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Dimensions of tree hollows used by birds and mammals in the jarrah forest: improving the dimensional description of potentially usable hollows

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ABSTRACT

A graphical method for describing the range of dimensions of hollows used by arboreal fauna is developed and applied to data from hollows used by six bird and four mammal species of the jarrah forest of south-west Western Australia. Pairs of hollow entry measurements and pairs of internal hollow measurements were graphed separately, and lines bounding the spread of these data defined the range of hollow sizes used by each species. This method can be used with small data sets. The descriptions provide a means of identifying hollows in felled trees that could have been used by these species. Measurements were collected from 82 hollows and combined with similar published data for hollows used by common brushtail possum (*Trichosurus vulpecula*), western ringtail possum (*Pseudocheirus occidentalis*), brush-tailed phascogale (*Phascogale tapoatafa*), mardo (*Antechinus flavipes*), red-tailed black cockatoo (*Calyptorhynchus banksii naso* and *Calyptorhynchus banksii samueli*), Australian ringneck (*Platycercus zonarius*), western rosella (*Platycercus icterotis*), red-capped parrot (*Platycercus spurius*), rufous treecreeper (*Climacteris rufa*), and striated pardalote (*Pardalotus striatus*).

The graphical presentation and interpretation of entry and internal dimensions is recommended for examining hollow sizes. This method can be used with the small data sets that often result because hollow dimensions are difficult, dangerous, and expensive to collect. A constant area function is proposed to describe the maximum hollow entry size used by a species. In studies of hollows used by fauna, maximum and minimum entry dimensions should be collected in preference to vertical and horizontal entry dimensions.

INTRODUCTION

Hollows in trees are an important attribute of forest environments (Recher *et al.* 1980; Kavanagh and Turner 1994; Kutt 1994). The importance of hollows to fauna that use them for denning and nesting is widely recognized (Cowley 1971; Tyndale-Biscoe and Calaby 1975; Newton 1994). In the jarrah forest of south-west Western Australia there are 9 mammal and 17 bird species that are obligate users of tree hollows (Serventy and Whittell 1976; Christensen *et al.* 1985; Strahan 1998) and 16 vertebrate species with lesser degrees of dependence on hollows for breeding and shelter (Ian Abbott[1], personal communication). The conservation of these species, (particularly the obligate hollow users) in a forest that is managed for water, timber and mineral production, conservation, and recreation, is in part dependent on the continued provision of suitable tree hollows.

Mackowski (1987), recommended describing the features of hollows used by individual species and interpreting hollow availability for each wildlife species based on these descriptions. Similarly, McComb *et al.* (1994) classified hollows as potentially suited to a species when the dimensions of the hollows fell within the range defined by the maximum and minimum dimensions reported by Saunders *et al.* (1982), Inions *et al.* (1989), Long (1990), and Haseler and Taylor (1993). Once hollows that are potentially suited to a species are identified, the relationship between hollow occurrence and tree characteristics can be examined. These relationships can then be used as a basis for selecting trees to retain after logging (Gibbons and Lindenmayer 1996, 1997).

This study describes the first phase of this process: the description of the dimensions of hollows that are potentially suited to ten arboreal hollow users (see Fig. 1). The species studied were: common brushtail possum (*Trichosurus vulpecula*), western ringtail possum (*Pseudocheirus occidentalis*), brush-tailed phascogale (*Phascogale tapoatafa*), mardo (*Antechinus flavipes*), red-tailed black cockatoo (*Calyptorhynchus banksii naso* and *Calyptorhynchus banksii samueli*), Australian ringneck (*Platycercus zonarius*), western rosella (*Platycercus icterotis*), red-capped parrot (*Platycercus spurius*), rufous treecreeper (*Climacteris rufa*), and striated pardalote (*Pardalotus striatus*) (nomenclature follows Strahan (1998), and Johnstone (in press)).

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[1] Dr I. Abbott, Department of Conservation and Land Management, Kennsington, WA.

In this paper I present a new method of describing the dimensions of hollows used by fauna. This new method was developed after the collected data were compared with published summaries of similar hollow dimensions. This comparison revealed that the published summaries provided incomplete and sometimes inconsistent descriptions of hollow size, and some small data sets provided limited information. These summaries could be misleading if used to classify hollows as potentially suited to a species. I apply this new method to the available data (including limited data sets) and present the descriptions of the range of hollow sizes used by 10 species from the jarrah forests of south-west Western Australia. I also explain the assumptions that were made in producing these descriptions, examine the reasons for applying limits to the descriptions and examine the distribution of hollow sizes classified as potentially usable by this system.

METHODS

This study was based on two data sets: one being measurements of hollows used by fauna, and the other measurements of all hollows located in a search of 239 trees (Whitford, in press). All new data collected for this work came from trees felled in logging operations. Data from the 239 trees were examined to determine whether applying the descriptions of potentially usable hollows to a sample of hollow measurements would result in a disproportionately large number of hollows with elongated entries being classified as potentially usable.

Hollows Used by Fauna

Data used to describe the dimensions of potentially usable hollows came from several studies. Hollow-bearing trees used by birds and mammals at Kingston Block, 20 km north-east of Manjimup, Western Australia, were identified by radio-tracking (K. Morris[2], personal communication; Rhind 1998), by the presence of scratch tracks made by possums, and by the observation of hollow use by rufous treecreepers (M. Craig[3], personal communication). Hollows were classified as used when clear evidence of occupation was found (nests, egg shell fragments, or scats, or identified hair samples associated with internal scratching, staining and wear). Dimensions of 59 used hollows were collected from 32 of these trees that were felled when the area was logged. Data from an additional 23 hollows in 18 trees were collected fortuitously in an examination of a random sample of 239 trees described in Whitford (in press). The dimensions collected from these used hollows were combined with similar data from: Saunders *et al.* (1982), Long (1990), Dickman[4] (1991 and unpublished data), Soderquist[5] (1993 and unpublished data), Craig[3] (unpublished data), Johnstone[6] (unpublished data), Rhind (1998), and nest box data from Wardell-Johnson (1986). These nest box dimensions for mardos were combined with data from natural hollows and interpreted in the same manner as data for other species.

