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Research Article

Tree cavity-using wildlife and the potential of artificial nest boxes for wildlife management in New Guinea

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Abstract

Little is known of the frequency of use and reliance upon tree cavities by wildlife, nor the natural availability of cavities in New Guinea forests. We surveyed the literature for records of cavity use by birds and mammals in New Guinea. We examined every standing tree on one hectare of primary forest and one hectare of secondary forest for cavities, then carefully assessed every tree for cavities after they were felled. We put up 190 artificial nest boxes of five designs in three sites and monitored occupancy. At least 50 species (23.6%) of New Guinea terrestrial mammals and 118 species (17.7%) of non-marine or aquatic bird species are recorded in the literature as using tree cavities. Ground observation identified 36 suspected cavities in a hectare of lowland primary forest and 10 in nearby secondary forest. Upon inspection of all trees after felling, these figures changed to 26 and 0 respectively. Ground censuses are not accurate. Cavities were more commonly found in large trees. In less than a year, nest box occupancy reached exceeded 33%, with *Phalanger* spp. and Sugar gliders, *Petaurus breviceps,* being most common. Some bird use was detected by the presence of feathers; snakes and geckos were also found in boxes. Occupancy increased with time and would probably be higher after a second year. The larger boxes had greater occupancy, as did boxes placed higher in the trees. Bees occupied and probably excluded other users from 10% of boxes. As Papuan forests are disturbed by logging, hunting practices and gardening, conservationists might need to manage practices to ensure cavity availability. Artificial nest boxes might have utility for wildlife conservation and research.

Keywords*:* Nest boxes, New Guinea, tree cavity, wildlife management

Received: 24 February 2013; Accepted 2 September 2013; Published: 16 December 2013

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Cite this paper as: Warakai, D., Okena, D. S., Igag, P., Opiang, M. and Mack, A. L. 2013. Tree cavity-using wildlife and the potential of artificial nest boxes for wildlife management in New Guinea. *Tropical Conservation Science* Vol.6 (6):711-733. Available online: www.tropicalconservationscience.org

Introduction

Cavities, or hollows, in trees are important because they provide protection from many kinds of predators [1] or provide essential and specialized microclimates [2-4]. Although not in all cases, the availability of nest cavities can be a limiting factor for populations of cavity-using species [5-7].

Wildlife that use cavities can be divided into obligate cavity users and opportunistic or facultative users. The loss of cavities in an area will most heavily impact obligate users and variably affect facultative users. Thus the availability of cavities can impact a wide range of species, depending upon each species' reliance on cavities [7]. Tree cavities are a single resource of high importance to a wide range of taxa, including invertebrates, reptiles, birds and mammals [5].

Cavity users can also be divided into two groups-- excavators or cavity producers and cavity consumers [8]. Excavators actively make cavities. These taxa are potentially important because the cavities they create are often later utilized by many non-excavating taxa [9-11]. They increase the availability of cavities over what is available due to natural processes (mainly relating to tree damage, tree age, and the decomposition and erosion of heartwood). The populations of excavators in a forest can affect a wide range of species [9,10,12,13].

Tree cavities fit the criteria for a keystone resource [14]. They are somewhat rare, they might limit populations of some species [5,15,16], and they possibly impact a wide diversity of taxa. Assessing the availability of cavities is difficult [17], as is knowing whether observed cavities are suitable for occupation [5]. Cavities are often hard to detect from the ground [18] and often can only be detected by following cavity-using animals to concealed cavities [19] or by inspecting downed trees [17]. Relatively few reliable data exist on the availability of cavities in tropical forests [20], and it is believed that logging often significantly reduces availability of cavities [5,16,21,22]. There are fewer cavities in secondary tropical forests than in unlogged primary forest [16,20].

Because cavities are a keystone resource and their availability is often reduced by human activities, nest boxes have been employed as a management tool to aid cavity-dependent wildlife [1,23-26].

New Guinea is home to the third largest block of rainforest in the world [27]. The biota of New Guinea is highly endemic. Over 70% of its forest birds and mammals are not found outside New Guinea and its associated offshore islands [28]. Although the mammal and bird faunas are related to those of Australia, where cavity-use is relatively more studied (e.g., [29-31]), New Guinea environments are quite different, being generally much wetter, more diverse, and more tropical--considered distinct from Australian ecoregions [32].

