

Roosting behaviour of the tawny frogmouth (*Podargus strigoides*)

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Abstract

We characterized the day roost sites of four pairs and one solitary tawny frogmouth *Podargus strigoides* in a woodland in south-eastern Australia. The birds were equipped with radio transmitters which enabled us to locate them daily from autumn 1997 to late summer 1998. Tree species, tree size, roost height and orientation of the roosting bird were recorded. Over the study period tawny frogmouths frequented a large number of day roosts (up to 71 per pair). Birds rarely used the same roost over extended time periods and most roosts were used for less than 3 days. Mature trees with a girth of more than 0.5 m were preferred as day roosts. Tawny frogmouths exhibited a significant preference for the coarse and dark-barked stringybark trees, but other tree species such as the smooth-barked, light-coloured gums were also frequented. However, when roosting in gum trees, dead branches were preferred, presumably as these have a coarser appearance than living branches and therefore provided better camouflaging. Especially during winter, the birds showed a significant selection of branches on the northern side of roost trees presumably to maximize sun exposure. During summer, two pairs maintained a significant northerly preference, whereas the others used roosts with random orientations. Small-scale seasonal movements in the area used for day roosting were also observed, with two pairs selecting a distinct area with a south-westerly aspect during summer which appeared to have less sun exposure. Our study suggests that tawny frogmouths select roosts to (1) minimize visibility from day predators and (2) to facilitate passive thermoregulation by sun-basking.

Key words: tawny frogmouth, Australia, behavioural thermoregulation, predator avoidance, roost selection, season

INTRODUCTION

Roosts of birds must fulfil at least two potentially important functions. Roosts must provide some protection or camouflaging from predators, as alertness of resting birds may be impaired. The second important function of roosts, particularly in cold climates, is to minimize heat loss and thus thermoregulatory costs (Dawson & Hudson, 1970; Reinertsen, 1983; Bech & Reintertsen, 1989). Unfortunately, roosting behaviour in many bird species is difficult to study, because most are diurnal and small, and difficult to locate at night. However, nest sites should fulfil similar functions as roosting sites (Nilsson, 1984; Zwartjies & Nordell, 1998) and nests are often easier to locate than the birds themselves. Accordingly, the selection of nest sites has been studied especially in cavity users, and it appears that in both hot and cold climates birds select roosts

primarily to minimize thermoregulatory costs (Ricklefs & Hainsworth, 1969; Finch, 1983; Zwartjies & Nordell, 1998). Nesting or roosting in cavities also has the advantage of good concealment from potential predators, but the drawbacks of such roosts are the often limited availability of suitable holes, the restriction to a relatively small body size, and a narrow scope for behavioural thermoregulation.

Roost selection of nocturnal birds which rest during the daytime is of course easier to study than that of diurnal birds, and is behaviourally more interesting, particularly when the birds roost in the open. For these birds camouflage is most important because of the increased visibility during daytime; sun radiation also provides them with a wide range of microhabitats and thus options for behavioural thermoregulation. We chose the nocturnal Australian tawny frogmouth (*Podargus strigoides*; Podargidae: Caprimulgiformes) to quantify roosting behaviour in the wild. The tawny frogmouth is one of the largest Caprimulgiformes (500 g) and feeds mainly on ground-dwelling invertebrates upon which it pounces from a low perch (Serventy, 1936;

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Rose & Eldridge, 1997). During the daytime frogmouths always roost exposed on a branch or occasionally on the ground (Schodde & Mason, 1980), and most roost selection should therefore not be limited by the availability of potential roost sites. The extremely cryptic plumage and the posture of frogmouths, which resembles a broken branch, provide an almost perfect camouflage from most diurnal predators. Moreover, frogmouths are extremely reluctant to fly during the day and their camouflage is therefore not jeopardized by movement. Nevertheless, raptors and mammalian carnivores are known occasionally to prey upon these birds (Serventy, 1936; Schodde & Mason, 1980).

