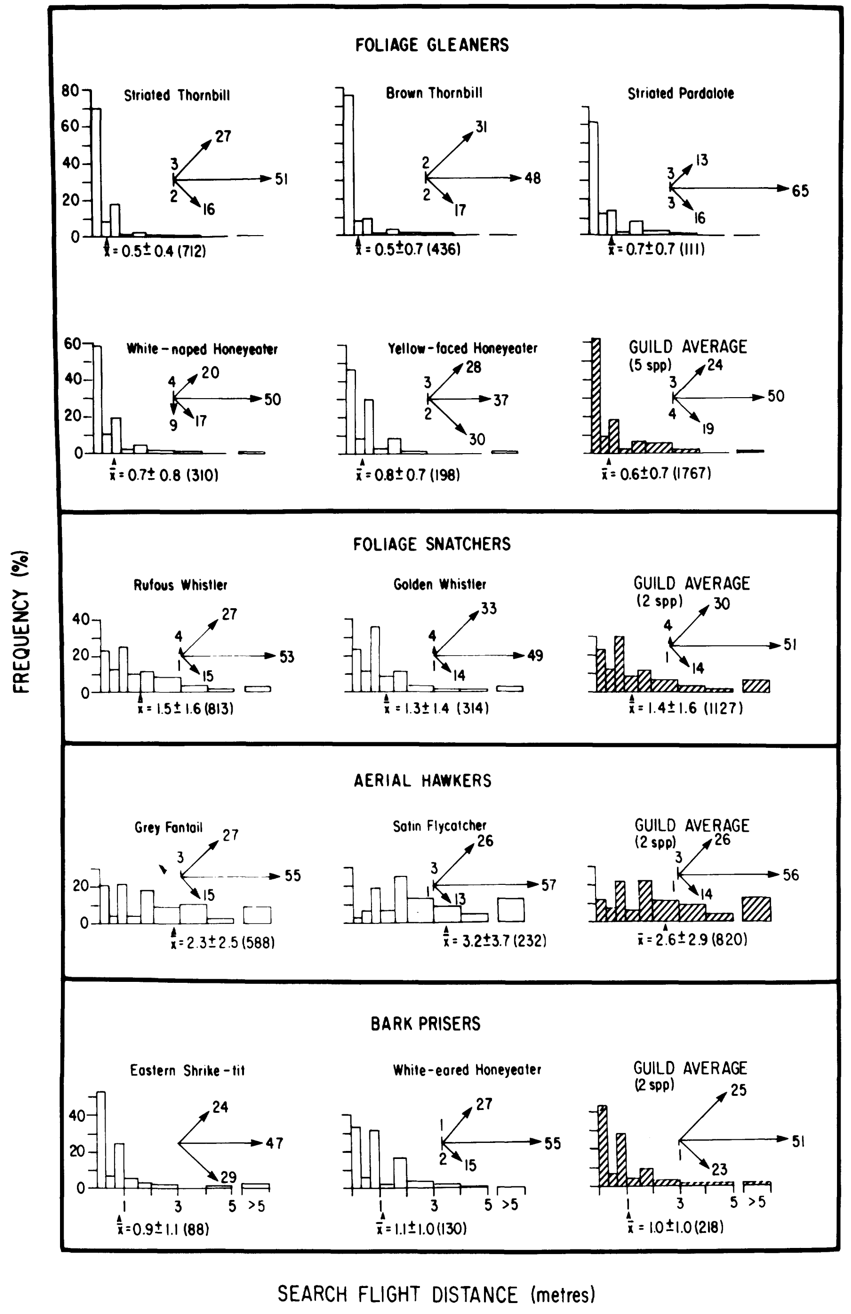


Fig. 1. Search flight characteristics of birds that foraged primarily above ground level in the eucalypt forests at Bondi, southeastern Australia. Species are grouped by foraging guilds (see Table 1); treecreepers are excluded due to insufficient sample sizes. Lengths and means (±SD) of search flights are given in the histograms, and angles of flights between perches are shown as vector diagrams. On the latter, arrows indicate flights that are straight up, 45° upward, horizontal, 45° downward, and straight down. Vector lengths are proportional to the percentages of flights in the directions indicated.

