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Roosts used by the golden-tipped bat *Kerivoula papuensis* (Chiroptera: Vespertilionidae)

M. Schulz

School of Resource Science and Management, Southern Cross University, Lismore, NSW 2480, Australia

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Abstract

Use of roosts by the golden-tipped bat *Kerivoula papuensis* was investigated principally in the Richmond Range National Park, north-eastern New South Wales and Mt Baldy State Forest in north-eastern Queensland, Australia. Roosts were located primarily using radiotelemetry; although others were found by light tagging, visual location and nest searching techniques. In the main study site in the Richmond Range a total of 54 *K. papuensis* diurnal roosts were located, 96.5% occurring in the suspended nests of the yellow-throated scrubwren *Sericornis citreogularis* (Pardalotidae) (93%) and the brown gerygone *Gerygone mouki* (Pardalotidae) (3.5%). At Mt Baldy, *K. papuensis* displayed greater variation in day roost selection, although 73% were in *S. citreogularis* nests. In both sites, day roosts were confined to the lower stratum of rainforest with a small proportion in eucalypt tall open forest with a rainforest subcanopy. Diurnal roosts were located at distances varying from 20 to 1200 m to the nearest major vegetation ecotone, ranging from along watercourses upslope to ridgelines. Diurnal roosts were predominantly occupied by single bats, with a maximum group size of eight individuals. All roosts in hanging nests were modified by the presence of a basal hole. Strong circumstantial evidence was provided that *K. papuensis* modified these roost structures in a manner allied to tent-making bats. A single maternity roost was located in the hollow of a rainforest canopy tree, *Flindersia australis* (Rutaceae).

Key words: roost, *Kerivoula papuensis*, bird nests, roost modification, maternity roost

INTRODUCTION

The roosting habits of bats are closely linked to morphology. Microchiropterans with an external-roosting strategy generally exhibit distinctive morphological characteristics such as bold and contrasting fur colour that serve as camouflage or assume cryptic roosting postures that make detection difficult (Constantine, 1966; Kunz, 1982). External roosting is suggested in many members of the genus *Kerivoula* due to the combination of thick long woolly fur and broken colour patterns of the pelage (Rosevear, 1965; Wallin, 1969; Kunz, 1982). It has been suggested that the thick pelage results in increased insulation while the broken colour patterns are a form of crypsis (Walker, 1975; Novick, 1977; Kunz, 1982). Use of roosts is poorly documented in the *Kerivoula*, with the scant roosting details gained primarily from anecdotal observations. In Africa and India, species within the genus have been recorded sheltering in the hanging nests of weaverbirds and sunbirds (Nectariniidae) (Sclater, 1900; Shortridge, 1934; Roberts, 1951; Rosevear, 1965; Brossett, 1966; Payne, Francis & Phillipps, 1985; Sharma, 1986; Skinner & Smithers, 1990; Nowak, 1994). Roosting in hanging bird nests has also been reported in the Australian species *K. papuensis*, with seven diurnal roosts located in the suspended nests of *Sericornis* spp. and *Gerygone mouki* (Pardalotidae) (Schulz, 1995). Species of *Kerivoula* have also been reported roosting in a variety of other situations such as tree hollows, trunks, foliage, flowers, caves and buildings (Rosevear, 1965; Nowak, 1994; Flannery, 1995*a*,*b*; Schulz, 1995). There are no published studies investigating the importance of hanging bird nests as roosts in the *Kerivoula*.

The objective of the present study was to characterize the roosting ecology of *K. papuensis* in eastern Australia, including the frequency suspended bird nests were used as diurnal roosts and whether nests were used as nursery or night roosts. *Kerivoula papuensis* is rare throughout its range which extends from eastern Australia north to New Guinea and the Biak-Supiori Islands (Flannery, 1995*a*,*b*) and little is known about its biology (Woodside, 1995). In the 1970s this species was considered to be extinct (Hall & Richards, 1979; Kennedy, 1990). Since its 'rediscovery' in 1981 until the beginning of the present study, a total of 71 individuals had been captured from 51 localities. The increase in captures of this species has been attributed to the use

Table 1. Details of the six study locations

Locality	Grid ref.	Land tenure	Altitude range (m)	Sample periods	Predominant vegetation[a]	No. of day roosts	Location method
Culmaran/Tryney Ck headwaters, Richmond Range NSW	28°48′S, 152°44′E	National Park	300–580	25–31 Dec 1993, 13–19 Feb 1994, 6–10 Apr 1994, 10–16 Aug 1994, 4–7 Sept 1994, 11–13 Apr 1995, 26 Apr –6 May 1995, 31 May–10 Jun 1995, 12–25 Oct 1995, 1–4 Nov 1995, 29 Nov–4 Dec 1995, 13 Feb–1 Mar 1996, 10–14 Apr 1996, 13–30 May 1996, 31 Jul–28 Aug 1996, 29 Nov–5 Dec 1996, 14–17 Dec 1996	Complex notophyll vine forest	54	Radio telemetry (51) Nest search (2) Visual detection (1)
Collins Ck headwaters, NSW	28°26′S, 153°08′E	National Park	400–1000	23 Oct 1993; 18 Dec 1996	Notophyll vine forest	1	Light tagging
Mebbin State Forest, NSW	28°27′S, 153°10′E	State Forest	100–400	18–19 Dec 1996	*Eucalyptus grandis* tall open forest with notophyll vine forest subcanopy	1	Radio telemetry
Beech Scientific Area, Kroombit Tops, Qld	24°24′S, 151°02′E	State Forest	500–930	7–14 Mar 1994, 22–28 Mar 1994	Complex notophyll vine forest	1	Radio telemetry
Walsh River headwaters, Qld	17°17′S, 145°25′E	State Forest	1000–1290	11–17 Dec 1995, 21–22 Dec 1995, 16–20 Apr 1996, 15–26 Jun 1996	Simple microphyll vine fern thicket	11	Radio telemetry
Ravenshoe State Forest, Qld	17°51′S, 145°35′E	State Forest	720–830	8–16 Dec 1995	Simple microphyll vine fern thicket	1	Radio telemetry

[a] After Tracey & Webb, 1975; Webb, 1978; Specht, 1970

and design modification of harp traps (Schulz, 1995; Rhodes, 1996). The only locality presently known where *K. papuensis* can regularly be trapped is in the Richmond Range National Park (28°48′S, 152°44′E) in north-eastern New South Wales (Schulz, 1995). This site was used as the primary study area for the present investigation and the results were compared with details of roost usage collected at five other localities.

STUDY AREAS AND METHODS

The main study area was in the headwaters of Culmaran and Tryney Creeks in the Richmond Range National Park (28°48′S, 152°44′E) near the town of Casino in north-eastern New South Wales. The altitude ranged from 300 to 580 m and the vegetation was dominated by complex notophyll vine forest (after Webb, 1978) abutting mixed eucalypt open forest (Floyd, 1980; Forestry Commission of New South Wales, 1987). Details on the use of roosts were collected during 17 visits to the site between December 1993 and December 1996 (Table 1).

Observations were made at 5 additional sites: Collins Creek headwaters, Border Ranges National Park (28°26′S, 153°08′E) and Mebbin State Forest (28°27′S, 153°10′E) in north-eastern New South Wales; Kroombit Tops State Forest (24°24′S, 151°02′E) in central eastern Queensland; and the Walsh River headwaters, Mt Baldy State Forest (17°17′S, 145°25′E) and Koombooloomba Creek headwaters, Ravenshoe State Forest (17°51′S, 145°35′E) in north-eastern Queensland. Broad characteristics and sample periods of these sites are summarized in Table 1.