The wide distribution range of the sedentary tawny frogmouth includes some of the colder areas of the Australian continent such as the Northern Tablelands of New South Wales where during winter nights and mornings air temperatures (T_a) regularly approach 0 °C. In these areas seeking sun exposure during the colder months, when prey availability is also decreased, could considerably reduce the energetic costs for thermoregulation. There are some anecdotal reports of frogmouths basking in the sun (Sedgwick, 1938; Lawrance, 1940; Coleman, 1946), but to date this behaviour has never been quantified. Furthermore, pair-roosting and huddling to share body heat seem to be common in this species (Tarr, 1985). The cool winters on the Northern Tablelands are followed by warm summers with an average maximum T_a of 26.4 °C and extremes up to 39 °C. Consequently, the hot summer climate combined with intense solar radiation also provides a potential thermoregulatory challenge for a bird roosting in the open.

The purpose of this study was, therefore, to quantify the nature of roost sites chosen by frogmouths living in a temperate region. Data were used to assess the extent to which roost selection is determined by predator avoidance and thermoregulation.

MATERIAL AND METHODS

Day roosts

The study was conducted between March 1997 and January 1998 in Eastwood state forest (*c.* 219 ha, 30° 35' S, 151° 44' E; altitude *c.* 1000 m) located about 10 km south-east of Armidale on the Northern Tablelands (New South Wales, Australia). The tree community includes broad-leaved stringybark *Eucalyptus caliginosa*, Blakely's red gum *E. blakelyi*, manna gum *E. viminalis*, yellow box *E. melliodora*, and fern-leaved wattle *Acacia filicifolia* as the most common species (Ford, Bridges & Noske, 1985). The area surrounding the state forest has been extensively cleared with the exception of a few patches of adjacent woodland situated on private property.

Spotlight surveys were conducted regularly from a vehicle along the established tracks (Fig. 1). When a bird was located we placed a raptor trap (Cam, 1985) close to

the bird. In all we trapped 6 birds (4 males, 2 females) between March and July 1997. Five of the birds were members of resident pairs (920, 940, 960, 980; numbers correspond to the transmitter frequency of tagged individuals). Two birds constituted the same pair (920). One frogmouth (180) was apparently a solitary bird, most likely a subadult without an established territory. Each bird captured was fitted with colour bands and a radio transmitter (Sirtrack, single stage). Transmitters were attached using a back-pack style harness made of elastic thread (Brigham, 1992). One bird was recaptured and the transmitter replaced. Birds were located daily by radio-tracking from the day of capture until the end of September when they started nesting or until the transmitter failed (2 occasions). Summer roost locations were recorded between 22 December and 26 January and juveniles which fledged in late November/early December (Körtner & Geiser, 1999) were included. The locations of roost trees were marked on a 1:10 000 topographical map of the study area and tree species and girth of the trunk at breast height were recorded. The characteristics of roost trees were compared to a random sample of trees. The random sample consisted of all trees with a girth at breast height of at least 0.2 m found in 74 randomly selected 50 × 20 m transects. Random trees were measured and grouped into three bark categories (i.e. light grey or cream-coloured smooth-barked 'gum', flaky or scaly-barked 'box', or dark and rough-barked 'stringybark'). We also sampled acacias which were larger than the size threshold. These were later excluded from the analysis, because their low and dense growth patterns apparently made them unsuitable as roosts for frogmouths.

In addition, roost height was measured using an inclinometer and the diameter of the roost branch and its vertical angle were estimated. The angle of the roost measured from the base of the tree and also the angle of the branch at the roost site were measured using a compass (magnetic north). We also noted whether or not members of a pair were huddling.

Air temperature

Data loggers at 2 locations in the woodland recorded T_a at hourly intervals. The loggers were based on a microprocessor (Basic Stamp II, Parallax) and equipped with 8 temperature transducers (AD 592; accuracy ± 0.35 °C) each. Data were down-loaded to a laptop computer in 3-week intervals and the average of the 2 locations was used for the analyses as T_a records were very similar.