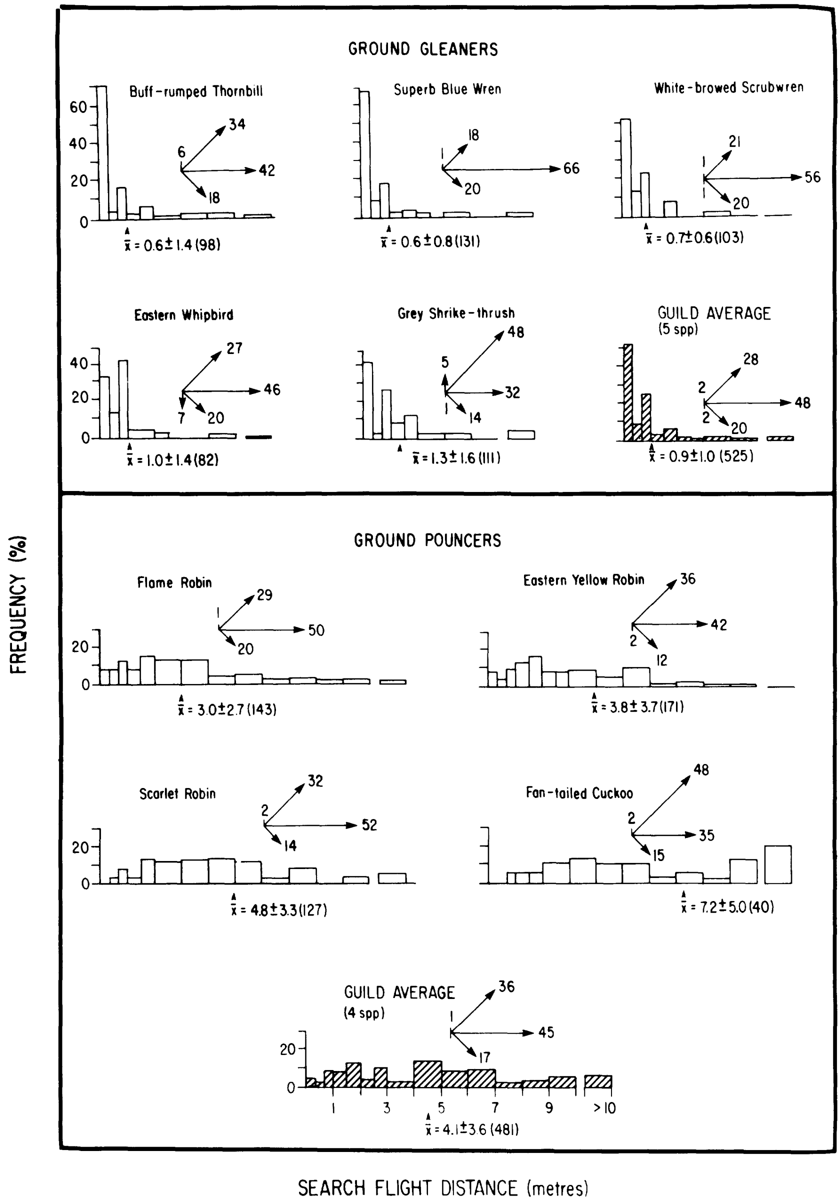


Fig. 2. Search flight characteristics of birds that foraged primarily on the ground in the eucalypt forests at Bondi. See Fig. 1 for further details.

ing modes are arranged in Table 3, using groupings and names consistent with those identified for birds in north temperate forests by Robinson and Holmes (1982), to which we contrast them in the following sections.

(1) *Open-perch searching.*—Birds that use this searching pattern sit and scan nearby substrates and the surrounding airspace. They fly from one perch to another and rarely hop (H/F ratios $\ll$ 1). Most of their prey attacks involve long flights, primarily pounces and hawks, and the prey obtained are mostly invertebrates active on the surface of the ground or in the air (Table 3). The main group of open-perch searchers at Bondi are the ground pouncers—the three robins and the Fan-tailed Cuckoo—which sit on perches in the subcanopy or shrub layer. From these perches they scan the forest

floor and trunks of nearby trees, and pounce on large prey such as beetles, grasshoppers, and moths. Eastern Yellow Robins occasionally took small lizards (Recher pers. obs.).