Roosts were primarily located using radio-tagged bats. *Kerivoula papuensis* was captured in harp traps (Tuttle, 1974; Tidemann & Woodside, 1978; modified as in Austbat, 1995) set over watercourses and trails. Captured individuals were sexed, and their age-class estimated. Juvenile bats were identified by the degree of ossification of the digital epiphyses of the wings, a characteristic that can only be used to age individuals up to between 3 and 4 months old (Anthony, 1988). Reproductive condition was assessed from external characteristics, after Phillips & Inwards (1985). All individuals in the Richmond Range were banded with either size 3 bat bands or size 2 bird bands issued by the Australian Bird and Bat Banding Scheme or numbered plastic size 2 finch bands. At all other sites, captured *K. papuensis* were not banded but marked with Shené Pink toluene-free nail polish on the thumb nails for short-term recognition. Two types of radio transmitters were used: Holohil model BD-2B with a 14 cm antenna having an expected battery life of 18–21 days and weighing 0.65 g and Titley LT1 transmitters with a 30 cm antenna having an expected battery life of 10 days and weighing 0.5 g. These transmitters weighed 9.7% and 7.5%, respectively, of the mean weight of 6.7 ± 0.1 g (range 5.0–9.4 g) of *K. papuensis* captured. This range exceeded the 5% 'rule' for transmitter mass for bats of Aldridge & Brigham (1988), but was below the transmitter weights of 10–13% of body weight used by other researchers in foraging and movement studies (e.g. Krull *et al*., 1991; Entwistle, Racey & Speakman, 1996; Robinson & Stebbings, 1997; Pavey, 1998). Transmitters were attached mid-dorsally between the shoulder blades on the fur with cold-curing Vetbond, with the antenna extending posteriorly.

In the main study area, 57 *K. papuensis*, comprising 30 females and 27 males were fitted with radio transmitters. This number of individuals represented 80% of the total number of *K. papuensis* previously recorded in Australia before the present study. Ten individuals were radio-tagged multiple times during different sample periods, with 1 male radio-tagged on 5 occasions over the 3 year period. At other sites, 1 male was radio-tagged in Mebbin State Forest, 1 male in Kroombit Tops, 7 (4 females and 3 males) in Mt Baldy State Forest and 1 male in Ravenshoe State Forest. Roosts of radio-tagged individuals were located by scanning using a hand-held collapsible 5-element Yagi-antenna coupled with a Telonics receiver. An intensive search of approx. 15 km^2 was mounted on foot for each radio-tagged bat until they were located or a maximum of 7 days had elapsed. Signals were followed to individual trees or vine tangles and the actual roost location was confirmed by visually locating the roosting bat or the aerial with the aid of binoculars (Luxon 8×25) or by observing the exit of the radio-tagged bat during emergence at dusk. Roost trees were marked with flagging tape. Radio-tagged bats were followed until the batteries failed, the transmitter dislodged or to the end of a field trip. In addition, roosts were located by 3 other techniques:

1. *Light tagging*: light tags (Buchler, 1974) weighing 0.5 g were glued to the fur between the shoulder blades of 28 individuals; 1 male was followed to a roost using this technique.
2. *Visual location*: dusk watches of 3 inaccessible suspended *Sericornis citreogularis* nests in the Richmond Range revealed 1 roost.
3. *Nest search*: 348 *S. citreogularis* nests were investigated for roosting *K. papuensis* in the Richmond Range. In addition, 280 *S. citreogularis* nests were checked in 11 known *K. papuensis* localities in north-eastern New South Wales and south-eastern Queensland. The height of the nest and the presence of a basal hole were recorded for all *S. citreogularis* nests investigated. Two individuals were located roosting using this technique.

In this paper 'diurnal roosts' are defined as the location used by each radio-tagged bat on each day. 'Nocturnal roosts' refer to resting sites of stationary individuals located at night and 'maternity roosts' are roosts consisting of pregnant or lactating females (Kunz, 1982; Ransome, 1990). For all roosts the location, altitude (± 10 m accuracy), surrounding vegetation type (following Specht, 1970; Webb, 1978), roost type, the species and growth form of the roost plant (following Walker & Hopkins, 1990) were recorded. In hanging nest-roosts the presence of a basal hole was recorded and roost condition identified using the

Table 2. Number of individuals of *K. papuensis* radio-tagged in the Richmond Range and Mt Baldy

	Richmond Range			Mt Baldy		
	Males	Females	Total	Males	Females	Total
No. of individuals tracked	27	30	57	3	4	7
No. of 'roost days'	152	139	291	5	12	17
No. of individuals not located	1	1	2	0	0	0
No. of days not located	8	9	17	6	2	8
No. of days captured in harp trap	4	4	8	1	0	1
No. of transmitters dropped, no information obtained	0	2	2	1	0	1

Table 3. Day roosts of *K. papuensis* located at six sites in north-eastern New South Wales and Queensland. The range is given in parentheses. *S.c*, *Sericornis citreogularis*

	New South Wales					Queensland			
Locality	Richmond Range	Collins Creek	Mebbin State Forest	Kroombit Tops	Ravenshoe State Forest	Mt Baldy			
Roost type	*S. c* ($n = 50$), *G. mouki* ($n = 2$) nests combined	*S. c* nest	*S. c* nest	Hollow trunk	*S. c* nest	*S. c* nest	Branch	Live foliage	Dead tree fern foliage cluster
No. of roosts located	50	1	1	1	1	8	1	1	1
Mean distance to nearest ecotone (m)	250 ± 24.3 (20–600)	48	80	120	1100	1087 ± 44 (900–1200)	1400	1300	700
Mean distance to water (m)	146 ± 21 (0–500)	3	0	20	85	45 ± 16 (0–122)	8	2	2
Mean distance to canopy opening (m)	6.4 ± 1.1 (0.1–38.0)	2.0	3.50	0.5	2.2	2.0 ± 1.1 (0.1–9.0)	11.0	23.0	0.5
Mean height of roost plant (m)	3.5 ± 0.2 (0.5–9.0)	1.5	4.1	5.0	7.5	5.1 ± 0.4 (3.8–6.5)	6.5	1.2	4.4
Mean plant height (m)	7.7 ± 0.6 (1.3–21)	2.0	6.0	7.0	18.0	8.0 ± 1.0 (5.0–14.0)	10.0	3.5	6.0
Mean DBH of roost plant (cm)	9.6 ± 0.9 (2.0–27.0)	4.0	5.2	18.1	18.5	2.6 ± 0.2 (2.10–3.60)	6.5	3.1	14.7
Mean distance to nearest foliage (m)	0.30 ± 0.05 (0.01–1.42)	0.30	0.14	0.50	0.50	0.11 ± 0.06 (0.01–0.43)	0.08	–	–
Mean distance to nearest trunk (m)	1.24 ± 0.10 (0.09–3.40)	1.10	2.10	1.10	1.20	1.35 ± 0.17 (0.9–2.6)	0.15	0.50	0.90
No. of nests with basal entrance	50	1	1	–	1	8	–	–	–
No. of bats in roost	1–8	1	1	1	1	1	1	1	1

following categories: type 1 nest, in good condition, retaining original shape without a basal hole (as described in Campbell, 1901; North, 1909; McGill, 1970; Beruldsen, 1980); type 2 nest, in good condition, retaining original shape but with a basal hole; type 3 nest, weathered, losing original shape, with a basal hole; type 4 nest, fragmented, lacking a distinct nest chamber; type 5 nest, as for type 3 nest but with basal hole absent. Roost longevity was estimated by recording the condition of known roosts during irregular visits. The number of *K. papuensis* in each roost was determined by direct observation or counting exiting bats at emergence.