Statistics

To test whether frogmouths selected certain tree species for use as roosts, the species composition of roost trees was compared with the random sample derived from the 74 transects. Samples were arranged in a 3 × 3

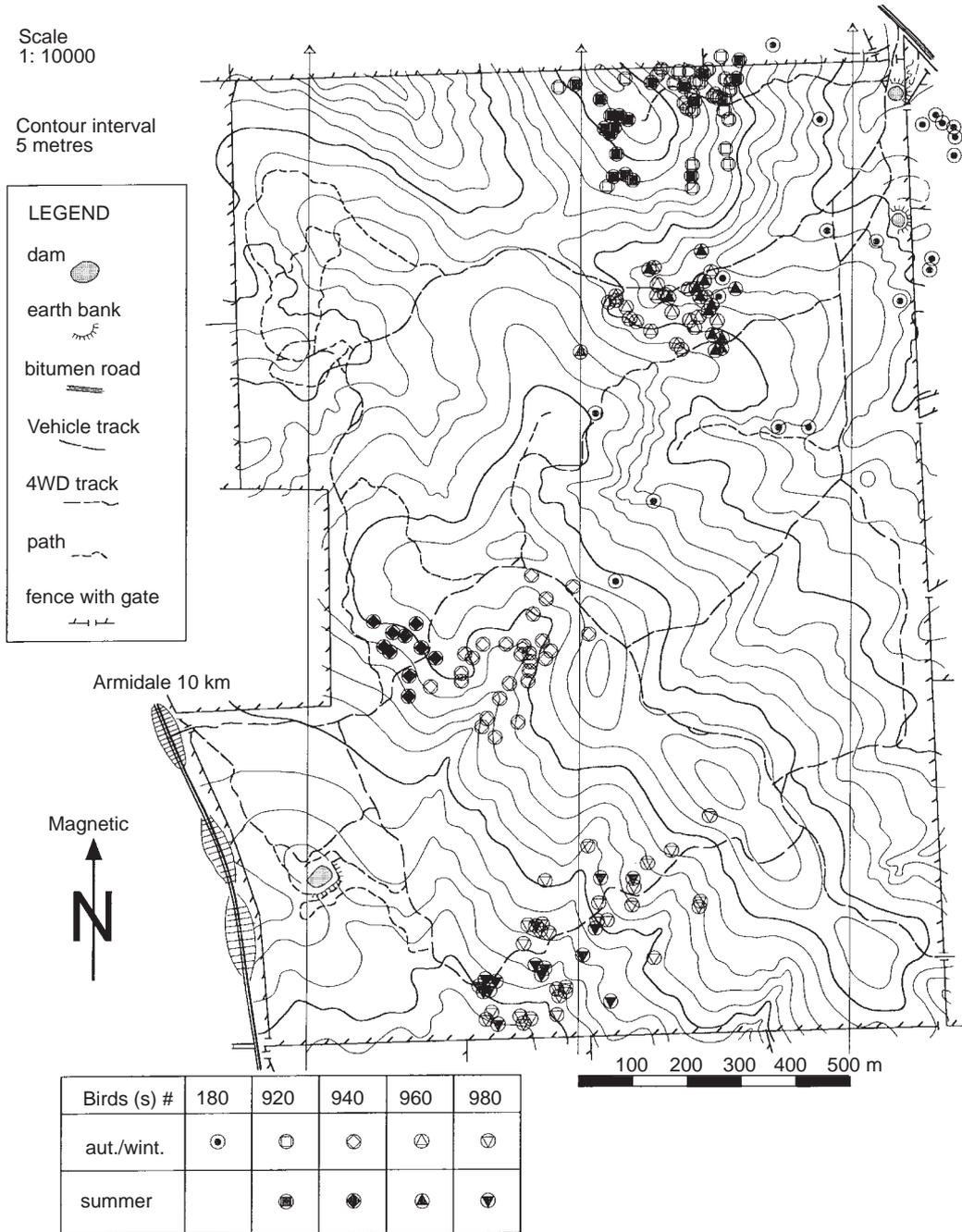


Fig. 1. Map of the study area showing the day roost locations for individuals from four pairs (920, 940, 960, 980) and one solitary tawny frogmouth (180).