The other species to use this search method is the Satin Flycatcher, which sits high above the ground, within the relatively open canopy or alongside a canopy gap, and sallies out after flying prey. It also snatches some prey from nearby foliage (Table 1). Its food consists of actively flying insects such as flies, wasps, and beetles (Table 3).

At Hubbard Brook, where the vegetation is relatively dense, the open-perch searchers (a tyrannid flycatcher, and a tanager: Thraupidae) sit on exposed perches, mainly in the subcanopy, and search nearby foliage. They then fly either horizontally or obliquely upward, mostly to hover at or snatch prey from leaves or relatively infrequently hawk insects from the air (Robinson and Holmes 1982). Their search-flight and prey-attack distances are significantly shorter ($P < 0.05$) than those of the Australian open-perch searchers. They also change perches significantly more often ($P < 0.05$), but the H/F ratios and prey-attack rates of the two groups are not statistically different ($P > 0.9$ and $P > 0.12$, respectively).

No species at Hubbard Brook are specialized as ground pouncers, but two thrushes (Swainson's Thrush, *Catharus ustulatus*; Veery, *C. fuscescens*) use this foraging method occasionally (15% of observed prey attacks, $n = 450$; Holmes and Robinson unpubl. data).

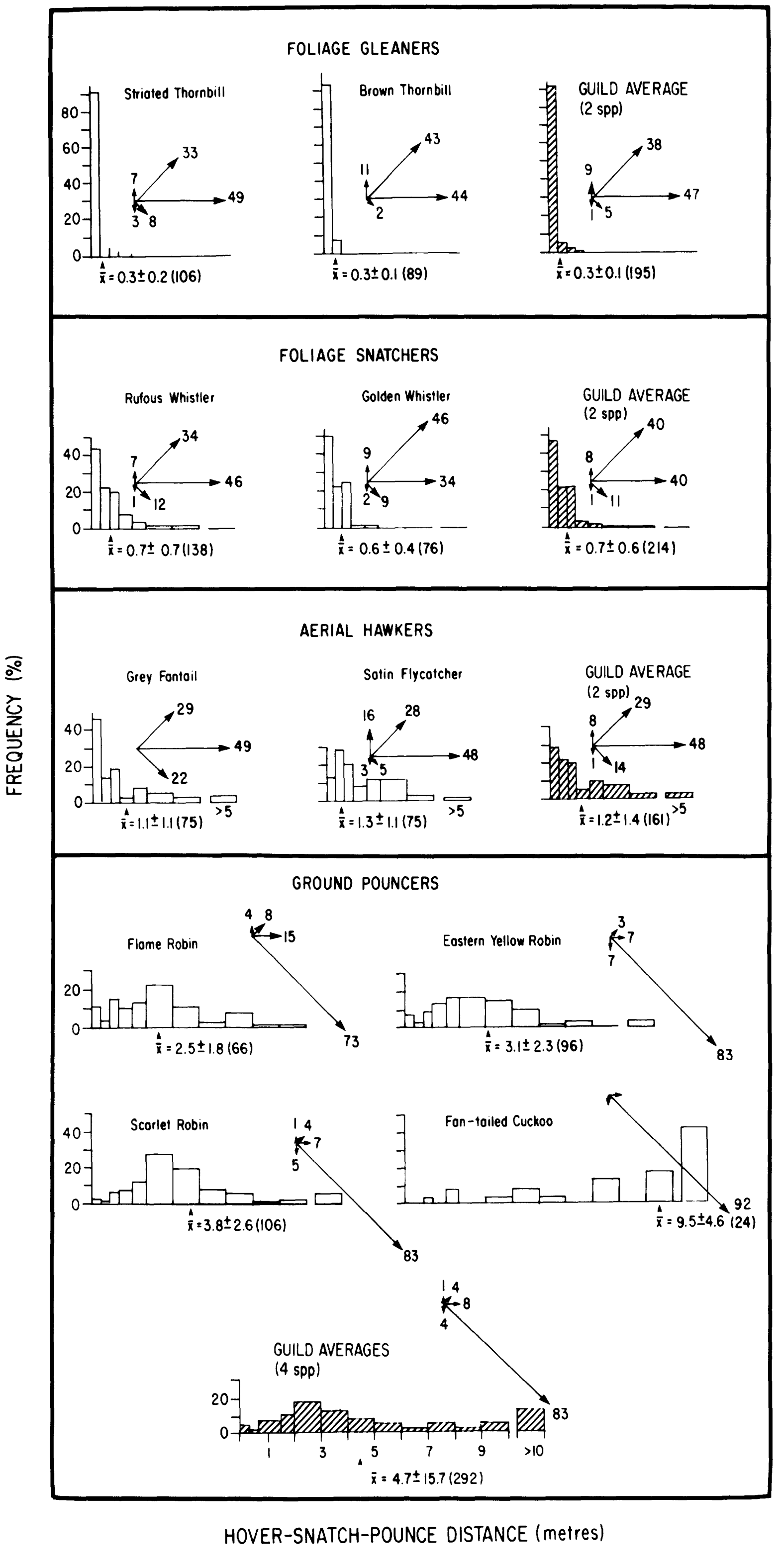
(2) *Flush-chasing.*—This search pattern involves an actively hopping or flying bird, moving among foliage and along branches from which prey are flushed and then pursued, often in a tumbling, erratic flight (Table 3). This is equivalent to the "flitting" category of Crome (1978) and Frith (1984). At Bondi, this search tactic is used by the Grey Fantail and the less common Rufous Fantail (*Rhipidura rufifrons*; Recher et al. 1985), and results in the pursuit and capture of small- to medium-size moths. Fantails also use this foraging technique to find and capture midges, wasps, and other highly mobile insects (Lea and Gray 1936, Cameron 1985).