Roosts are a critical resource for many species of bats owing to species specific requirements (Law, 1996). In order to identify characteristics of roosts used by *K. papuensis* 10 external characteristics were measured: (1) diameter at breast height (DBH) of the roost plant; (2) roost height; (3) plant height; (4) roost height below the forest canopy; (5) distance to the nearest trunk; (6) distance to the nearest foliage; (7) distance to the closest foliage on a north, south, east and west bearing; (8) estimated foliage projection cover in a 1 m^3 area above the roost; (9) foliage layers above the roost, using the following categories: multiple layers of foliage, single layer of dense foliage, little foliage and partly a canopy opening above the roost; (10) the presence of other sheltering vertebrate species.

To provide an understanding of the location of roosts within a rainforest patch, 6 landscape characteristics

Table 4. Sex combinations of *K. papuensis* using *S. citreogularis* nests as roosts in the Richmond Range

	Dry season (Jun–Aug)	Pre-wet season (Sept–Nov)	Wet season (Dec–Feb)	Post-wet season (Mar–May)	Total
Female(s) only in roost	7	1	5	4	17
Male(s) only in roost	2	6	6	8	22
Both sexes in roost	3	3	3	7	16
Unknown	0	1	2	5	8
Total	12	11	16	24	63

were measured: (1) distance to the closest surface water (to the nearest 50 m when > 200 m from water); (2) distance to the nearest canopy opening where the opening was identified using the following categories: created by a natural tree fall, road or track, watercourse, rock outcrop, past logging activities and ecotone; (3) approximate distance (to the nearest 50 m when > 200 m away) to the closest major vegetation ecotone, characterized by a change in the canopy structure (Specht, 1970); (4) slope (following Speight, 1990); (5) aspect; (6) position in the catchment (following Speight, 1990).

RESULTS

Day roosts in the Richmond Range

Fifty-four *K. papuensis* diurnal roosts were located in the Richmond Range in 291 'roost days' (where one 'roost day' referred to an individual bat being successfully tracked to a roost on a particular day) (Table 2). Two bats were not located at all perhaps because of transmitter failure. Individual radio-tagged bats were not located on 17 days. However, all these same individuals were found occupying roosts on subsequent days. All roosts were situated within rainforest, predominantly complex notophyll vine forest (CNVF) without a tall open forest canopy ($n = 47$), while a single roost was found in Araucarian notophyll vine forest. Six roosts were located in CNVF with a tall open forest canopy (after Specht, 1970) dominated by *Eucalyptus saligna*, *E. seeana* and/or *Lophostemon confertus* (Myrtaceae). The average straight-line distance to the closest ecotone with open forest lacking a rainforest subcanopy was 250 m (SE 24.3, note that distances > 200 m were to the nearest 50 m), varying in distance from 20 to 600 m (Table 3). Seven roosts (13%) were situated within 50 m of a rainforest/open forest ecotone; with the closest being 20 m.

Kerivoula papuensis was most frequently found roosting in the hanging nests of *S. citreogularis* ($n = 50$) in the Richmond Range. Both sexes were found in these nests throughout the year, roosting either singly, with other members of the same sex or with a combination of individuals from the two sexes (Table 4). These nests were used as roosts under a variety of climatic conditions ranging from dry weather to extended periods of heavy rain and with diurnal maximum temperatures up to 29 °C and minimum diurnal temperatures down to 9 °C. The nest of *S. citreogularis* is a bulky pear-shaped structure. It is constructed from pieces of dry vegetation such as bark and fern fibre, rootlets, leaves, moss, and frequently coated over the outside with moss and horsehair fungus, the ends of which often hang up to 18 cm below the nest. The nest chamber is lined with bark, fern fibre and feathers, with a steeply downward-sloping tunnel-like entrance on one side. The size of the domed section of the nest ranges externally from 17 to 27 cm in length and 11 to 18 cm in diameter; the entrances varied from 2.5 to 5 cm in diameter ($n = 30$). Up to 18 cm of nesting material may be built around the supporting branch or vine tendril before the domed section of the nest is constructed.

All *S. citreogularis* nests occupied by *K. papuensis* included a circular hole in the base of the nest chamber, ranging from 2.5 to 5.5 cm in diameter ($n = 16$). The majority (90%) of these roosts were in type 2 *S. citreogularis* nests, with the remainder in type 3 nests. Where nests were subsequently re-occupied by *S. citreogularis* (one nest on two occasions in December 1995 and December 1996) or used by *S. magnirostris* ($n = 2$) for breeding purposes, the hole in the base of the nest chamber was covered over with new nesting material.

Sericornis citreogularis nests located in the Richmond Range were suspended from the ends of live branchlets, at a mean distance of 1.23 ± 0.10 m ($n = 50$) to the trunk or main branch of the roost tree or shrub. Roosts in *S. citreogularis* nests were found in 16 rainforest subcanopy or shrub species, with the dominant species being *Baloghia inophylla* (Euphorbiaceae) ($n = 11$) and *Actephila lindleyi* (Euphorbiaceae) ($n = 8$) (Table 5). Three nests were suspended from tendrils of the rainforest vines, *Pandorea baileyana* (Bignoniaceae) ($n = 2$) and *Ripogonum elseyanum* (Ripogonaceae) ($n = 1$). The nests used as roosts were typically in open situations. When the distance to foliage on bearings of 90°, 180°, 270° and 360° was measured, the most distant foliage from the nest base averaged 4.3 ± 0.4 m (range 14–0.3 m); while the mean distance to the nearest tree or sapling trunk was 1.24 ± 0.10 m ($n = 50$).

Two diurnal roosts, both occupied by single males, were located in the enclosed nests of *Gerygone mouki*, suspended from the branches of a *Sloanea australis* (Elaeocarpaceae) and *Podocarpus elatus* (Podocarpaceae). Similar to *S. citreogularis*, *G. mouki* builds a dome-shaped nest constructed of fern and bark fibre,

Table 5. Frequency of roost plant species supporting *S. citreogularis* nests used as roosts by *K. papuensis* in the Richmond Range. Growth form: 2, mid-canopy tree; 3, lower stratum tree; 4, shrub; 5, vine

Plant species	Growth form	Richmond Range
Araucaria cunninghamii	3	4
Actephila lindleyi	3, 4	8
Austromyrtus bidwillii	3	1
Baloghia inophylla	2, 3	11
Capparis arborea	3	2
Castanospermum australe	3, 4	2
Cinnamomum virens	3	1
Cleistanthus cunninghamii	3	2
Croton verreauxii	2	1
Elattostachys nervosa	2, 4	2
Flindersia bennettiana	3	1
Guilfoylia monostylis	2	1
Pandorea baileyana	5	2
Podocarpus elatus	2, 3	3
Ripogonum elseyanum	5	1
Sloanea australis	2, 3, 4	4
Syzygium corynanthum	2	1
S. francisii	3	3

mosses, spider web and is lined with moss and feathers. The domed nest chamber is smaller measuring 5–9 cm in length and 3–5 cm in diameter ($n = 6$), with a long 'tail-like appendage' suspended to 8 cm below the chamber. The nest has a long spout-like entrance 2.5–5.5 cm in length and 1–2 cm in diameter. The two *G. mouki* nests had been modified by the presence of a circular hole in the base of the nest chamber in a similar way to the *S. citreogularis* nests used as roosts by *K. papuensis*.