Hollow Measurement

Felled trees were thoroughly searched for hollows, and hollows used by birds and mammals were identified from the contents (hair samples, nests, egg shell fragments, scats, internal scratching, staining and wear). Each hollow was measured for: height of the hollow entry above the ground, depth of the hollow from the lower lip of the entry to the base of the hollow, and the width of the hollow at the widest point (the average of minimum and maximum dimensions at that point). The maximum and minimum widths of the hollow entry, termed the maximum entry dimension and minimum entry dimension, were also measured (usually at right angles to one another). Figure 1 illustrates these measurements.

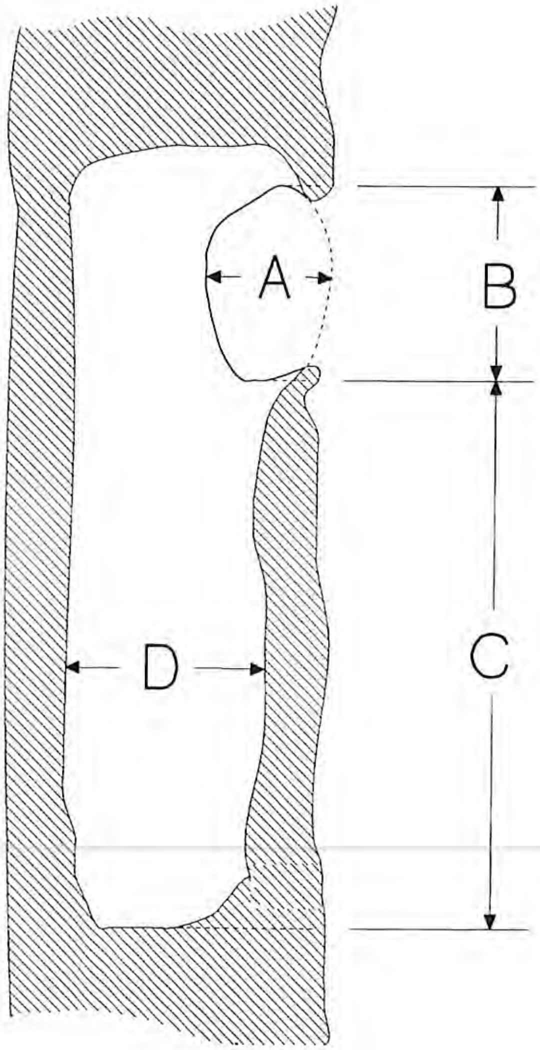

Figure 1. The measurements of tree hollow dimensions: A, minimum entry dimension; B, maximum entry dimension; C, depth of the hollow; D, average width of the hollow at the widest point (after Fig. 2 of Saunders et al. *1982).*

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[2] K. Morris, Department of Conservation and Land Management, Woodvale, WA.

[3] Dr M. Craig, Centre for Rainforest Studies, Yungaburra, Queensland.

[4] Dr C. Dickman, School of Biological Sciences University of Sydney, NSW.

[5] Dr T. Soderquist, National Parks and Wildlife Service, Dubbo, NSW

[6] R. Johnstone, Western Australian Museum, Perth, WA.

Western ringtail possums were observed using shallow hollows that were as wide as they were deep. These refuges, such as depressions in tree forks, would not commonly be referred to as hollows, and have not been included in this study.

Descriptions of the Dimensions of Potentially Usable Hollows

The system I developed to describe the dimensions of hollows had five main attributes:

1. Pairs of hollow dimensions collected from a single hollow were examined as pairs.
2. From each hollow I collected a pair of maximum and minimum entry dimensions, and a pair of internal hollow depth and width (see Fig. 1).
3. The dispersion of these pairs was examined on two-dimensional graphs to identify lines that bounded the spread of the data for each species.
4. For hollow entries the bounds were: the line y = x; a minimum hollow entry size determined from the smallest single hollow entry dimension; and a maximum entry size that was described by a constant area function (see Fig. 2).
5. For hollow internal dimensions the bounds were: the line y = x; the largest and smallest hollow depths and widths observed; and for hollows used by mammals, an additional restriction to ensure that very small hollows were not classified incorrectly as potentially usable.

Where I combined my data with the vertical and horizontal hollow entry dimensions collected by other researchers I assumed these vertical and horizontal dimensions approximated pairs of maximum and minimum entry dimensions. Hollow entries commonly approximate an ellipse, with the vertical entry dimension usually larger than the horizontal dimension. For this reason, the combination of vertical and horizontal dimensions with maximum and minimum measurements was considered appropriate.

I graphed the maximum and minimum dimensions of all hollow entries used by each species. Hollows with at least one small entry dimension defined the lower limit for the minimum hollow entry dimension (the horizontal line shown in Fig. 2). The line y = x occurs as a boundary because the y values (minimum entry dimension) cannot exceed the x values (maximum entry dimension). The third boundary, the maximum size of the hollow entries, was a constant area function that describes all elliptical shapes that have equal areas (Fig. 2). This function can be defined by a single pair of maximum and minimum entry dimensions, or the area of this entry. The exact function used for each species was determined by the largest single observed hollow entry, or where more than one entry had a similar area, by the mean area of a group of the largest observed hollow entries. Hollows with entries that occurred outside the area A and C shown in Figure 2 would be classed as unsuited to the species.

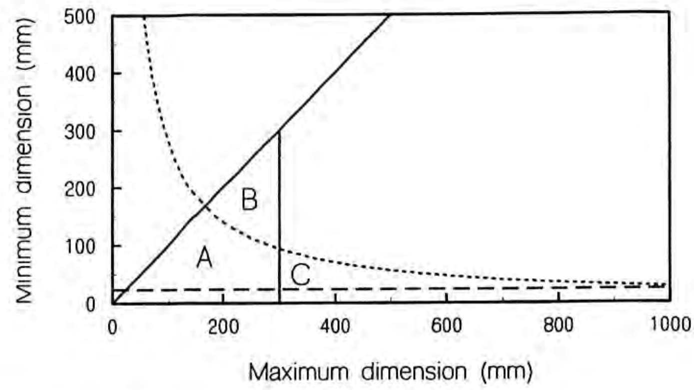

Figure 2. When the range of potentially usable hollow entries is determined from maximum and minimum bounds selected from data summaries, potentially usable hollow entries are those within the right triangular area A and B. The area B can incorrectly indicate that very large hollow entries will be used by the species. The range of potentially usable hollow entries is more correctly described by the area A and C. This area is bounded by three lines; y = x (solid diagonal line), y = the minimum usable dimension (broken straight line), and the constant area function for a set of ellipses, y = constant/x (broken curve). All lines shown including the solid vertical line are for phascogale tapoatafa. Lines for other species are given in Table 1.