New Guinea and Australia lack woodpeckers (Picidae), the main family of cavity excavators found in almost all other forests worldwide. Woodpeckers are crucial components of many forests and substantially increase the availability of tree cavities [20,33,34]. The absence of woodpeckers in New Guinea suggests tree cavities might be less available and more limiting than some other forests, and that cavity-using species are more reliant on processes of decay that create cavities [10]. Furthermore, New Guinea is experiencing a rapid expansion of industrial logging and other forms of forest conversion [35] that could dramatically reduce the availability of tree cavities. Traditional and widely employed methods of wildlife harvesting in New Guinea also reduce cavity availability, because hunters often cut down trees with cavities in order to extract wildlife from them [36]. This practice eliminates a cavity that might otherwise have sheltered wildlife for years. Circumstantial evidence therefore suggests that tree cavities might be vitally important in New Guinea and under threat, but few quantitative data are available.

We undertook this study to explore the importance of tree cavities to wildlife in New Guinea and the potential use of artificial nest boxes as a management tool. We are unaware of any published surveys of cavity availability on mainland New Guinea, and only one study on New Britain [16], nor of any systematic assessment of cavity use by New Guinea fauna. Moreover, we are unaware of any published study on the placement and occupancy of artificial nest boxes in New Guinea. With this preliminary investigation we:

1) surveyed the literature and compiled information on cavity use by birds and mammals;
2) censused cavity availability, using two techniques, in lowland primary and secondary forest;
3) experimented with placement of artificial nest boxes in three different elevations and monitored occupancy after 8 months.

Methods

Cavity-using wildlife of New Guinea

We surveyed recent compendiums of mammal biology [[37-39], and bird nesting sites [40,41] supplemented with primary literature [42,43] to determine a provisional list of wildlife that use tree cavities. Where nesting information for a bird species was unavailable, but there were reports of cavity use for congeners, we categorized these species as "presumed" cavity users.

Tree plot cavity census

Natural occurrence of tree cavities was censused at Wanang, 100-200 m a.s.l. (05°15’S, 145°16.115’E), Madang Province, in a study site established by the New Guinea Binatang Research Centre (NGBRC – Madang) (Fig. 1a). The area is a mosaic of mixed evergreen lowland primary and secondary forests with 3.5 m mean annual rainfall [44,45]. The NGBRC established two one-ha research forest plots, one in primary forest and one in secondary forest, and all trees >5 cm DBH were identified, tagged and mapped. The NGBRC study involved the felling of all trees and lianas in the two plots [46].

D. Warakai carried out cavity census of all trees >5 cm DBH on these two forest plots, from 18 February 2006 to 3 March 2006, before the trees were felled. NGBRC subsequently closely examined all felled trees and recorded any cavities found. This provided a unique and reliable means of testing the reliability of the observer's census and a reliable count of the actual number of cavities.

The search for tree cavities by ground observation in the current study is comparable to those done in other studies [20,47,48]. Every tagged tree was first tapped to assess if the bole sounded hollow. The tree was then carefully inspected from all sides, with the aid of binoculars, for holes in the bole, primary branches, and secondary branches. Features that might indicate cavities were recorded, such as snapped branches and parts that were dead, dying, or partly rotten.

To determine the precision of the cavity census carried out on standing trees, the NGBRC examined all the trees on the plots after they felled them. This involved walking the entire length of the trees looking for any holes (including openings at the tops of snags) with diameter >5cm that connected to a cavity judged large enough to be occupied by any of the known cavity-using taxa, and looking for any nests in these holes or hollows. Trees were sectioned and removed, enabling the team to examine all parts of the tree, including that which initially was against the ground.

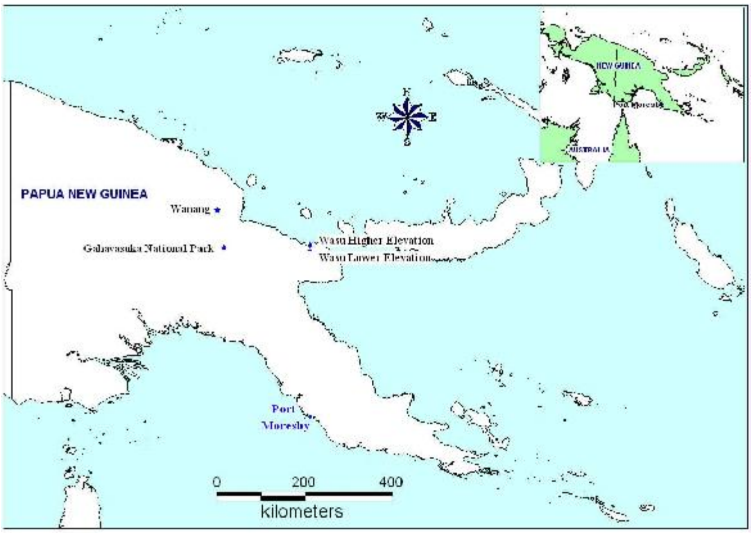

Fig. 1a Location of study areas in Papua New Guinea on the eastern half of the island of New Guinea. Fig. 1b. Detail of the Wasu study area showing the boundaries of the four nest box plots.