All but two diurnal roosts were located in suspended bird nests, and these two appeared to be the result of stressed individuals. A female was located roosting 1.1 m above a pool, 18 m upstream from the release site on a bare branch of a *Sloanea australis*. This female was located on the morning of 15 October 1995, did not leave during a 2 h period after dusk, did not display any reaction when a *Melomys cervinipes* (Muridae) ran along adjacent branches and was again present in the same situation on the following morning. A male was located resting in filtered sunlight in an exposed situation on the side of a fallen *L. confertus* trunk over a pool on the morning of 14 October 1995, approx. 350 m downstream of the release site. Six species of birds, *Sericornis magnirostris*, *Meliphaga lewinii* (Meliphagidae), *Lichenostomus chrysops* (Meliphagidae), *Tregellasia capito* (Petroicidae), *Monarcha melanopsis* (Dicruridae), and *Neochmia temporalis* (Passeridae) were actively preening, bathing and drinking within 1.5 m of the bat without it showing any reaction. As with the female, the male did not leave after dusk and was again present on the following day. Since both individuals had been roosting in exposed situations for over 24 h and appeared in a state of stress, the transmitters were removed off the back fur, the bats were fed crushed meal worms and honeyed water and then released after dusk. The details of these roosts have been excluded from any further roost calculations.

All *K. papuensis* diurnal roosts were in the lower stratum of the rainforest, ranging from 0.5 to 9.0 m above the ground, at a mean height of 3.5 ± 0.2 m ($n = 52$); and a mean height below the canopy level of 26.4 ± 0.8 m. The height of roosts in which only males were recorded did not differ significantly from the height of roosts in which only females were found ($t = 1.62$, $P > 0.05$, d.f. = 24). Roosts were present in trees and shrubs averaging 7.7 ± 0.6 m ($n = 49$) in height and with a mean DBH of 9.6 ± 0.9 cm; comprising 67% lower stratum trees ($n = 33$), 27% mid-stratum trees ($n = 13$) and 6% shrubs ($n = 3$). No day roosts were located in canopy trees. Roosts were predominantly (83%) in situations with a high foliage projection cover of > 80% ($n = 43$), consisting of multiple layers of foliage above the nest. The distance to the nearest canopy opening penetrating to the shrub level within the rainforest varied from 0.1 to 38.0 m, averaging 6.4 ± 1.1 m ($n = 52$). These canopy openings were principally a result of treefalls ($n = 31$), watercourses ($n = 10$), and canopy gaps that may have been caused by past logging activities ($n = 7$).

Roosts were distributed across the site in a range of landform elements from ridgelines ($n = 4$) and upper slopes ($n = 14$) to lower slopes ($n = 15$) and over watercourses ($n = 11$), with no significant preference for position within the catchment ($X^2 = 7.80$, $P > 0.05$, d.f. = 3). Correspondingly, the distance to the nearest surface water ranged from 0 m where roosts were located in *S. citreogularis* nests hanging over watercourses ($n = 6$) up to 500 m on ridgelines ($n = 2$). The average distance to surface water was 145.9 ± 21.3 m ($n = 52$) (Table 3). Roosts were predominantly located on slopes with a southerly aspect, particularly south-east facing ($n = 17$). However, this apparent bias to southerly facing slopes may have been a function of sampling a population in valleys with a southerly orientation. Roosts were situated on slopes varying from very gently inclined ($n = 3$) to cliffed ($n = 1$), with the majority (69%) occurring on gently inclined ($n = 17$) or moderately inclined slopes ($n = 19$).

The majority of diurnal roosts (70%) were occupied by single males ($n = 23$) or single females ($n = 18$). Group sizes greater than two individuals comprised 28% of all roosts located, with a maximum number of eight individuals recorded on two occasions. All day roosts occupied by more than two individuals consisted either of both sexes or were comprised of individuals where the sexes were not ascertained. No other species of bats were recorded roosting in *S. citreogularis* or *G. mouki* nests within the site. One adult male eastern pigmy-possum *Cercartetus nanus* (Burramyidae) was encountered in a *S. citreogularis* nest that had previously been used by *K. papuensis*. This nest had subsequently been used by nesting *S. magnirostris* and the hole in the chamber base had been covered over with new nesting material.

Day roosts at other sites

Fifteen diurnal roosts were located at five other localities, with 11 found in Mt Baldy State Forest, north-eastern Queensland (Table 1). The Collins Creek roost was located by following a light-tagged individual, while the remainder of the roosts were found by tracking radio-tagged bats. All roosts were situated within rainforest, with the exception of the Mebbin State Forest roost which was located in tall open forest with a rainforest subcanopy. Roosts at Mt Baldy and Ravenshoe State Forests were located significantly further from the nearest rainforest/open forest ecotone than roosts in the Richmond Range ($t = 14.15$, $P < 0.001$, d.f. = 62). While roosts at the other three sites were within the range of roost distances from ecotones recorded in the Richmond Range (Table 3).

Kerivoula papuensis was located in the suspended nests of *S. citreogularis* at four sites, with all nests modified by the presence of a circular hole in the base of the nest chamber. The *S. citreogularis* nests occupied in Collins Creek and Mebbin State Forest were similar to those occupied in the Richmond Range. In these sites, height of the roost, height and DBH of the roost plant, distance to the nearest foliage and trunk, the distance to the nearest canopy opening and surface water were within the range of measurements for the Richmond Range roosts (Table 3). The roost trees were similar species to the Richmond Range, the Collins Creek roost occurring in a *Sloanea australis* and the Mebbin State Forest site occurring in an *Austromyrtus* sp. aff. *acmenoides* (Myrtaceae). The roost in Ravenshoe State Forest was located in a *Davidsonia pruriens* (Davidsoniaceae) 7.5 m above the ground in simple microphyll vine fern thicket (Table 3). In contrast, the *S. citreogularis* nests used as roosts at Mt Baldy were all located amongst foliage in lawyer vine *Calamus* spp., compared with 5.8% of roosts suspended from vines in the Richmond Range (Table 5). The nests were significantly higher above the ground at Mt Baldy ($t = 3.72$, $P < 0.001$, d.f. = 56) than roosts in the Richmond Range.

Four other roost types were occupied by *K. papuensis*. The only diurnal roost located in a tree hollow was in Kroombit Tops, where a single male was tracked to the top section of a broken-off hollowed-out trunk of a rainforest tree *Endiandra sieberi* (Lauraceae). The bat was located roosting approx. 5 m above the ground on a mid slope with a south-west aspect in CNVF (Table 3). Two individuals in Mt Baldy State Forest were detected roosting singly amongst foliage. A male was found sheltering for a single day on the underside of a leaf of a live *Ceratopetalum succirubrum* (Cunoniaceae) 1.2 m above the ground and 2 m from the edge of a flowing creek on a slight slope with a north-east aspect. He was roosting in a sheltered situation with foliage projection cover of > 80% and was protected from filtered sunlight that penetrated the rainforest canopy. An adult female was tracked to a cluster of three dead *Cyathea* spp. (Cyatheaceae) fronds that had fallen and become vertically suspended over a branch 4.4 m above the ground on a bank of the Walsh River. The site was located on the edge of a canopy opening under a dense screen of live *Cyathea* fronds, with a foliage projection cover of > 80%. The bat remained in the site for at least 2 days during periods of heavy rain. The fourth roost type was on a bare branch of a *C. succirubrum* on a moderately inclined lower slope with a north-west aspect in Mt Baldy. Here a male was located roosting on the underside of the join between two branchlets 6.5 m above the ground, shaded from filtered sunlight. Unlike the bats found roosting in two similar situations in the Richmond Range, this bat appeared in good condition and on dusk vacated the roost.

All roosts located in the five sites supported only single individuals. As in the Richmond Range no other species of bats were located roosting with *K. papuensis*. Although a female *Murina florium* (Vespertilionidae) was tracked in June 1996 to the same *S. citreogularis* nest used by a female *K. papuensis* in December 1996.

Night roosts

Little information was collected on the use of roosts at night because of the difficulty of radio-tracking in steep trackless terrain. On five nights radio-tagged bats were found roosting in *S. citreogularis* nests used by the same individuals as diurnal roosts in the Richmond Range.