The internal hollow dimensions of width and depth were also graphed as pairs of minimum and maximum dimensions (typically internal width is less than depth). The resulting scatter was examined to define the bounds of the dimensions of used hollows. The ranges of hollow sizes used by mammals were described differently than those of bird hollows. There are two reasons for this: (1) mammals curl their bodies up to fit into a variety of shapes because they do not have relatively rigid wings and tail feathers; (2) the mammal hollows were used for both nesting and diurnal shelter, while all the bird hollows were used for breeding. Consequently, I assumed a mammal species would use a wider range of hollow shapes and orientations than a bird species. The data for birds were interpreted as descriptions of approximately cylindrical hollows that are deeper than they are wide, while the data for mammals were interpreted as coming from a range of hollow shapes (ranging from cylinders, to ellipsoids and spheres). Consequently, for mammals other than mardos (nest box data), the minimum dimensions of small spherical hollows were limited by a negatively sloped line that excluded the smallest combinations of depth and width dimensions. This reduces the number of hollows classified as potentially suited to these species by eliminating hollows that are smaller than those observed in use.

The data used to develop these descriptions were collected from a variety of forest types and sites, and a portion from tree species other than jarrah and for bird subspecies other than those that inhabit the jarrah forest. In using these data I assumed that: the dimensions of hollows used by bird or mammal species primarily reflect the hollow preferences of those species; the physical size and hollow related behaviour of the subspecies were equivalent for these purposes; these dimensions can be applied to other tree species in other areas; and the predators and competitors on sites where these data were collected had a secondary or minor effect on the range of these dimensions. I also assumed that the range of hollow sizes used by each species was fully expressed in the data. Where this is not the case, the use of the available data was a conservative interpretation, and the application of these descriptions of hollow size will not lead to over-estimation of the number of potentially usable hollows. There may be physical, social, and environmental factors that determine whether a hollow that has suitable dimensions is used by a bird or mammal, but hollow and entry size are primary attributes that determine the suitability of a hollow. For these reasons I refer to the hollows I identify by applying these dimensional descriptions as 'potentially suited to' a species, or 'potentially usable'. Hollows described in this way are the same size and height above the ground as hollows observed in use by a species, i.e. the height of the entry, and the entry dimensions and internal dimensions fall within the range of dimensions of hollows observed in use.

Distribution of Hollow Entry Shapes Found in 239 Trees

The bounded area shown in Figure 2 implies the occurrence and suitability of extremely elongated hollow entries occupying the right hand side of area C, even though for most species such entries were not observed in use. I wanted to determine whether the hollows that I classified as potentially usable included a disproportionately high number of hollows with extremely elongated hollow entries (when compared with the distribution of hollow entries observed in use). I identified which of the 665 hollows found in 239 trees had entry dimensions, internal dimensions, and height to entry, consistent with the hollows used by each species, and compared the distribution of entry shapes for these potentially usable hollows with the distribution of entry shapes for hollows observed in use.

RESULTS

Used Hollows

Clear evidence of hollow use was found in 82 hollows from 50 trees. These consisted of 17 hollows used by western ringtail possums, 24 by common brushtail possums, 19 by brush-tailed phascogales, 12 by rufous treecreepers, and 10 by striated pardalotes. Twenty-three of these used hollows (2 western ringtail possum, 8 common brushtail possum, 3 brush-tailed phascogale, 3 rufous treecreeper, and 7 striated pardalote hollows) were found in 18 trees that came from the sample of 239 trees.

Entry Dimensions of Hollows Used by Fauna

The range of entry sizes used by each of the six bird and four mammal species is shown in Figure 3 and the equations of the lines bounding the range of hollow entry sizes used by each species, and the minimum height above the ground of hollow entries, are given in Table 1 (appropriate internal dimensions would also be required for the hollow to be potentially usable). For brush-tailed phascogale, mardo, western rosella, and rufous treecreeper, the bounding lines in Figure 3 followed directly from the data, i.e. these lines were positioned to pass through the smallest hollow entry, and the largest entry (or entries). For other species, interpretation of the data was required to resolve inconsistencies. In all cases, except for the upper limit applied to common brushtail possums, and the lower

TABLE 1

Dimensional limits to hollow entry size and entry height. The lines describing the area on the graph of maximum hollow entry dimension (x) versus minimum entry dimension (y) that were used to describe the range of hollow entry sizes suited to each of six bird and four mammal species. The third side of the triangular area is described by the line y = x. Hollow entry heights are the minimum height above ground of entries to used hollows. Sample sizes are given in Figure 3.

SPECIES	LOWER LIMIT (mm)	UPPER LIMIT (mm)	MINIMUM ENTRY HEIGHT (m)
Common brushtail possum	y = 60	y = 72000/x	0.5[a]
Western ringtail possum	y = 55	y = 72000/x	0.5[a]
Brush-tailed phascogale	y = 24	y = 28000/x	0.0[b]
Mardo	y = 20	y = 30000/x	0.0[c]
Red-tailed black cockatoo	y = 100	y = 168833/x	4.4[d]
Australian ringneck	y = 50	y = 33000/x	3.19[e]
Western rosella	y = 48	y = 11025/x	6.22[e]
Red-capped parrot	y = 50	y = 20090/x	4.75[e]
Rufous treecreeper	y = 40	y = 12100/x	2.4
Striated pardalote	y = 24	y = 8000/x	2.2[f]

[a] Inions *et al.* (1989); [b] Soderquist (1993); [c] C. Dickman unpublished data; [d] Saunders *et al.* (1982); [e] Long (1990); [f] Woinarski and Bulman (1985).