contingency table (i.e. 3 tree types: stringybarks, gums, and box vs 3 size classes: 0.5–0.9 m, 0.9–1.6 m and > 1.6 m girth at breast height). Chi-square analyses were performed whereby the expected Chi-squares represented the overall species composition in the woodland.

The angle of the roost measured from the base of the tree and the angle of the branch at roost position, both determined by compass, were tested for randomness (Raleigh test; circular statistics, Zar, 1996). For the test each recorded roost location represented one data point regardless of how many days it was used or how many birds used it. For non-random distributions the mean angle and 99% confidence interval were calculated. The

nesting period plus the 2 weeks following fledging were excluded from all analyses.

Unless stated otherwise, all data are presented as means \pm SD for the number of observations 'N' or the number of pairs/families and also the one individual bird 'n'. A test result was assumed significant when $P < 0.05$.

RESULTS

Our spotlight surveys revealed that the woodland harboured seven or eight resident frogmouth pairs. Five

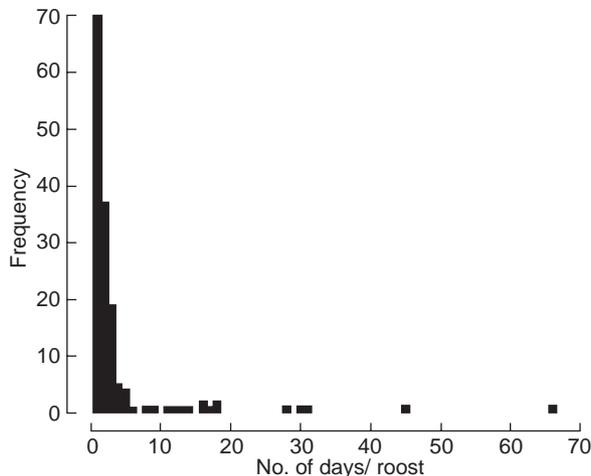


Fig. 2. Bar graph illustrating the number of day roosts used over the study period.

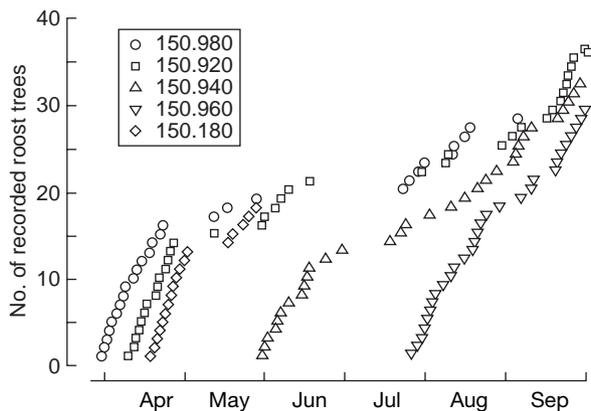


Fig. 3. Cumulative total of roost locations from the autumn winter survey. Note how number of roost trees levelled off at approximately 20 after initial capture between April and July, but the use of new roosts increased again in September indicating seasonal change in roost preference.

of the trapped birds belonged to four resident pairs. One radio-tagged individual moved between the territories of a least three resident pairs and eventually left the forest altogether. This bird probably was a dispersing subadult from the previous year. In general, pairs used relatively small areas for day roosting (Fig. 1). Over the course of the study, birds were observed to change roost sites only twice during the daytime.