Maternity roosts

The only maternity roost located was situated in a hollowed-out spout of a *Flindersia australis* (Rutaceae) in CNVF on an upper moderately inclined slope with a southerly aspect in the Tryney Creek catchment, Richmond Range. This rainforest canopy tree was 28 m high with a DBH of 147 cm. The roost tree was situated 450 m upslope from the closest surface water and 1000 m from the nearest ecotone. The roost entrance was 15 m above the ground and 13 m below the rainforest canopy level, with a foliage projection cover of > 80%, consisting of multiple layers of foliage above the hollow entrance. The hollow was situated at the end of a broken-off bough with an orientation of approx. 45° from horizontal. The entrance had a south-westerly aspect and had a 12 cm diameter at the widest point. The tree was located on the edge of a canopy opening that was the result of past timber extraction activities.

A single lactating female, trapped on Tryney Creek, a straight line distance of 750 m, was located in the roost on 3 December 1995. A further two lactating females captured in the same trap site were radio-tagged on 3 December and detected in the roost on 4 December 1995. Counts of *K. papuensis* as they emerged revealed a minimum of 18 individuals on 3 December 1995 and 20 individuals on 4 December 1995. The same roost was used in December 1996, with 19 individuals observed emerging at dusk on 2 December 1996. On 3 December 1996, 14 emerging bats were captured in a monofilament

Table 6. *Sericornis citreogularis* nest search summary at known *K. papuensis* localities in north-eastern New South Wales and south-eastern Queensland

Locality	No. of search periods	No. of nests checked	No. of nests checked with basal holes	No. of *K. papuensis*	Other vertebrates
Richmond Range, NSW	11	348	213	2	2 *Cercartetus nanus*
Forest Land State Forest, NSW	1	26	1	0	–
Spirabo State Forest, NSW	1	4	0	0	–
Chaelundi State Forest, NSW	1	20	1	0	–
Irishman State Forest, NSW	1	32	8	0	–
Marsh State Forest, NSW	1	6	0	0	–
Border Ranges National Park, NSW	3	31	3	0	–
Tooloom National Park, NSW	1	2	0	0	–
Mebbin State Forest, NSW	1	7	1	0	–
Brisbane Forest Park, Qld	1	72	18	0	–
Kenilworth State Forest, Qld	2	35	3	0	–
Lamington National Park, Qld	1	45	2	0	–
Total	25	628	250	2	2

mist net. All these bats were lactating females, including one individual (Band No. 47716) that had been recorded in the site the previous year.

Nest search

In April 1994 a single male *K. papuensis* was located when searching a *S. citreogularis* nest in the Richmond Range. To test the feasibility of using *S. citreogularis* nest searching as a technique to capture *K. papuensis* a total of 340 nests (type 1, 2, 3 and 5 nests) that had not previously been identified as roosts were censused between May 1995 and December 1996 (Table 6). A single additional *K. papuensis* was located using this technique. The mean height of nests manually checked for roosting bats was 2.5 ± 0.1 m (range 0.5–6.3 m), which fell within the range of known roost heights in the Richmond Range. The only other vertebrate located in these nests were single males of *C. nanus* in October 1995 and December 1996. Both individuals were found in type 1 *S. citreogularis* nests lacking a basal hole.

In addition, 280 *S. citreogularis* nests, including 40 nests with basal holes, were searched for roosting *K. papuensis* between April 1994 and December 1996 in 11 localities where this species had previously been recorded (Table 6). The nest searches in these localities failed to record any *K. papuensis*.

Roost longevity

Known *K. papuensis* roosts in *S. citreogularis* nests in the Richmond Range were revisited to establish the fate of these roosts. Of 47 nests located at various times before December 1996, 66% ($n = 31$) were no longer available to *K. papuensis*. The principal causes were that the nests had fragmented ($n = 15$), fallen ($n = 5$) or a canopy tree had dropped on the roost plant ($n = 5$). Three nests were re-occupied by *S. citreogularis* or *S. magnirostris* and were not available in the short-term.

It was not possible to accurately determine the time *S. citreogularis* nests were suitable *K. papuensis* roosts, because the date of construction was not known and the nests were not visited regularly enough to obtain an accurate date when the nests ceased being used. The longest period of roost availability was 25 months, in which a single *K. papuensis* was located in a nest in April 1994 and again in December 1996. During this time the nest had fragmented from a type 2 to a type 3 nest. Three new *S. citreogularis* nests were constructed on the same or adjacent branches to old nest sites that had been used as roosts by *K. papuensis*.

At Mt Baldy, three of the five *S. citreogularis* nests located as roosts in December 1995 had fallen or fragmented by June 1996. The only roost located in a *S. citreogularis* nest in April 1996 was still present 2 months later. In contrast, the cluster of suspended dead *Cyathea* fronds used as a roost in April 1996 was no longer present in June 1996.

DISCUSSION

Diurnal roosts

Anecdotal evidence indicates that many species within the genus *Kerivoula* roost in the hanging nests of passerine bird species, primarily those of the Nectariniidae. No published studies have examined the incidence in which such roosts are used. The present study found that 96.5% of diurnal roosts of *K. papuensis* were located in the suspended nests of *S. citreogularis* (93%) and *G. mouki* (3.5%) in the Richmond Range National Park. In the five other sites investigated, suspended nests accounted for 73% of the day roosts of *K. papuensis*, all found in *S. citreogularis* nests. External roosting either on exposed surfaces or amongst foliage accounted for five diurnal roosts. Three external roosts were located in Mt Baldy State Forest, north-eastern Queensland. The other two external roosts were of single apparently stressed individuals found resting on

exposed surfaces in the Richmond Range. Transmitters can influence roosting behaviour, sometimes as a result of infections occurring at the site of attachment. However, the influence of transmitters on the use of roosts appears to be small as 23 *K. papuensis* previously radio-tagged on at least one occasion were recaptured and showed no evidence of infection or skin irritation. The lack of observed injuries might in part be due to transmitters being attached to the fur rather than the skin.

The nearly exclusive use of bird nests as roosts by *K. papuensis* contrasts with the majority of Australian microchiropterans which primarily roost in tree cavities, caves, disused mineshafts or rock crevices (Strahan, 1995). A variety of bats has been recorded using bird nests on occasions as shelter sites in Australia. In a review of bats roosting in bird nests, Schulz (1997) listed 10 species (Molossidae and Vespertilionidae) from the enclosed bottle-shaped mud nests of *Hirundo aerial* (Hirundinidae), two species in the enclosed plant material nests of *Pomatostomus temporalis* (Pomatostomidae) and *Oreoscopus gutturalis* (Pardalotidae), and one species in the open spoon-shaped nest of *Collocalia spodiopygia* (Apodidae). However, all these species have been recorded sheltering in a range of roost types including tree holes and/or caves (Tidemann & Flavel, 1987; Menkhorst, 1995; Strahan, 1995). The use of *Sericornis* nests as bat roosts was first noted by Allen (1939) who reported a small unidentified microchiropteran in old nests of *S. citreogularis* and *S. frontalis* in central coastal New South Wales. The possibility of these bats belonging to the genus *Kerivoula* was discounted by Allen (1939) since at the time members of this genus were not known from Australia and *K. papuensis* was included in the genus *Phoniscus* (Thomas, 1914). However, it is considered possible that these individuals were *K. papuensis* (Schulz, 1995). Unidentified bats have also been encountered in *S. citreogularis* nests in the Conondale Ranges, south-eastern Queensland and near Wauchope in north-eastern New South Wales, both localities situated close to known *K. papuensis* sites (Schulz, 1997).