Wasu nest box experiment

The main component of the nest box study was done near Wasu Station on the north shore of the Huon Peninsula, Morobe Province (Figure 1a) (05°57’44.7”S, 147°11’35.3”E, sea level). Boxes were placed 3-25 August 2006 at two sites, one at lower elevation and the second 4.6 km away at higher elevation, in areas along a road that links Wasu to Kabwum District (Fig. 1b). The lower elevation site at Movorong (06°00’12.7”S, 147°12’05.9”E) was less than 200 m a.s.l. The higher elevation site, Hongo (06°02’33.6”S, 147°11’18.5”E) was 800-1,200 m a.s.l. At both sites primary and secondary forests were identified. Four 700 X 500m plots were established, differentiated by elevation (low/high) and forest type (primary/secondary) (Fig. 1b). In each plot a nest box was placed on a grid every 100m.

Eight months after placement at Wasu, the nest boxes were checked (13 April - 5 May 2007) for evidence of use. Any new material (e.g., fur, scats, feathers) in the boxes was collected and other evidence photographed (tooth or claw marks) to help identify taxa using the box. When checking nest boxes, climbers were careful to minimize disturbance of occupants and we often secured photographs of resting mammals.

Nest box design

On the four Wasu plots 160 boxes (40/plot) were placed: 32 boxes each of five different types. The tallest nest box was King Parrot (KP); Cuscus (CC) was the widest; Ringtail (RT) was of middle size; then there was the smaller Rosella (RS); and Sugar Glider (SG) was smallest and shortest. Nest boxes were made according to designs of boxes used in Australia [49] (Table 1). We extended the lids with a longer overhang due to PNG’s wet climate. Shade cloth was secured to RS and SG nest box interiors, to accommodate micro-bats. Nest boxes were made from waterproof plywood, with front panels (where entrance holes are) made of untreated timber. Boxes were not painted or further treated; joints were not glued. Wood was "aged" in open air at least eight months before construction and placement.

Table 1. Nest box dimensions. Boxes followed specifications[49]., with minor modifications
Abbreviations for box styles: KP= King Parrot, CC= Cuscus, RT= Ringtail, RS= Rosella, SG= Sugar Glider.

Nest box type	Back Panel (mm) L x w	Front Panel (mm) L x w	Sides (x2) (mm)	Lid (mm)	Base (mm)	Entrance hole diameter (mm)	Extra features	Height above ground in tree (m)
King Parrot (KP)	1000 x 250	950x250	Lx250	310x310	250x250	100	spout	10-20
Cuscus (CC)	575 x 340	495x340	Lx340	460x410	340x275	120	-	4-10
Ringtail (RT)	475 x 250	450x250	Lx250	390x310	250x250	105	Perch	4-10
Rosella (RS)	490 x 150	460x150	Lx240	330x200	200x150	70	Perch; shade cloth on inside.	4-10
Sugar Glider (SG)	360 x 150	330x150	Lx240	330x200	200x150	40	Perch; shade cloth on inside	4-10

Nest box placement

Eight of each type of nest box were placed in each Wasu plot. The nest boxes were staggered so that no two same nest boxes were directly adjacent on a grid 100 m apart. Nest boxes were placed on the nearest suitable tree to each designated grid marker. However, due to land ownership issues, the Movorong secondary plot had to be configured differently, and boxes were spaced every 80m on a modified grid. Eighty nest boxes were erected at Movorong and 80 were placed at Hongo for a total of 160 boxes. Within each site, 40 nest boxes were placed in a primary forest plot and the other 40 nest boxes in a secondary forest plot (Table 2). Boxes were placed 4-20 m above ground, mean = 9.5m.

Nest boxes were fastened in trees as described by Franks and Franks [49] to be stable with minimal injury to the tree by means of a cable inside a length of garden hose passed over a branch on the opposite side of the tree (Fig. 2). Where no branch was available two 4-inch nails secured the cable. Boxes were secured by climbers using either the single rope technique or free climbing using branches and lianas for support.