Some trees were favoured and repeatedly used as roosts, but always by the same individual or pair. One roost was used for 52 days with only two interruptions. On average, however, each individual or pair used 11.1 ± 5.3 (range 1–22) roosts per month. Of all the recorded roost trees ($n = 205$) 87% were used for 3 days or less (Fig. 2). If a tree was used as a roost more than once birds usually selected the same branch.

As expected the cumulative number of roost trees used per pair or individual increased sharply after first capture. The accumulation of new roosts typically

levelled off between 15 and 20 (Fig. 3) and few new roosts were frequented during mid-winter. However, a large number of new roosts was used from September (spring), indicative of a seasonal change in roost preference (Fig. 3). The roosts used by the birds during the summer survey again comprised a large number of new sites. For two pairs (920, 940) summer roosts were predominantly situated in distinct parts of their territory that differed in aspect from the winter roost areas (Fig. 1). The use of roost locations of pair 980 also varied with season. In autumn (1997) this pair preferred higher elevations, whereas during the following winter the pair typically roosted near the bottom of a hill. Towards the end of the following summer survey (January 1998) this pair was again found at higher elevations. We found no distinct seasonal movements for pair 960 (Fig. 1), but summer roosts were predominantly situated in the eastern part of the area used for roosting while during winter roosting occurred in a larger area. The limited seasonal variation in this pair may be attributed to the fact that the male was not trapped until 21 July 1997 and this pair was therefore monitored only over a relatively short time.

The overall tree community in the small woodland was relatively uniform with only small clearings and a few dense patches of regrowth. However, gums were slightly more common along the wetter gullies. Therefore, random plots inside the roosting areas showed no differences in species composition, tree density, or tree sizes relative to plots situated outside the roosting areas. Overall tree density was $348 \text{ trees ha}^{-1}$ (tree girth $\geq 0.2 \text{ m}$). Frogmouths preferred large mature trees with a girth of at least 0.5 m and trees with a girth between 1.1 and 1.7 m were used most frequently (Fig. 4). Of the 212 trees selected as day roosts, 75.9% were stringybarks, 17.5% were gums and 5.7% were box. When compared with species composition in the relevant size classes, stringybarks were significantly over-represented as day roosts ($P < 0.001$) (Fig. 4).

The height of the day roosts ranged from 4.8 to 19.3 m (mean: $12.8 \pm 2.5 \text{ m}$; $N = 259$, $n = 5$) and birds were never observed roosting on the ground during the day. The branch selected as a day roost was often exposed and birds never appeared to shelter or hide within the foliage. Particularly when roosting in gums, dead branches were preferred as roost sites (54%), but in only two instances were birds observed to roost in a dead tree. Birds often roosted in a vertical fork or next to the trunk. The vertical angle of the selected branch relative to horizontal was never steeper than 50° ($24.7 \pm 14.4^\circ$; $N = 275$) and the branch diameter ranged from *c.* 3 to 20 cm.

During autumn/winter the angle of the roost measured from the base of the tree and the angle measured along the branch at roost site were significantly north-facing ($P < 0.001$) for all birds monitored (Fig. 5). The average angle measured from the base of the tree ranged between 2.1 and 30.6° (average for the pooled data set: $14.7 \pm 9.8^\circ$, 99% confidence interval, $r = 0.66$, $N = 159$,