Tidemann & Flavel (1987), in examining roost choice in tree-hole roosting microchiropterans, suggested that competition has a major influence on roost selection, particularly with birds and other bat species. *Kerivoula papuensis* exhibits wing morphology characteristics and wide-band echolocation calls typical of a species that can travel within cluttered environments (Aldridge & Rautenbach, 1987; Rhodes, 1996). Such characteristics coupled with the woolly pelage may predict an ability to use a roost resource not frequented by other microchiropterans. Such ability was suggested where in the Richmond Range no other species of bats were encountered in suspended bird nests. Although at Mt Baldy, a second species with similar wing morphology and echolocation call characteristics, *Murina florium*, was also recorded using suspended bird nests. In 10 roosts of this species, 60% occurred in *S. citreogularis* nests (Schulz & Hannah, 1998).

The advantages of *K. papuensis* using suspended nests may in part be a response to predation pressures with the roosting bats deriving benefits from the placement of the birds' nests. Nest predation is a principal factor determining reproductive success in birds and has been observed to be the primary source of nest losses across a wide diversity of species, vegetation types and geographic locations (Ricklefs, 1969; Cody, 1971; Nilsson *et al*., 1985; Martin, 1993*a*). Predation rates are expected to be lower in species that use nest sites that are different to those used by most other species within a forest environment (Martin, 1993*b*). *Sericornis citreogularis* and *G. mouki* are the only species to construct hanging closed nests in the subcanopy of rainforests in south- and central-eastern Australia (Beruldsen, 1980; Blakers, Davies & Reilly, 1984). In north-eastern Queensland, three additional species use such nest placement within rainforest; *G. magnirostris*, *G. palpebrosa* and *Nectarinia jugularis* (Nectarinidae). The placement of nests in the subcanopy may impede the ability of mobile predators to locate the suspended nests even when they are poorly concealed (Martin, 1993*b*). For example, members of the Falconidae and Artamidae are known predators of microchiropterans (Key, 1938; Young, 1980; Czechura, 1983) but rarely penetrate into the subcanopy regions of rainforests in eastern Australia. Closed nests such as those of *S. citreogularis* and *G. mouki* have been found to be less susceptible to predation than open nests (Lack, 1968; Oniki, 1975; Loiselle & Hoppes, 1983; Cooper & Francis, 1998). One explanation accounting for lower predation rates is that closed nests may be difficult to break open (Oniki, 1979). The nests of *S. citreogularis* and *G. mouki* were suspended from the ends of thin branchlets and vine tendrils, at a mean distance of 1.24 m from the nearest trunk or main branch in the Richmond Range. Such nest placement may represent a strategy to avoid predation from arboreal snakes, lizards and rodents. Nests above ground may be less frequently encountered by mammalian predators (Ricklefs, 1969). Loiselle & Hoppes (1983) proposed that predation by snakes above ground may play an important role in nesting success. Many climbing predators would be unlikely to reach *S. citreogularis* and *G. mouki* nests either because of the light-weight terminal branches and vine tendrils or the distance span from the nearest trunk or major branch. Where a climbing predator does attempt to approach the nest, roosting bats may be alerted by the body mass and movement resulting in disturbance to the branch or vine tendril, causing the nest to move (Timm & Mortimer, 1976; Boinski & Timm, 1985).

Moreover, the alternate use of different nests within a bat's home range may be advantageous by introducing uncertainty into the search tactics of the potential predator (Foster, 1992; Kunz *et al*., 1994). The location of only two individuals in a nest search of 340 *S. citreogularis* nests in the Richmond Range and a further 280 nests elsewhere suggested a low occupancy rate that would further discourage the development of predator search strategies (Martin, 1993*b*). The low

encounter rate may partly be a result of the alertness of the roosting bats. While attempting to gain access using a stepladder, bats in some nests may have escaped without my knowledge. The advantage of alertness in external roosting is possibly a predator avoidance response (Kunz, 1982; Tidemann & Flavel, 1987).

Roost modification

Bird nests used by microchiropterans principally are of two construction types: either enclosed with a downward orientated entrance (e.g. *H. aerial*) or open cup-shaped structures situated in the twilight zone of caves or man-made structures (e.g. *C. spodiopygius* and *H. neoxena*; Schulz, 1997). Both nest types allow escape routes for bats, either by taking off from an open surface or through a downward-facing entrance which allows the occupants unobstructed views of the environment below (Brooke, 1990; Kunz & McCracken, 1996). In contrast, the entrance of *S. citreogularis* nests are located on the side of the nest chamber, facing outwards (Campbell, 1901; North, 1909; McGill, 1970; Beruldsen, 1980). In *G. mouki* nests a bottle-neck entrance is connected to the upper side of the nest chamber. In neither case does the nest provide unobstructed views of the environment below or a ready escape route unless roosting on the edge of the entrance hole.

All suspended nests used as roosts were characterized by the presence of a basal hole. Circumstantial evidence suggested that *K. papuensis* modified these nests by the construction of these basal holes. Such evidence includes the presence of these holes in 100% of nests occupied as roosts, the observation that all individuals emerged at dusk through the basal holes ($n = 28$) and during daytime all disturbed individuals were observed to escape through the basal holes. Three *S. citreogularis* nests known to have been occupied by roosting *K. papuensis* were subsequently reused by either *S. citreogularis* or *S. magnirostris*. The basal hole in all these nest chambers was covered over with new nesting material. Examination of the nest material around the edge of the basal holes failed to reveal any chew marks. However, the fine nature of the material did not lend itself to providing this evidence. The modification of the hanging nests would offer unobstructed views of the ground below. It would also allow a quick exit route in the opposite direction to where a climbing predator was reaching the nest from the supporting branchlet or vine tendril or through the original entrance. Similar modifications of weaverbird or sunbird nests used by *Kerivoula* species in Africa and India has not been documented (e.g. Rosevear, 1965; Sharma, 1986; Skinner & Smithers, 1990).

Roost modification in the form of 'tent-making' has been reported in 18 species of bats in the families Pteropodidae, Phyllostomidae and Vespertilionidae (Kunz *et al*., 1994; Kunz & McCracken, 1996; Tan, Zubaid & Kunz, 1997). The majority of these tents are formed when bats partially chew the veins and/or midrib of selected leaves, leaflets or stems (Kunz *et al*., 1994). Only a single species of vespertilionid bat, *Scotophilus kuhlii*, has been reported as tent roosting (Rickart, Heideman & Utzurrum, 1989). Kunz *et al*. (1994) questioned whether *S. kuhlii* actually made the tents or was simply using tents constructed by another species. Roost modification of suspended nests in *K. papuensis* seems to be allied to the tent-making behaviours of both neotropical and palaeotropical bats. The hanging nests with basal holes resemble the stem tent roost type described in Kunz *et al*. (1994). Stem tents have a bell-shaped cavity surrounded by uncut stems and leaves or fruits (Bhat & Kunz, 1995). This tent structure differs from other tents in that it is constructed from the stems of small vines, tree branches and fruit/flower strings rather than leaves.

Sericornis citreogularis nests are ephemeral in nature, with 66% of all nests used as roosts in the Richmond Range no longer available by December 1996; while at Mt Baldy three out of five nests located in December 1995 were no longer present 6 months later in June 1996. Some nests provided suitable conditions for roosting for at least 12 months and one nest showed little sign of deterioration after 25 months. Tents constructed by *Artibeus jamaicensis* and *Uroderma bilobatum* (Phyllostomidae) similarly provided suitable roosting conditions after 1 year (Kunz & McCracken, 1996), and after 10 months in *Cynopterus brachyotis* (Pteropodidae) (Tan *et al*., 1997).