Flush-chasing is very similar to the search and prey-attack behavior of American Redstarts (*Setophaga ruticilla*) at Hubbard Brook (Robinson and Holmes 1982). Redstarts change perches more often than fantails (27 vs. 15/min) but make shorter search flights (0.9 vs. 2.3 m). Fantails pursue their prey in acrobatic flights for long distances, often for 5 m or more (Holmes and Recher unpubl. data).

(3) *Medium-distance searching.*—This mode is characterized by birds that hop frequently along branches and among foliage and make short- to medium-length (1–2 m) horizontal flights between perches. They scan foliage up to 1 m away and fly horizontally or obliquely upward to snatch relatively large insects from foliage and small branches (Table 3). The two whistlers were the major species that used this pattern, but the less common Black-faced Flycatchers (*Monarcha menalopsis*) and Rose Robins (*Petroica rosea*) also snatched most of their prey from foliage (Recher et al. 1985) and searched in a similar manner. The prey obtained by whistlers using this search pattern included a variety of adult insects (81% of 68 observed captures consisted of beetles, flies, adult moths, and cicadas), while larvae, mostly Lepidoptera but also some sawfly (Hymenoptera: Tenthredinidae), also were taken (Holmes and Recher unpubl. data).

These tactics are similar to those of three *Vireo* species and a fringillid, the Rose-breasted Grosbeak (*Pheucticus ludovicianus*), at Hubbard Brook, which feed mostly on Lepidoptera larvae (Robinson and Holmes 1982). As a group, their rates of movement, H/F ratios, and prey-attack rates were not statistically different ($P > 0.35$) from those of the whistlers. The whistlers, however, differed from the vireos by hopping more than flying, with H/F ratios of 1.3–1.6 and 0.3–0.7, respectively, and, subjectively, by not moving as steadily through the foliage as they searched for insects (Holmes and Recher pers. obs.). Whistlers often sat for long periods, scanning nearby foliage and branches for cryptic prey. Although the vireos were listed as hoverers by Robinson and Holmes (1982), they snatch most of their food from leaves, as determined more recently when snatching was distinguished as a separate category (Holmes unpubl. data); thus, they are similar to the whistlers. The grosbeak, however, gleans more often (56%) than either the vireos (Robinson and Holmes 1982) or the whistlers (Table 1).