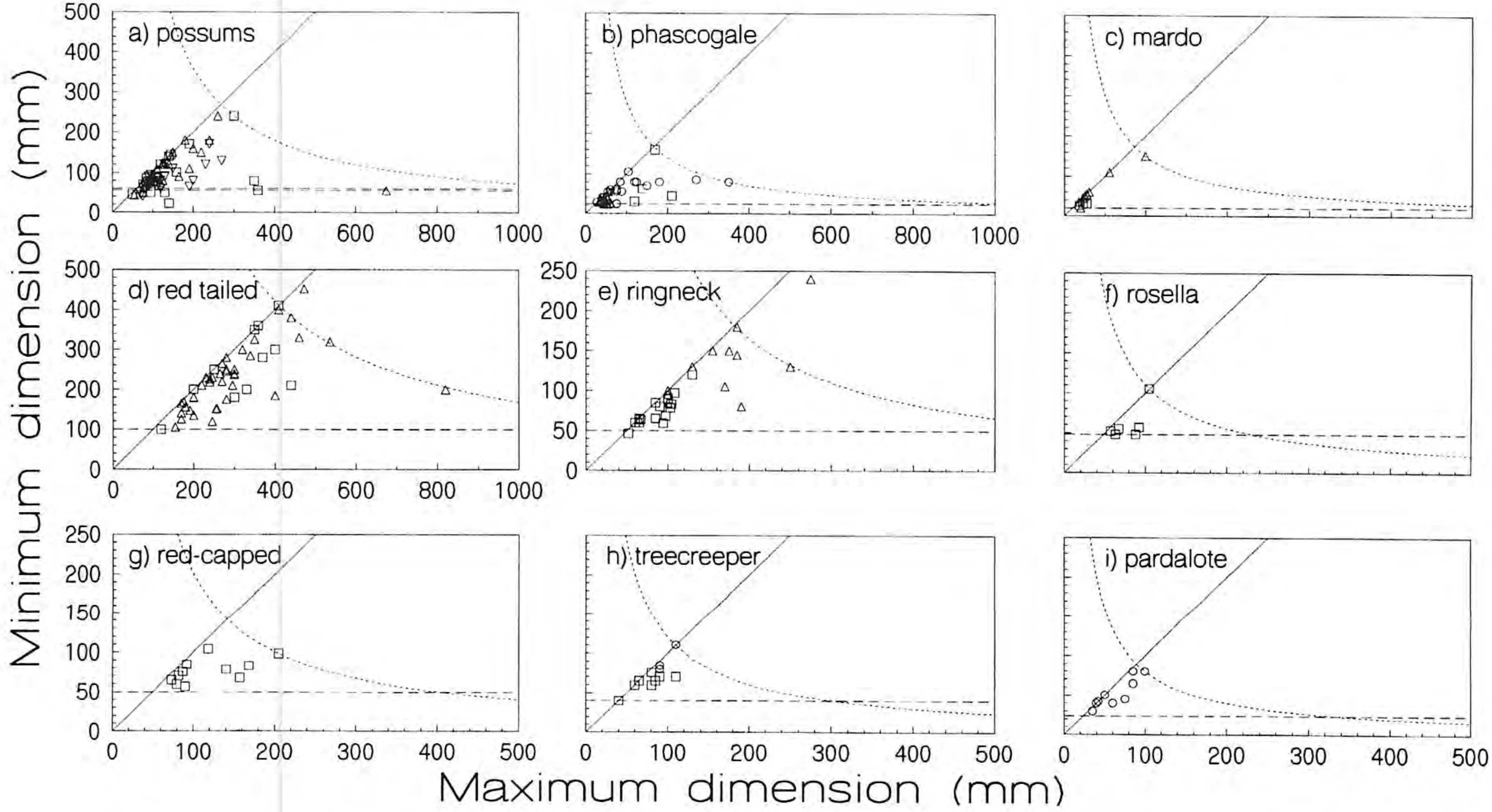

Figure 3. Entry dimensions of hollows used by: (a) common brushtail possums (n = 29), Δ and ∇ (Rhind 1998); western ringtail possums (n = 19), □ and ◊ (Rhind 1998); (b) brush-tailed phascogale (n = 23), O and □ (Rhind 1998), and Δ (Soderquist, unpublished data); (c) mardo (n = 7), Δ (Wardell-Johnson 1986), and □ (Dickman, unpublished data); (d) red-tailed black cockatoo (n = 49), Δ (Saunders et al. *1982), and □ (Johnstone, unpublished data); (e) Australian ringneck (n = 30), □ (Long 1990), and Δ (Saunders* et al. *1982); (f) western rosella (n = 6) (Long 1990); (g) red-capped parrot (n = 11), (Long 1990); (h) rufous treecreeper (n = 12), O and □ (Craig, unpublished data); and (i) striated pardalote (n = 11). The dashed horizontal line is the minimum usable entry dimension. The curved line defines the maximum entry size and is a constant area function for elliptical entries (see Table 1).*

limit applied to pardalotes and red-capped parrots, the interpretation of the data was conservative, i.e. it would result in fewer hollow entries being classified as potentially usable. The reasons for the locations of these bounding lines are given below.

All entries to possum hollows which were smaller than 55 mm were secondary entries into hollows that had other larger primary entries. One unusually long and thin primary entry of 55 mm x 675 mm was set aside, and following Inions *et al.* (1989) and Menkhorst (1984), the larger and more conservative dimension of 60 mm was taken as the lower limit for hollow entry use by common brushtail possums (Fig. 3a). A common upper limit was chosen for both possum species (Fig. 3a). This was selected because western ringtail possums are smaller than common brushtail possums, yet the largest hollow entry used by a possum came from a hollow used by a western ringtail possum.

Five of the largest red-tailed black cockatoo entries, which had nearly equivalent area, were used to set the maximum entry dimensions in preference to a single larger entry that was assumed to be atypical. This was a conservative interpretation of the data which would reduce the number of hollow entries classified as potentially suited to red-tailed black cockatoos.

Two Australian ringneck entries were set aside (Fig. 3e). One small entry of Long (1990) was ignored as it was noticeably smaller than all other entries, smaller than the entries used by western rosellas (a smaller species), and smaller than the minimum of the range reported by Long (1990). Following Long (1990), the lower limit for potentially usable hollow entries was set at 50 mm. The largest hollow entry recorded for Australian ringnecks was much larger than other entries used by this species and very much larger than entries used by other parrot species. The next two largest entries, which had nearly equivalent area, were chosen as more conservative indicators of the upper limit for Australian ringneck hollow entry size (Fig. 3e).