Maternity roosts

In Australia, tree hollows provide an important shelter resource for many mammals, with more than half of the microchiropterans known to roost and breed in tree holes (Tidemann & Flavel, 1987; Strahan, 1995). *Kerivoula papuensis* was recorded roosting in tree holes on two occasions. At Kroombit Tops State Forest the only roost located for a single male in 3 days of radio-tracking was in the broken-off, hollowed-out trunk of a rainforest tree. In this rainforest, *S. citreogularis* does not occur, although *G. mouki* is present (Horton & Jahnke, 1986; Schulz, 1994). The second record of a tree hole was in December 1995 in Tryney Creek headwaters in the Richmond Range. At this site up to 20 lactating females were found using a hollow spout of a rainforest canopy tree as a maternity site. This same hollow was used as a maternity site the following year, with one female recorded at the location in both years. The shift of females into specific nursery sites has been observed in many microchiropterans (e.g. Dwyer & Harris, 1972; McNab, 1982; Winchell & Kunz, 1996). The shift of female *K. papuensis* into tree hollows for the formation of a nursery roost may be associated with such factors as roost microclimate or the re-use of these nests by *Sericornis* spp. at this time of the year. The only other maternity site recorded for *K. papuensis* was in a cave on Biak Island, north of New Guinea (Flannery, 1995*a*). In this cave, two lactating and one pregnant female and two juveniles were located roosting in a solution cavity

on the ceiling. In Australia, *K. papuensis* has not been recorded roosting in caves or mineshafts (Schulz, 1995). Natural caves, used by known cave-dwelling species such as *Miniopterus australis* (Vespertilionidae), *M. schreibersii* and *Rhinolophus megaphyllus* (Rhinolophidae) were present both in the Richmond Range and Mt Baldy sites. A search of accessible sections of known caves and rock overhangs in December 1995 and 1996 in the Richmond Range and December 1995 at Mt Baldy failed to locate any *K. papuensis*. However, this species may have been overlooked as a result of cryptic roosting habits or a preference for deep inaccessible crevices. Cryptic roosting habits have been found in some uncommon cave-dwelling species in Australia such as *Hipposideros semoni* and *H. stenotis* (Hipposideridae) (Schulz & Menkhorst, 1985; de Oliveira & Schulz, 1997). Until additional maternity sites are located, it is not possible to characterize the maternity roost requirements of this rare species.

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REFERENCES

Aldridge, H. D. J. N. & Brigham, R. M. (1988). Load carrying and maneuvrability in an insectivorous bat: a test of the 5% 'rule' of radio-telemetry. *J. Mammal*. **69**: 379–382.

Aldridge, H. D. J. N. & Rautenbach, I. L. (1987). Morphology, echolocation and resource partitioning in insectivorous bats. *J. Anim. Ecol*. **56**: 763–778.

Allen, G. M. (1939). *Bats*. New York: Dover.

Anthony, E. L. P. (1988). Age determination in bats. In *Ecological and behavioural methods for the study of bats*: 47–58. Kunz, T. H. (Ed.). Washington, D. C.: Smithsonian Institution Press.

Austbat (1995). *Harp trap information*. Lower Plenty, Victoria: Austbat Research Equipment.

Beruldsen, G. (1980). *A field guide to nests and eggs of Australian birds*. Sydney: Rigby.

Bhat, H. R. & Kunz, T. H. (1995). Altered flower/fruit clusters of the kitul palm used as roosts by the short-nosed fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae). *J. Zool. (Lond.)* **235**: 597–604.

Blakers, M., Davies, S. J. J. F. & Reilly, P. N. (1984). *The atlas of Australian birds*. Melbourne: Melbourne University Press.

Boinski, S. & Timm, R. M. (1985). Predation by squirrel monkeys and double-toothed kites on tent-making bats. *Am. J. Primatol*. **9**: 121–127.

Brooke, A. P. (1990). Tent construction and social organization in *Vampyressa nymphaea* (Chiroptera: Phyllostomidae) in Costa Rica. *J. trop. Ecol*. **3**: 171–175.

Brosset, A. (1966). *La Biologie des Chiroptères*. Paris: Masson.

Buchler, E. R. (1974). A chemoluminescent tag for tracking bats and other small nocturnal animals. *J. Mammal*. **57**: 173–176.

Campbell, A. J. (1901). *Nests and eggs of Australian birds*. Melbourne: A. J. Campbell.

Cody, M. L. (1971). Ecological aspects of reproduction. In *Avian biology*: 462–512. Farner, D. S. & King, J. R. (Eds). New York: Academic Press.

Constantine, D. G. (1966). Ecological observations on lasiurine bats in Iowa. *J. Mammal*. **47**: 34–41.

Cooper, D. S. & Francis, C. M. (1998). Nest predation in a Malaysian lowland rain forest. *Biol. Conserv*. **85**: 199–202.

Czechura, G. V. (1983). Predation on a small colony of bats by an Australian hobby, *Falco longipennis*. *Victorian Nat*. **98**: 200–203.

de Oliveira, M. C. & Schulz, M. (1997). Echolocation and roost selection in Semon's leaf-nosed bat *Hipposideros semoni*. *Mem. Qld Mus*. **42**: 158.

Dwyer, P. D. & Harris, J. A. (1972). Behavioral acclimatization to temperature by pregnant *Miniopterus* (Chiroptera). *Physiol. Zool*. **45**: 14–21.

Entwistle, A. C., Racey, P. A. & Speakman, J. R. (1996). Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Philos. Trans. R. Soc. Lond. B Biol. Sci*. **351**: 921–931.

Flannery, T. (1995*a*). *Mammals of New Guinea*. Sydney: Reed.

Flannery, T. (1995*b*). *Mammals of the South-west Pacific & Moluccan Islands*. Sydney: Reed.

Floyd, A. G. (1980). *Rainforest report: Richmond Range*. Hurstville, New South Wales: New South Wales National Parks and Wildlife Service.

Forestry Commission of New South Wales (1987). *Management plan for Urbenville management area*. Sydney: Forestry Commission of New South Wales.

Foster, M. S. (1992). Tent roosts of Macconnelli's bat (*Vampyressa macconnelli*). *Biotropica* **24**: 447–454.

Hall, L. S. & Richards, G. C. (1979). *Bats of eastern Australia*. Brisbane: Queensland Museum.

Horton, W. & Jahnke, B. R. (1986). Birds recorded from Kroombit Tops, Queensland, in December 1983. *Qld Nat*. **27**: 72–75.

Kennedy, M. (Ed.). (1990). *Australia's endangered species. The extinction dilemma*. Brookvale: Simon Schuster.

Key, H. J. (1938). A little falcon (*Falco longipennis*) kills a bat. *S. Aust. Ornithol*. **January 1**: 122.

Krull, D., Schumm, A., Metzner, W. & Neuweiler, G. (1991). Foraging areas and foraging behavior in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). *Behav. Ecol. Sociobiol*. **28**: 247-253.

Kunz, T. H. (1982). Roosting ecology of bats. In *Ecology of bats*: 1-55. Kunz, T. H. (Ed.). New York: Plenum Press.

Kunz, T. H., Fujita, M. S., Brooke, A. P. & McCracken, G. F. (1994). Convergence in tent architecture and tent-making behavior among neotropical and paleotropical bats. *J. Mammal. Evol*. **2**: 57–78.

Kunz, T. H. & McCracken, G. F. (1996). Tents and harems: apparent defence of foliage roosts by tent-making bats. *J. trop. Ecol*. **12**: 121–137.

Lack, D. (1968). *Ecological adaptations for breeding in birds*. London: Metheun.

Law, B. S. 1996. The ecology of bats in south-east Australian forests and potential impacts of forestry practices: a review. *Pacific Conserv. Biol*. **2**: 363–374.

Loiselle, B. A. & Hoppes, W. G. (1983). Nest predation in insular and mainland lowland rainforest in Panama. *Condor* **85**: 93–95.