(4) *Near-surface searching.*—This pattern involves birds hopping along a substrate and gleaning or picking small insects from nearby


FOLIAGE GLEANERS
Striated Thornbill
x̄ = 0.3 ± 0.2 (106)
Brown Thornbill
x̄ = 0.3 ± 0.1 (89)
GUILD AVERAGE
(2 spp)
x̄ = 0.3 ± 0.1 (195)
FOLIAGE SNATCHERS
Rufous Whistler
x̄ = 0.7 ± 0.7 (138)
Golden Whistler
x̄ = 0.6 ± 0.4 (76)
GUILD AVERAGE
(2 spp)
x̄ = 0.7 ± 0.6 (214)
AERIAL HAWKERS
Grey Fantail
x̄ = 1.1 ± 1.1 (75)
Satin Flycatcher
x̄ = 1.3 ± 1.1 (75)
GUILD AVERAGE
(2 spp)
x̄ = 1.2 ± 1.4 (161)
GROUND POUNCERS
Flame Robin
x̄ = 2.5 ± 1.8 (66)
Eastern Yellow Robin
x̄ = 3.1 ± 2.3 (96)
Scarlet Robin
x̄ = 3.8 ± 2.6 (106)
Fan-tailed Cuckoo
x̄ = 9.5 ± 4.6 (24)
GUILD AVERAGES
(4 spp)
x̄ = 4.7 ± 15.7 (292)
FREQUENCY (%)
HOVER-SNATCH-POUNCE DISTANCE (metres)