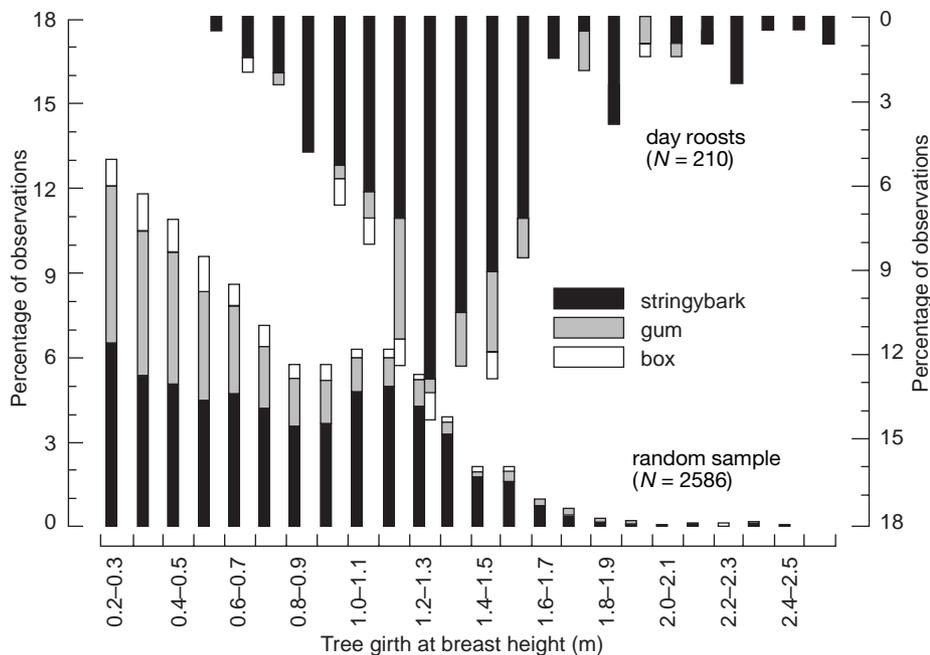


Fig. 4. Size class distribution of the day roosts used by frogmouths vs a random sample of trees. Trees were separated into three different bark categories (stringybark, box and gum).

$n = 5$, Fig. 5). Mean angle measured along the branch was $13.6 \pm 8.6^\circ$, 99% confidence interval, $r = 0.73$, $N = 164$, $n = 5$).

Only a slightly smaller number of roost sites was found during the shorter summer survey, because the young, which were usually in the vicinity of their parents, were included. The northerly preference by roosting birds was less pronounced in summer than in winter, but prevailed in two pairs. For one pair, both the northerly angle of the roosting bird measured from the base of the tree and the branch angle were significant. In the other pair only the angle measured along the roost branch was significant. When all summer data were pooled, the results were also significant (angle from base shown in Fig. 5: $26.3 \pm 17.2^\circ$, 99% confidence interval, $r = 0.23$, $N = 117$, $n = 4$, $P < 0.01$; branch angle: $28.1 \pm 15.6^\circ$, 99% confidence interval, $r = 0.34$, $N = 121$, $n = 4$, $P < 0.001$).

When a human observer, or large birds such as ravens (*Corvus* spp.) or currawongs (*Strepera graculina*), were in the vicinity of the day roost frogmouths assumed a typical outstretched, branch-like position which presumably decreases the likelihood of being detected. Observed from a distance, however, birds would assume a more relaxed position and especially on cold mornings feathers were fluffed up to maximize insulation. During most days members of a pair roosted in close vicinity to each other, whether in neighbouring trees, different branches of the same tree, or huddled together. Since it was easy to miss birds even when they were roosting close to a radio-tagged individual, only huddling was quantified. From April to the end of August huddling occurred in $66.3 \pm 7.8\%$ of all observations with no significant differences

between months. Frequency of huddling was not correlated with the average daily T_a nor with its daily minimum.

During most of the summer survey young roosted with their parents; roosting together in a family group may only partly reflect thermoregulatory behaviour, and may also have a social component.

DISCUSSION

Our study shows that tawny frogmouths select roost locations and tree species that are likely to facilitate two major functions: behavioural thermoregulation and predator avoidance. Area selection and roost orientation changed with season, but birds remained within the same relative small area throughout the year.