Martin, T. E. (1993*a*). Nest predation among vegetation layers and habitats: revising the dogmas. *Am. Nat*. **141**: 897–913.

Martin, T. E. (1993*b*). Nest predation and nest sites. *BioScience* **43**: 523–532.

McGill, A. R. (1970). *Australian warblers*. Melbourne: Bird Observer's Club.

McNab, B. K. (1982). Evolutionary alternatives in the physiological ecology of bats. In *Ecology of bats*: 151–200. Kunz, T. H. (Ed.). New York: Plenum Press.

Menkhorst, P. W. (Ed.). (1995). *Mammals of Victoria: distribution, ecology and conservation*. Melbourne: Oxford University Press.

Nilsson, S. G., Björkman, C., Forslund, P. & Höglund, J. (1985). Egg predation in forest bird communities on islands and mainland. *Oecologia (Berl.)* **66**: 511–515.

North, A. J. (1909). *Nests and eggs of birds found breeding in Australia and Tasmania* **II**. Sydney: F. W. White.

Novick, A. (1977). Biology of bats. In *Biology of bats* **1**: 73–287. Wimsatt, W. A. (Ed.). New York: Academic Press.

Nowak, R. M. (1994). *Walker's bats of the world*. Baltimore: John Hopkins University Press.

Oniki, Y. (1975). The behavior and ecology of slaty antshrikes (*Thamnophilus punctatus*) on Barro Colorado Island, Panama Canal Zone. *An. Acad. Bras. Cienc*. **47**: 477–515.

Oniki, Y. (1979). Is nesting success of birds low in the tropics? *Biotropica* **11**: 60–69.

Pavey, C. R. (1998). Habitat use by the eastern horseshoe bat, *Rhinolophus megaphyllus*, in a fragmented woodland mosaic. *Wildl. Res*. **25**: 489–498.

Payne, J., Francis, C. M. & Phillipps, K. (1985). *A field guide to the mammals of Borneo*. Malaysia: Sabah Society.

Phillips, W. R. & Inwards, S. J. (1985). The annual activity and breeding cycles of Gould's long-eared bat, *Nyctophilus gouldi* (Microchiroptera: Vespertilionidae). *Aust. J. Zool*. **33**: 111–126.

Ransome, R. (1990). *The natural history of hibernating bats*. London: Christopher Helm.

Rhodes, M. P. (1996). Wing morphology and flight behaviour of the golden-tipped bat, *Phoniscus papuensis* (Dobson) (Chiroptera: Vespertilionidae). *Aust. J. Zool*. **43**: 657–663.

Rickart, E. A., Heideman, P. D. & Utzurrum, R. C. B. (1989). Tent-roosting by *Scotophilus kuhlii* (Chiroptera: Vespertilionidae) in the Philippines. *J. Trop. Ecol*. **5**: 433–436.

Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. *Smithson. Contrib. Zool*. **9**: 1–48.

Roberts, A. (1951). *The mammals of South Africa*. Johannesburg: CNA.

Robinson, M. F. & Stebbings, R. E. (1997). Home range and habitat use by the serotine bat, *Eptesicus serotinus*, in England. *J. Zool. (Lond.)* **243**: 117–136.

Rosevear, D. R. (1965). *The bats of West Africa*. London: British Museum of Natural History.

Schulz, M. (1994). *The fauna of Kroombit Tops*. Report to Queensland Department of Primary Industries (Forestry), Brisbane.

Schulz, M. (1995). Utilisation of suspended bird nests by the golden-tipped bat (*Kerivoula papuensis*) in Australia. *Mammalia* **59**: 280–283.

Schulz, M. (1997). Bats in bird nests in Australia: a review. *Mammal. Rev*. **28**: 69–76.

Schulz, M. & Hannah, D. (1998). Relative abundance, diet and roost selection of the tube-nosed insect bat, *Murina florium*, on the Atherton Tablelands, Australia. *Wildl. Res*. **25**: 261–271.

Schulz, M. & Menkhorst, K. A. (1985). Notes on the lesser warty-nosed horseshoe-bat (*Hipposideros stenotis*). *Aust. Bat Res. News* **20**: 14–16.

Sclater, W. L. (1900). *The mammals of South Africa*. London: Porter.

Sharma, S. K. (1986). Painted bats and nests of Baya weaver bird. *J. Bombay Nat. Hist. Soc*. **81**: 196.

Shortridge, G. C. (1934). *The mammals of South West Africa: a biological account of the forms occurring in that region*. London: Heinemann.

Skinner, J. D. & Smithers, R. H. N. (1990). *The mammals of the Southern African subregion*. Pretoria: University of Pretoria.

Specht, R. L. (1970). Vegetation. In *The Australian environment*: 44–67. Leeper, G. W. (Ed.). Melbourne: Melbourne University Press.

Speight, J. G. (1990). Landform. In *Australian soil and land survey. Field handbook*: 9–57. McDonald, R. C., Isbell, R. F., Speight, J. G., Walker, J. & Hopkins, M. S. (Eds). Melbourne: Inkata.

Strahan, R. (Ed.). (1995). *The mammals of Australia*. Sydney: Reed.

Tan, K. H., Zubaid, A. & Kunz, T. H. (1997). Tent construction and social organization in *Cynopterus brachyotis* (Muller) (Chiroptera: Pteropodidae) in Peninsular Malaysia. *J. Nat. Hist*. **31**: 1605–1621.

Thomas, O. (1914). On mammals from Manus Island, Admiralty Group and Ruk Island, Bismarck Archipelago. *Ann. Mag. Nat. Hist*. **13**: 434–439.

Tidemann, C. R. & Flavel, S. C. (1987). Factors affecting choice of diurnal roost site by tree hole bats (Microchiroptera) in south-eastern Australia. *Aust. Wildl. Res*. **14**: 459–473.

Tidemann, C. R. & Woodside, D. P. (1978). A collapsible bat trap and a comparison of results obtained with the trap and mist-nets. *Aust. Wildl. Res*. **5**: 355–362.

Timm, R. M. & Mortimer, J. (1976). Selection of roost sites by the Honduran white bats, *Ectophylla alba* (Chiroptera: Phyllostomatidae). *Ecology* **57**: 385–389.

Tracey, J. G. & Webb, L. J. (1975). *Vegetation of the humid tropical region of north Queensland*. Indooroopilly: CSIRO.

Tuttle, M. D. (1974). An improved trap for bats. *J. Mammal*. **55**: 475–477.

Walker, E. P. (1975). *Mammals of the world* **1**. Baltimore: John Hopkins University Press.

Walker, J. & Hopkins, M. S. (1990). Vegetation. In *Australian soil and land survey. Field handbook*: 58–86. McDonald, R. C., Isbell, R. F., Speight, J. G., Walker, J. & Hopkins, M. S. (Eds). Melbourne: Inkata.

Wallin, L. (1969). The Japanese bat fauna. A comparative study of chorology, species diversity and ecological differentiation. *Zool. Bidrag., Uppsala* **37**: 226–440.

Webb, L. J. (1978). A general classification of Australian rainforests. *Aust. Plants* **9**: 349–359.

Winchell, J. M. & Kunz, T. H. (1996). Day-roosting activity budgets of the eastern pipistrelle bat, *Pipistrellus subflavus* (Chiroptera: Vespertilionidae). *Can. J. Zool*. **74**: 431–441.

Woodside, D. P. (1995). Golden-tipped bat *Kerivoula papuensis*. In *The mammals of Australia*: 490–491. Strahan, R. (Ed.). Sydney: Reed.

Young, R. A. (1980). Observations on the vulnerability of two species of wattled bats (*Chalinolobus*) to diurnal avian predators. *Victorian Nat*. **97**: 258–262.