In the case of red-capped parrots, the minimum entry size was set at 50 mm, slightly smaller than the smallest entry observed in use (90 mm x 57 mm). As red-capped parrots are smaller than Australian ringnecks, and Australian ringnecks use hollows with entries as small as 50 mm, this was seen as a consistent interpretation of the available data. The minimum entry dimension used by rufous treecreepers was 40 mm (Fig. 3h). Though only one entry of this size was observed, this value was used as it is consistent with the relatively small size of this bird. For striated pardalotes, Haseler and Taylor's (1993) minimum entry dimension of 24 mm was used as the lower limit for entry dimensions (Fig. 3i) because these authors examined a much larger data set.

Internal Dimensions of Hollows Used by Fauna

The internal depth and width dimensions of used hollows and the lines bounding the range of hollow sizes used by eight species are shown in Figure 4. Individual data were not available for red-tailed black cockatoos, and in Table 2 the summary values of Saunders *et al.* (1982) were used to define the range of internal dimensions of these hollows. Very few data on the internal dimensions of hollows used by mardos were available and these are not graphed. Equations for the lines that define the range of hollow sizes used by all species are given in Table 2. For all bird species, the maximum and minimum restrictions placed on the internal hollow depths and widths were based on the largest and smallest dimensions observed in use. For the mammals, common brushtail possum, western ringtail

TABLE 2

Dimensional limits to hollow depth and width. The lines describe the area on the graph of hollow depth (x) versus hollow width (y), that were used to describe the range of internal dimensions of hollows suited to each of six bird and four mammal species. In cases indicated by an asterisk, a fifth side is described by the line, y = x (see Fig. 4). All values correspond to dimensions in millimetres. Sample sizes are given in Figure 4.

SPECIES	MINIMUM INTERNAL WIDTH	MAXIMUM INTERNAL WIDTH	MINIMUM HOLLOW DEPTH	MAXIMUM HOLLOW DEPTH
Common brushtail possum*	y = 120	y = 480	y = -0.4 x + 300	x = 11200
Western ringtail possum*	y = 80	y = 480	y = -0.1 x + 150	x = 5340
Brush-tailed phascogale*	y = 80	y = 330	y = -0.08 x + 110	x = 3860
Mardo	y = 100	y = 200	x = 190	x = 540
Red-tailed black cockatoo	y = 190	y = 540	x = 450	x = 7250
Australian ringneck	y = 95	y = 320	x = 360	x = 4005
Western rosella	y = 95	y = 275	x = 356	x = 1510
Red-capped parrot	y = 95	y = 232	x = 190	x = 976
Rufous treecreeper	y = 60	y = 160	x = 240	x = 600
Striated pardalote	y = 60	y = 150	x = 170	x = 950