The 219 ha Eastwood State Forest contained at least seven resident pairs. The reason for the small territory sizes probably reflects the ample foraging opportunities provided by the open woodland with a dense network of vehicle tracks plus the surrounding grassland. Although these territories may appear rather small for a bird of this size, similar territory sizes, as small as 20 ha, have been reported for this species elsewhere on the Northern Tablelands (Schodde & Mason, 1980).

Only a part of these small territories was used for day roosting, but the number of roost trees was considerable and records for new roosts accumulated throughout the study. This suggests that previous reports of high roost fidelity by frogmouths with birds rotating between a few established day roosts (Schodde & Mason, 1980; Ingram, 1994) may not always apply. Previous data are likely to reflect either short-term observations or might

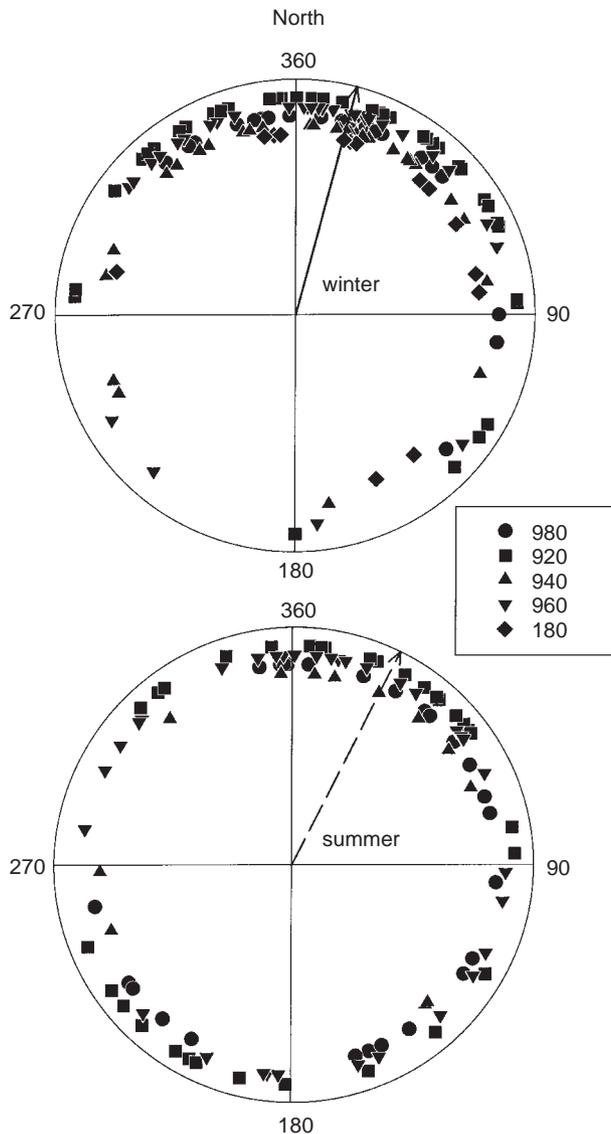


Fig. 5. Compass orientation of the roosting bird measured from the base of the tree of all roost locations recorded between April and September 1997 (top) and December 1997 to January 1998 (bottom). Data for different individuals/pairs are plotted on separate radii to increase clarity. During winter all pairs/individuals showed a significant northerly orientation, whereas in summer this was restricted to only one pair. The arrows indicate the mean angle for the pooled records which were significant for both winter ($P < 0.001$; $r = 0.66$; solid line) and summer ($P < 0.01$; $r = 0.23$; broken line).

apply to birds in urban situations where few suitable roost trees are available.

Presumably day roosts are chosen to meet certain criteria. For birds such as frogmouths which must roost in exposed places, avoidance of day-time predators should be an important consideration. As foxes, cats and domestic dogs are common in Eastwood State Forest it is not surprising that tawny frogmouths were never observed roosting on the ground, compared with other sites (Schodde & Mason, 1980). Most birds also

selected mature thick trees (Fig. 4) and roosted at considerable height (> 4.8 m).