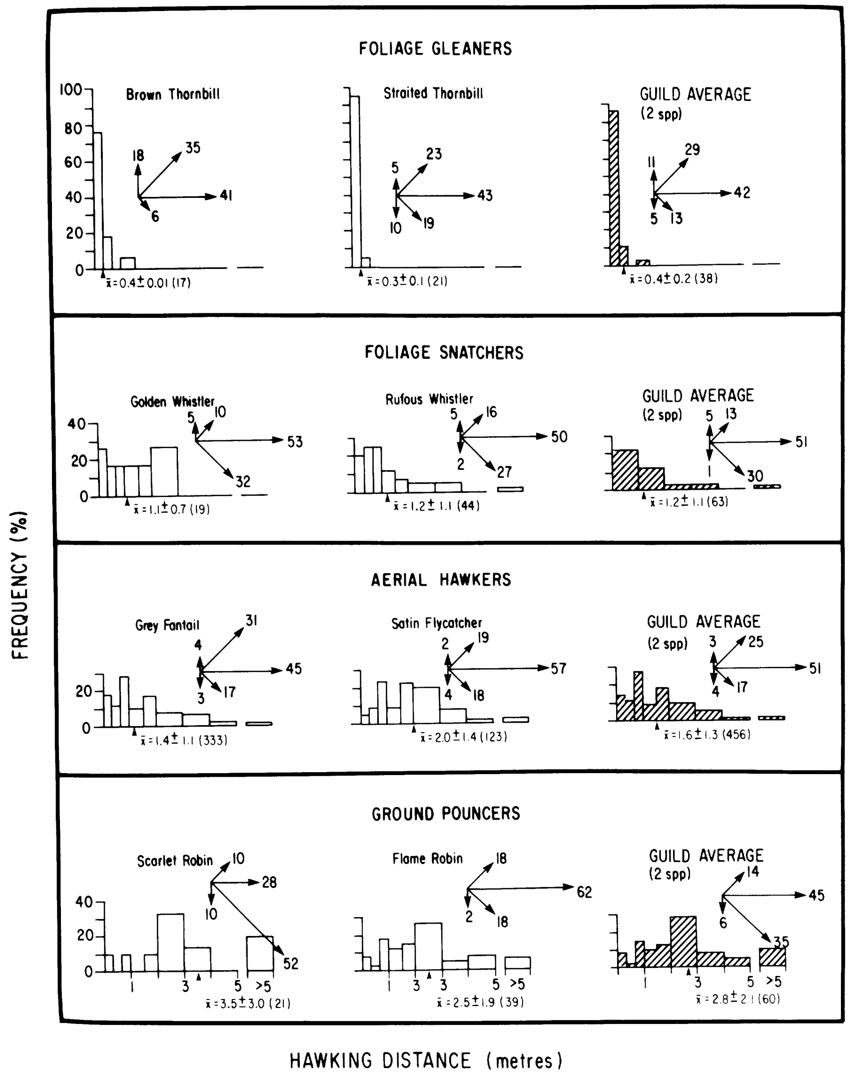


Fig. 4. Characteristics of prey-attack flights directed toward the capture of flying prey (i.e. hawking maneuvers). Only species that hawked prey frequently are considered. See Figs. 1 and 3 for further details.

surfaces. Flights to new searching places are relatively infrequent. Three groups of species used this mode: the foliage gleaners, bark gleaners, and ground foragers (Table 3).

The foliage gleaners at Bondi exhibited a search pattern similar to that of *Dendroica* warblers at Hubbard Brook (Robinson and Holmes 1982). These two groups have H/F ratios >1 and similar search velocities (30.8 vs. 26.4 perch changes/min for the Australian and Hubbard Brook species, respectively; $P > 0.18$). The Australian species, however, hopped significantly more often and flew less often than their Hubbard Brook counterparts (average H/F ratios of

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Fig. 3. Characteristics of prey-attack flights that terminated in snatching, hovering, or pouncing (see text). Lengths (distances traveled from perch to substrate on which prey was located) are indicated as histograms and angles of flights as vector diagrams (see Fig. 1 for further details). Only species that used these prey-attack maneuvers frequently are considered.

TABLE 3. Searching patterns of small insectivorous birds in *Eucalyptus* forests of southeastern Australia.

Searching patterns and representative species/guilds	Hop/flight ratio	Search flight distance	Search velocity	Primary attack maneuver	Attack rate	Attack distance	Prey-type obtained
Open-perch searchers							
Ground pouncers[a]	$\ll 1$	Long (>3 m)	Very slow (1–4)[b]	Pounce	Low (1.7)[c]	Long (4.7 m)	Large, ground-dwelling beetles, grasshoppers, lizards
Satin Flycatcher	$\ll 1$	Long (3.2 m)	Very slow (3)	Hawk	Low (2.3)	Medium (1.3 m)	Small flying insects
Flush-chasers							
Grey Fantail	>1	Medium-long (2.3 m)	Medium-fast (15)	Hawk (flush/chase)	Medium (6)	Medium (1.1 m)	Small, mobile foliage-dwelling insects
Medium-distance searchers							
Foliage snatchers[a]	≥ 1	Medium-short (1.4 m)	Slow (7–11)	Snatch	Low (1.9)	Short–medium (0.6–1 m)	Sawfly and moth larvae, large adult beetles, moths, and other insects sitting on foliage
Near-surface searchers							
Foliage gleaners[a]	$\gg 1$	Short (0.6 m)	Fast (30)	Glean	High (11)	Short (<0.3 m)	Small insects, lerps, and carbohydrate resources on foliage
Bark gleaners[a]	$\gg 1$	Short (<1 m)	Very fast (34)	Glean	High (12)	Short ($\ll$0.3 m)	Ants, moths on bark
Ground gleaners[a]	$\gg 1$	Short (0.9 m)	Very fast (36)	Glean	High (9)	Short ($\ll$0.3 m)	Ants, flies, and other small arthropods on ground
Special substrate-restricted searcher							
Loose-bark prisers[a]	$\gg 1$	Short (1.0 m)	Medium-fast (23)	Prise, probe	High (9)	Short (<0.3 m)	Larval and adult beetles, bark exudates

[a] Species for each guild are listed in Table 2.
[b] Average searching moves or perch changes/min (see Table 2).
[c] Average prey attacks/min (see Table 2).

5.0 vs. 1.9, $P < 0.05$); they also attacked prey more often (average of 11 vs. 3.6 times/min; $P < 0.05$). In addition, Striated and Brown thornbills were classed as very fast searchers, with a mean of 35.5 perch changes/min (Table 2). No foliage gleaners at Hubbard Brook moved this rapidly.