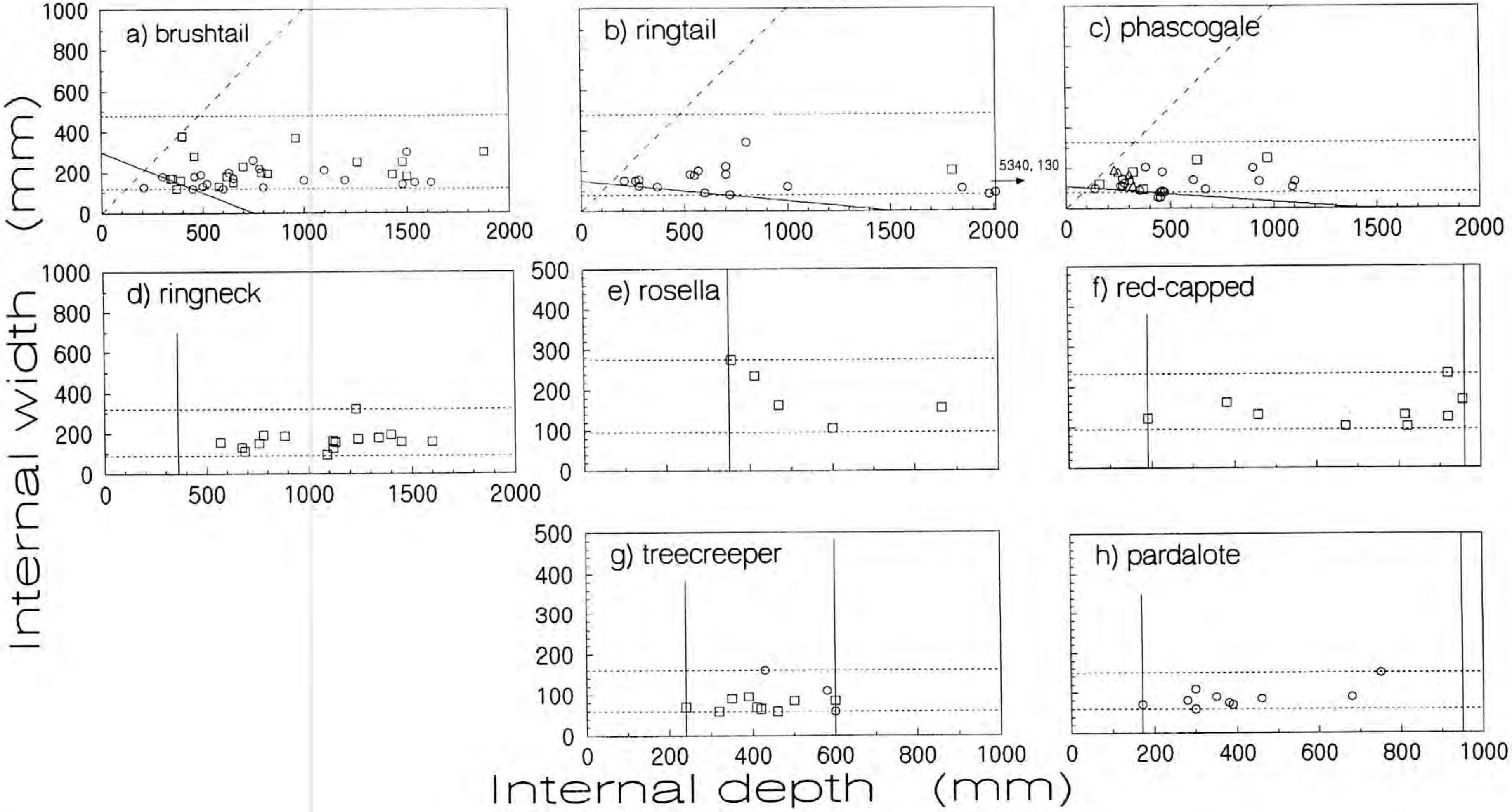

Figure 4. Internal dimensions of hollows used by; (a) common brushtail possums (n = 29), O and □ (Rhind 1998); (b) western ringtail possums (n = 19), O and □ (Rhind 1998); (c) brush-tailed phascogale (n = 26), O and □ (Rhind 1998), and Δ (Soderquist, unpublished data); (d) Australian ringneck (n = 16), □ (Long 1990); (e) western rosella (n = 5), (Long 1990); (f) red-capped parrot (n = 10), (Long 1990); (g) rufous treecreeper (n = 12), O and □ (Craig, unpublished data); and (h) striated pardalote (n = 10). The lower horizontal line is the minimum usable width and the upper horizontal line the maximum usable width (see Table 2). The maximum hollow depths are not shown for common brushtail possum, western ringtail possum, phascogale tapoatafa, Australian ring-necked parrot, and western rosella. The minimum and maximum hollow depths and other limits to minimum combinations of hollow dimensions are given in Table 2.

possum, and brush-tailed phascogale, additional restrictions were applied to exclude hollows with both small depth and small width dimensions from being classified as potentially usable. These restrictions reduce the number of hollows that would be classified as potentially suited to these species.

The upper limit for internal hollow width shown for common brushtail possums and for western ringtail possums is the 480 mm nominated by Inions *et al.* (1989) (Figs 4a, 4b, Table 2). The negatively sloped line of Figure 4a excludes two small hollows that were too small to be used to define potentially usable hollows. Small hollows like these are relatively common, but are rarely used by common brushtail possums and the exclusion of these points is conservative as it reduces the number of small hollows that can be classified as potentially usable.

One phascogale hollow with a very small width was not considered in setting the limits for internal dimensions. This hollow was unusually narrow (55 mm), and I considered this hollow to be too small to use in classifying other hollows as potentially usable.

Two of the three internal widths (60, 90, and 125 mm) of natural hollows used by mardos (Dickman[7]) were smaller than the 100 mm of Wardell-Johnson's (1986) nest box 8. Nest box 8 was least preferred, but still used by breeding females. The minimum internal hollow width for mardos was set at 100 mm.

As the western rosella is smaller than the Australian ringneck, the minimum dimension used by Australian ringnecks (95 mm) was set as the lower limit for hollows used by western rosellas (Fig. 4e, Table 2).

The smallest hollow widths used by red-capped parrots were 102 mm (Fig. 4f). As there were limited data and the red-capped parrot is smaller than the Australian ringneck, the minimum width used by Australian ringnecks (95 mm) (Long 1990) was set as the lower limit for hollows used by red-capped parrots.

The minimum depth of hollows used by striated pardalotes (170 mm)(Fig. 4g, and Table 2) was consistent with Haseler and Taylor's (1993) observation of a minimum distance to the nest of 90 mm, and the dimension of a nest chamber in a tree 'excavated to the dimensions required' of 70 x 80 mm.

The Range of Entry Shapes of Potentially Usable Hollows

I examined the dimensions of 665 hollows found in 239 trees and found 204 hollows had entry heights, entry dimensions, and internal hollow dimensions that fitted the descriptions given in Tables 1 and 2. Figure 5 shows the dispersion of hollow entry shapes from these hollows that were classified as potentially suited to each of 10 fauna species.

DISCUSSION

Why a Constant Area Function is Appropriate

A major failing of summaries of hollow dimensions is that they separate related pairs of dimensions. The summary data of Saunders *et al.* (1982) can be used to demonstrate this problem (which can also be observed in the red-tailed black cockatoo, phascogale, possum, and red-capped parrot data presented in Fig. 3). Saunders *et al.* (1982) properly reported a maximum horizontal dimension for hollow entries used by red-tailed black cockatoo of 820 mm, and a maximum vertical dimension of 535 mm. Though correct, these summary data do not describe the dimensions of the largest hollow entry that Saunders *et al.* (1982) observed in use. Red-tailed black cockatoos were **not** observed using hollow entries as large as 820 x 820 mm, 820 x 535 mm, or even 535 x 535 mm. Similar incorrect interpretations would be made if the data presented here for possums, phascogale, red-tailed black cockatoos, and red-capped parrots, were summarized. Summaries that separate the two entry dimensions can be misleading when used to identify the largest hollow entries that are suited to a species because they incorrectly indicate that hollow entries in area B of Figure 2 are potentially suited to the species. The use of a maximum area limit constrains the two related hollow dimensions in a realistic manner.

A related, but opposite, effect occurs when summary entry dimensions from the most common, slightly elliptical entries, are used to define potentially usable entries. This eliminates from consideration entries which may well be suitable but are more elongated than the typical slightly elliptical entry. These are the entries described by area C of Figure 2. Where data are more numerous (e.g. Figs 3a, b, and d), the range of entry shapes tends to increase from the most common circular and elliptical entry shapes to those that are quite elongated. A small sample of used entries (such as Figs 3f, h, and i) will tend to include the most commonly occurring entry shape, i.e. round to slightly elliptical. Strict interpretation of dimensional limits from summaries based on such small sets of dimensions will inappropriately exclude from consideration elongated entries of equivalent area that, from the data in Figures 3 a, b, d, e and g, are acceptable to several species of birds and mammals.

Hollows used by fauna are difficult and expensive to measure and consequently the amount of data is often small. The constant area limit enables the interpretation and description of the dimensions of a variety of hollow entry shapes, and enables these interpretations to be made from limited data (including the extremes of one large and one small hollow entry). A wide range of potential entry shapes can be described from a limited data set. Examples of this are shown in Figures 3f, g, h, and i, where a range of hollow entry shapes are defined using data from only 6 to 12 used hollow entries.

As well as these practical reasons for applying this constant area function, the use of this limit was supported by the spread of the data. The scatter of data in Figures 3a,

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[7] Unpublished data, Dr C. Dickman, School of Biological Sciences, University of Sydney, NSW.