Tawny frogmouths preferred stringybarks presumably because the rough bark is so similar in appearance to the bird's mottled plumage. If a gum was chosen as day roost, then dead grey-coloured branches blending with the plumage of the resting bird were frequently selected as roosts. To conceal the bulk of the body further, frogmouths either roosted along medium sized branches or in a fork. Particularly when sitting on a thin branch, frogmouths tended to press their body against the trunk or another larger branch. Camouflage thus appears to be an important criterion for roost selection by frogmouths. In contrast, the closely related owl-nightjar *Aegotheles cristatus* which was studied in the same woodland does not select roosts in certain tree species (i.e. bark appearance; Brigham, Debus & Geiser, 1998). However, owl-nightjars roost within tree hollows and therefore are hidden from daytime predators and external appearance of the tree thus seems irrelevant.

The seasonal movements we observed by most pairs are not accounted for by the need for camouflaging and predator avoidance. Such movements extended over not more than a few hundred metres and could be either gradual (980) or abrupt (920, 940). Since abrupt movements occurred shortly after the young had fledged (see also Le Souëf, 1937; Sedgwick, 1938), it is possible that enforced inflexibility in roost selection during the preceding 2-month nesting period prevented a gradual adjustment. The areas selected for roosting in summer and winter appeared to differ in the level of sun exposure and the topographical features within a territory seemed to govern such movements to some extent. During summer, two pairs (920, 940) and their young predominantly roosted in areas characterized by a south-westerly aspect with little sun exposure. In winter, these birds preferred either easterly aspects (920) or were roosting along a gully with a north-south orientation (940) which would increase morning and midday sun exposure and also decrease shading by the canopy.

Exposure to the sun also appears to influence the position the birds assume in the roost tree itself. During the colder months of the year all frogmouths preferred a northerly orientation, suggesting that roost sites were selected for sun exposure. During winter T_a frequently approaches 0°C around Armidale and exposure to these low T_a values would demand heat production 3–4 times that at thermoneutrality (McNab & Bonaccorso, 1995). Sun basking together with huddling, which we commonly observed and which has been described in the literature (Lawrance, 1940; Coleman, 1946; Schodde & Mason, 1980), are therefore probably employed to reduce thermoregulatory costs (Boix-Hinzen & Lovegrove, 1998). In summer T_a is more favourable and, as expected, preferences for a northerly direction were less pronounced. However, preference for north-facing roosts did prevail in some pairs. This may be explained by the high ($> 30^\circ\text{C}$) thermoneutral zone of tawny frogmouths (McNab & Bonaccorso, 1995) which is usually

above the T_a that is encountered. Even in summer it therefore appears to be advantageous to be sun exposed, particularly in the early morning. Later in the day a shaded position might be more desirable, but frogmouths like other Caprimulgiformes possess remarkable heat tolerance (Lasiewski, Dawson & Bartholomew, 1970; McNab & Bonaccorso, 1995). Even above thermoneutrality frogmouths are able to dissipate heat by panting at exceptionally low energetic cost (Lasiewski & Bartholomew, 1966; Lasiewski *et al.*, 1970).

In conclusion, it appears that reducing detection by potential predators and behavioural thermoregulation are both important factors implicated in roost site selection by tawny frogmouths. These birds seek sun exposure even during summer at least under the moderate climatic conditions of the Northern Tablelands. Nevertheless, the overall large number of day roosts used only once, together with the selection of whole sets of new roost locations over short time intervals, suggests that frogmouths constantly adjust to seasonal climatic changes. Moving between areas with different aspect and sun exposure and selecting suitable roost trees within these areas, are at least two strategies to minimize energy expenditure in a climate characterized by pronounced daily and seasonal temperature fluctuations. So, by selecting appropriate tree species, position of trees and direction of roosts, frogmouths appear to be able to minimize both predation risks and thermoregulatory costs.

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