The foliage gleaners at Bondi took food that could not always be identified, but included insects, spiders, and a variety of energy-rich carbohydrates. The carbohydrate food available included manna (a sugary exudate of *Eucalyptus* leaves and bark), honeydew (polysaccharide secretions of aphids and coccids), and lerp (the sugary covering of psyllids), which are important sources of energy for some birds in eucalypt forests (Paton 1980). The two foliage-gleaning honeyeaters and the Striated Pardalote probably fed mainly on manna and lerp, whereas the Brown and Striated thornbills took mostly insects (Woinarski and Cullen 1984, Bell 1985, Woinarski 1985). At Hubbard Brook, the only species that feed on carbohydrates are the Yellow-bellied Sapsucker (*Sphyrapicus varius*) and its commensal, the Ruby-throated Hummingbird (*Archilochus colubris*) (Miller and Nero 1983). These birds feed on sap oozing from wounds in tree trunks made by the sapsucker.

The second group of near-surface searchers at Bondi are those that glean prey from bark, mainly the two species of treecreeper but also the less common Orange-winged Sittella (*Neositta chrysoptera*) and Brown-headed Honeyeater (*Melithreptus brevirostris*) (Recher et al. 1985). These species have essentially the same search patterns as the foliage searchers in that they hopped frequently, made short search flights, and gleaned prey from nearby substrates (Table 3). This search pattern on bark yields ants as a major food (Noske 1979, 1985), which are picked up in rapid succession, accounting for the high prey-attack rates of the treecreepers (Table 2). In north temperate forests, this search pattern is typical of nuthatches (*Sitta* spp.), creepers (*Certhia* spp.), some woodpeckers, and certain paruline warblers (e.g. the Black-and-white Warbler, *Mniotilta varia*). These northern species search for and attack prey more slowly, however, and take mostly cryptic insects and spiders from bark crevices, rather than ants (Holmes pers. obs.).

The third group of species that used the near-surface searching technique included the ground-gleaning thornbills, the White-browed Scrubwren, the Superb Blue Wren, and the Eastern Whipbird. These hopped rapidly along the ground and made frequent pecks at small surface-active prey (Table 3) or, in the case of the whipbird, rummaged among fallen bark and other ground litter. In addition to the species included in this study, the Superb Lyrebird (*Menura novaehollandiae*) and Ground Thursh (*Zoothera dauma*) were also ground foragers at Bondi (Recher et al. 1985), but they are large birds (>100 g body mass) that search and forage by scratching and turning over litter or by probing rather than taking prey from the surface.

At Hubbard Brook, the ground gleaners—a paruline warbler (Ovenbird, *Seiurus aurocapillus*), a fringillid (Dark-eyed Junco, *Junco hyemalis*), and the thrushes (*Catharus* spp. and *Hylocichla*)—search for prey by walking or hopping actively along the forest floor (Holmes pers. obs.). The thrushes, like the larger Australian Ground Thrush, forage by probing into the leaf litter and upper layers of the soil to obtain prey (Holmes et al. 1979). The Winter Wren (*Troglodytes troglodytes*) at Hubbard Brook gleans extensively from the surfaces of logs and other fallen dead wood, leaf litter, and herb and shrub foliage, and, although unquantified, its search behavior and foraging actions appear similar to those of the Superb Blue Wren at Bondi (Holmes pers. obs.).

(5) *Specialized substrate-restricted searching.*—Although the near-surface gleaners are substrate specific (see above), two species in this Australian community, the Eastern Shrike-Tit and the White-eared Honeyeater, searched for food among exfoliating bark in the forest canopy (Table 3). The shrike-tit flew from one clump of bark to another and prised apart strips of hanging curled bark to locate concealed invertebrates. Indeed, we often located shrike-tits by hearing them crunching or prising apart the brittle coils of bark. They also peeled loose bark from trees in their search for prey. White-eared Honeyeaters searched and fed in a similar manner but probably took more carbohydrates from under the loose bark than did shrike-tits.