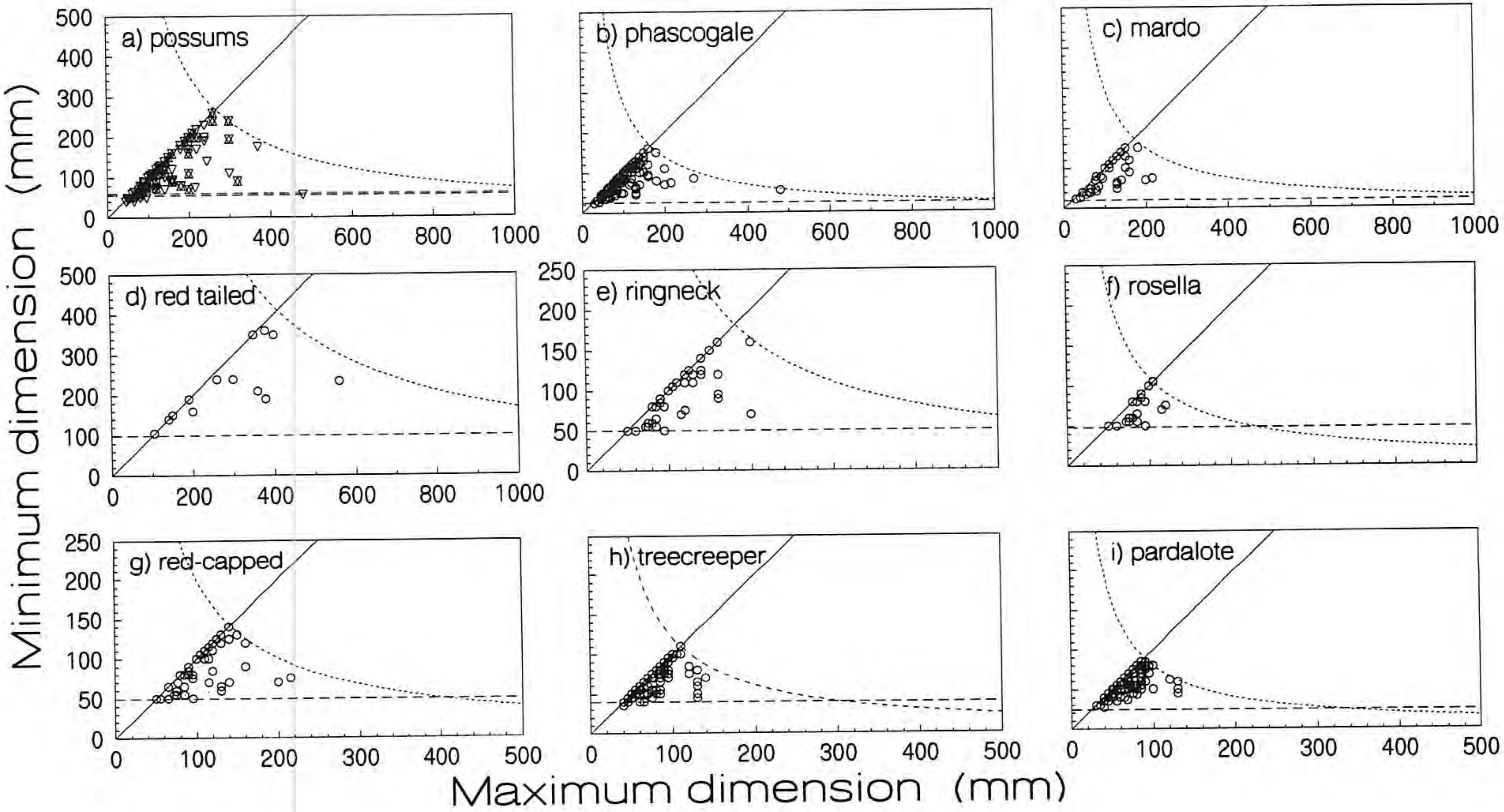

Figure 5. The disposition of 204 hollow entries from hollows classified as potentially suited to 10 fauna species. Graphs are for: (a) common brushtail, Δ (n = 35) and western ringtail ∇ possums (n = 84); (b) brush-tailed phascogale (n = 106); (c) mardo (n = 34); (d) red-tailed black cockatoo (n = 13); (e) Australian ringneck (n = 37); (f) western rosella (n = 19); (g) red-capped parrot (n = 46); (h) rufous treecreeper (n = 73); and (i) striated pardalote (n = 91). The dashed horizontal line is the specified minimum usable dimension and the curved line is the maximum entry size specified (see Table 1).

b, d, e and g shows a range of entry shapes that are contained within the dimensional descriptions given in Table 1. In the case of Figure 3b the two largest entries, though very different in shape, fall along the constant area curve that is defined by a single pair of entry dimensions. In Figure 3d, five entries fall along this curve. Figures 3a and 3g show a range of entry shapes contained within this limiting description. The constant area function is a simple expression that satisfactorily caters for and describes the range of entry dimensions and shapes observed.

The use of this constant area function as an upper limit is a variation of the boundary line analysis expounded by Webb (1972). Here, this analysis technique has been used on small data sets where the absolute limit of the response (the boundary) has not necessarily been reached. The true boundary may lie beyond the position indicated by these relatively small data sets. However, with the upper limit on entry size, the bounding function has a fixed shape, there is a rational basis for selecting the function shape (i.e. entries are elliptical), and the function can be defined by a single datum point. In cases where the upper extent of hollow entry size has not been demonstrated in the available data, the use of a lower limit is a conservative interpretation based on available data, and the application of this specification will not lead to over-estimation of the number of potentially usable hollows.

Minimum Hollow Entry Size

I assume a constant minimum hollow entry dimension for each species. Predator avoidance is often cited to explain the tendency of animals to seek small entry sizes (e.g. Tidemann and Flavel 1987; Traill 1995). Competition for hollows has also been suggested as a factor determining the entry size of occupied hollows (Van Balen *et al.* 1982; Newton 1994). Whatever the mechanism, the tendency for hollow entry size to follow body size is both logical and commonly observed (e.g. Saunders *et al.* 1982; Tidemann and Flavel 1987; Traill 1995). Clearly, a minimum hollow size will be determined by the smallest opening which the occupying species can pass through. This should be a relatively consistent minimum for a species because it will be determined by adult body size.

Additional Restrictions on the Internal Dimensions of Mammal Hollows.

The data of Figures 4a, b, and c show that mammals use some small hollows that are as wide as they are deep (ranging from cylinders, to ellipsoids and spheres), while birds use approximately cylindrical hollows that are much deeper than they are wide (Figs 4d, e, f, g, h). The dimensions collected from deep cylindrical hollows used by birds require only maximum and minimum bounds to define the range of potentially usable hollows. The data collected from small spherical and ellipsoidal hollows used by some mammals require an additional restriction to exclude hollows with both small depth and small width dimensions from being classified as potentially usable. These negatively sloped lines in Figures 4a, b, and c, were a conservative interpretation that reduce the number of hollows classified as potentially suited to the species by excluding hollows that were small in both dimensions.

This problem is similar to that caused by the separation of pairs of dimensions measured on a single hollow. Just as summaries of separated hollow entry dimensions drawn from two hollows can be misleading, unrelated internal dimensions drawn from two hollows can incorrectly imply that hollows with both small widths and small depths are potentially suited to a species. Pairs of hollow dimensions collected from individual hollows should be analysed and summarized as pairs.

Limited Data Sets and Excluded Data

Hollow dimensions are difficult, dangerous, and expensive to collect; consequently data sets are often small. One major strength of the method described in this paper is the capacity to sensibly interpret these relatively small data sets. The risk is in producing misleading interpretations that over- or underestimate the number of potentially usable hollows. However, a more usual interpretation of these data, based on means and ranges, carries a similar or greater probability of being misleading. If descriptions of potentially usable hollows are based on mean hollow dimensions, the number of potentially usable hollows will always be underestimated, as both large and small entries (and hollows) will be excluded. If summarized maximum and minimum dimensions are used, both under- and overestimates can occur. With some species the observation of a used entry that is large and elongated will lead to the inclusion of much larger and rounder entries, and an overestimation of available hollows (the inclusion of area B of Fig. 2). With other species, limited observations that only include entries that are close to round, will lead to the exclusion of slightly elongated entries and an underestimation of potentially usable hollows (the exclusion of area C of Fig. 2). By consistently applying this method of interpreting the data, an orderly and rational progression of hollow entry descriptions is produced. These are consistent with the progression of body sizes for these species, and the hollows identified as 'potentially usable' have the same range of dimensions as those observed in use. Consequently, the number of these hollows should be correctly estimated. Ultimately the correctness of these descriptions of hollow size can only be assessed against larger data sets.

In interpreting this data, atypically large or small hollow dimensions were ignored in the analysis. The excluded values were: one large red-tailed black cockatoo entry, one large and one small Australian ring-necked parrot entry, two small internal hollow dimensions for common brushtail possums, and two small internal hollow dimensions for *Phascogale tapoatafa*. Individuals of a species may at times use hollows that are outside the range of sizes typically used by these species and these values are inappropriate as the basis for this type of analysis, and the proposed subsequent modelling exercise. The exclusion of these data produce a conservative result as it reduces the number of hollows that are classified as potentially usable.

Distribution of Entry Shapes for Classified Hollows

The 204 hollows classified as potentially suited to fauna were examined to determine whether extremely elongated hollow entries occurred, and whether they were ever classified as potentially suited to any species. Comparison of the distribution of points on Figure 3 and Figure 5 shows that the range of entry dimensions classified as potentially suited to fauna is consistent with those observed in actual use by fauna. A disproportionate number of extremely elongated hollow entries do not occur on hollows that also have suitable internal dimensions and suitable entry height. For this reason a bound on the right hand side of Figure 3 was not seen as necessary.

Ringnecks

Figure 3e clearly shows that the Australian ringnecks of Saunders *et al.* (1982), in *Eucalyptus salmonophloia,* used larger hollow entries than those of Long (1990) in *E. wandoo* and *E. longicornis*. It is unlikely that these differences are owing to the effects of competition for hollows. Long (1990) stated that competition between birds that used similar sized hollows was not affecting his data set, as few other species nested in his study area. Australian ringnecks were the smallest hollow users on the site studied by Saunders *et al.* (1982): a site also used by galahs, corellas, and red-tailed black cockatoos. It seems most unlikely that competition with these larger birds forced Australian ringnecks to use larger hollows. Predators on Long's site may have forced Australian ringnecks to use only small entries, however, this does not explain why the Australian ringnecks on Saunders' site used only large entries. I interpret this difference as indicating differences in the sizes of hollows occurring on the two sites. This difference is owing to a difference in the available hollows in the different tree species at the two sites, and/or a difference in tree sizes between the two sites.

CONCLUSION

In the many areas of the jarrah forest that density of medium sized mammal species is low, fox predation is assumed to be a major cause (Christensen 1980a, b). While factors in addition to predation are proposed as causes of decline in bird and mammal densities (Calver and Dell 1998), fox control is expected to increase the abundance of mammals in these forests (Morris *et al.* 1995). With low animal abundance, hollow use is not a meaningful indicator of hollow abundance. These descriptions of used hollows provide a means of identifying other hollows that are potentially usable. The attributes of trees with and without hollows can be assessed, and regression techniques used to identify which attributes are associated with hollow bearing trees, and then to predict the availability of potentially usable hollows (the validation of predictive models is essential in the latter step). The number of potentially usable hollows that are actually used may depend on: species abundance, population densities, predator population density, stand vegetation structure and composition, spatial dispersion of the hollows, and other environmental and behavioural factors; however, hollow size is fundamental and will be the primary determinant of hollow suitability, and a sound basis for estimating general hollow availability across the forest. In using these descriptions, it is also important to consider that the descriptions of mammal hollows given here differ from those for bird hollows, as not all mammal hollows were used for breeding.

Ideally hollows, which are three-dimensional objects, could be described and analysed as three-dimensional objects. For such analyses to be useful they would require a greater amount of data and more detailed measurements than were available for this work. The two-dimensional descriptions of internal hollow dimensions presented here are the best available approximation of the three-dimensional reality and an improvement on dimensional summaries. For most hollow entries, two-dimensional descriptions will contain as much information as three-dimensional descriptions, and these two-dimensional descriptions of hollow entry shape are substantially more descriptive than data summaries. This paper brings together available information on the dimensions of hollows used by these species, combines this with new data, and presents a sensible system for interpreting this information in a rational and consistent manner. The interpretations provide an improvement on existing published summaries and this simple system is useful for examining hollow shapes and sizes. Graphical presentations of hollow entry dimensions and the internal dimensions of used hollows should be presented in preference, or as a supplement, to summaries, and paired measurements from individual hollows should not be analysed separately. Researchers are encouraged to examine the area of hollow entries as one of the descriptors of the range of hollow dimensions.

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