This search pattern is similar to that of tropical antwrens (Formicariidae) that specialize in feeding on insects in dead hanging leaves

(Gradwohl and Greenberg 1982, Remsen and Parker 1984). It is also similar to Black-capped Chickadees (*Parus atricapillus*) foraging for insects among dead curled leaves at Hubbard Brook (Robinson and Holmes 1982).

SEARCHING MODES AND ENVIRONMENT: BONDI VS. HUBBARD BROOK

Our analysis of food-searching behavior illustrates the relationships between search tactics, methods of prey capture, and types of food consumed: birds searching in different ways encounter (and capture) different kinds of prey. The general similarity in searching patterns between the Australian species and their north temperate counterparts suggests that these geographically isolated forests offer much the same ways for birds to search for and capture arthropod prey. Although the details of foliage structure differ in certain ways (see below), the vegetation at the two sites is broadly similar (Holmes and Recher unpubl. data) and provides the same basic substrates on which prey can be found. This results in a general convergence on a similar set of searching patterns by birds in the two communities, despite the independent phylogenetic histories of the two avifaunas.

Differences exist in searching patterns between birds at Bondi and Hubbard Brook. These seem to be related to differences in vegetation structure and food resources at the two sites. Most of the Australian birds had searching and prey-attack flights that averaged 2-3 times longer than those of Hubbard Brook species (see above and contrast Figs. 1-3 in this paper with Figs. 1 and 2 in Robinson and Holmes 1982). This is probably due to the more widely spaced distribution of *Eucalyptus* foliage and branches, which forces birds to look for prey over longer distances and to move longer distances between perches. At Hubbard Brook, the leaves of the dominant trees are spaced at closer and more regular intervals on relatively short branches so that birds, on average, search over shorter distances, hop more frequently, and attack prey on leaves that are close to their perches. This effect of leaf spacing on the foraging behavior of insectivorous birds seems analogous to that of fructescence structure on fruit-eating birds in which food accessibility is influenced by habitat structure and by the physical and behavioral abilities of the birds to perceive and obtain that food (Denslow and Moermond 1982, Levey et al. 1984). Experimental studies of the effects of different foliage structures on the foraging behavior of insectivorous birds, however, have not yet been made.

The kinds and abundances of food resources present at Bondi and Hubbard Brook also influence searching and foraging patterns. The near-surface foliage-searching birds at Bondi gleaned significantly more often than comparable Hubbard Brook species, which probably is related to a greater abundance of small insects on *Eucalyptus* foliage (Recher and Gowing unpubl. data). At Hubbard Brook, the main prey available to foliage-searching birds are large but relatively rare Lepidoptera larvae (Holmes unpubl. data). *Eucalyptus* foliage and bark also offer an abundance of carbohydrate resources (Paton 1980, Woinarski 1985), used by honeyeaters, Striated Pardalotes, and occasionally other foliage- and bark-foraging birds (Recher et al. 1985), which provide different and unique foraging opportunities. In addition, the high abundance of ants on the trunks and branches of *Eucalyptus* provide resources not found at Hubbard Brook. Again, the rapid gleaning rates of the treecreepers reflect the abundance of these small-size prey.

These observations and interpretations are consistent with the hypotheses that vegetation structure and food resources act together to influence and perhaps determine the ways in which birds can search for and capture prey in a particular environment (Robinson and Holmes 1982). Further comparisons of bird foraging tactics in similar and in contrasting habitats will provide additional insight into the constraints and opportunities imposed by these environmental characteristics. In addition, experimental verification is needed to evaluate these proposed relationships between vegetation structure and bird foraging success.

We believe that these findings suggest that the vegetation matrix and associated food resources limit the ways in which insectivorous forest birds can find food and thus survive in a particular place. These in turn, perhaps coupled with biotic interactions and other factors, may significantly influence species distributions and abundances and, ultimately, bird community structure.

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Charles G. Sibley, president-elect of the A.O.U., has been elected to the National Academy of Sciences.

Visual Resources for Ornithology (VIREO) accession numbers for study-site slides for Andersen and MacMahon (Auk 103: 622–626) are A07-1-001 through A07-1-004.

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