Gahavasuka nest boxes

Additional testing of nest boxes was conducted at Mt. Gahavasuka Provincial Park (6°00'53"S, 145° 24'45"E) in the Bismarck Range, 11 km northwest of Goroka, Eastern Highlands Province. Thirty nest boxes were placed in two 400 X 200 m grids (Table 2). Nest box designs were identical to those used at Wasu (KP, CC, RT, RS, SG) with three of each design on each grid. All were placed 5-10 m above the ground, except KP boxes, which were placed 10-20 m above the ground. Boxes were placed in December 2008-January 2009 and monitored by climbing and inspecting the interior. Boxes were checked monthly for the first six months, then every three months thereafter through December 2010.

Table 2. Placement and occupancy of different box styles at several sites in Papua New Guinea. Occupancy means the number of boxes of a style that were occupied by mammals during the study. Box styles follow designs in Franks and Franks [49]; abbreviations as in Table 1. Details of sites are given in the methods.

		Nest box numbers				
Site	**Forest type**	**KP**	**CC**	**RT**	**RS**	**SG**
Wasu/Hongo	Primary mid-montane	8	8	8	8	8
Wasu/Hongo	Secondary mid-montane	8	8	8	8	8
Wasu/Movorong	Primary lowland	8	8	8	8	8
Wasu/Movorong	Secondary lowland	8	8	8	8	8
Gahavasuka	Primary montane	6	6	6	6	6
Mammal Occupancy Wasu		14	7	4	3	3
Mammal Occupancy Gahavasuka		4	1	2	1	2

Statistical Analyses

Most tests were non-parametric tests, or t-tests for differences of means. Tests were made using online Chi-square test [50]; online Mann-Whitney U-test [51]; and online independent *t*-test [52].

Fig. 2. Examples of placement of nest boxes at Wasu and types of boxes. A- Ringtail (RT) box, B- Cuscus (CC) box, C- King Parrot (KP) box, D- Rosella (RS) box, E- Sugarglider (SG) box. Dimensions follow [49].

Results

Cavity-using wildlife of New Guinea

There are approximately 212 species of terrestrial mammals in New Guinea [37,38,53]. Of these, at least 50 species (23.6%) from 12 families are recorded as using standing tree cavities (Appendix 1). Of these, seven are listed as vulnerable to critically endangered [54]. Another 47 species (22%) had records of using fallen hollow logs.

There are roughly 668 bird species in the New Guinea region, excluding aquatic and marine taxa[55-57]. We classified species as obligate cavity nesters (51 species) or opportunistic cavity nesters (14 species), and where there was not direct information from New Guinea we classified as presumed obligate (37 species) or presumed opportunistic (16 species) based on our knowledge of the taxa and of known close relatives. Thus about 88 species (13.2%) are obligate cavity users and 30 (4.5%) opportunistically use tree cavities (Appendix 2).

The families most dependent on tree cavities include the parrots, cockatoos and lories (Psittacidae), owlet-nightjars (Aegothelidae), hornbills (Bucerotidae), and owls (Tytonidae and Strigidae) (Appendix 2). Among the cavity-using species are 19 species considered vulnerable to endangered [54].

Tree plot cavity census

There were 1,375 trees with dbh >5 cm and 232 species in the primary forest plot, and 1,217 trees with dbh >5 cm and 92 species in the secondary plot. The mean dbh of trees in the primary forest plot (12.7 cm) was significantly larger than that of trees in secondary forest plot (10.3 cm) (t =20.5, p<.05) with 200 (14.5%) trees >20 cm dbh on the primary plot and only 65 (5.3%) of the trees in the secondary plot.

By ground observation for tree cavities, 36 potential cavities were identified in the primary forest plot and 10 potential cavities were identified in the secondary forest. The cavity assessment on felled trees revealed 26 cavity trees in the primary forest plot and no cavity trees in the secondary forest plot. Nine (25%) of the potential cavity trees identified by a ground observer actually proved to have cavities when the tree was felled. Seventeen cavity trees were identified only after felling, and had not been identified during the ground survey. Three of the cavity trees had more than one cavity.

The 26 cavity trees were found in 21 tree species from 14 families. Four trees of *Teijsmanniodendron bogoriense* had cavities, followed by *Horsfieldia basifissa* and *Chionanthus ramiflora* (2 trees each). All other cavity tree species had one cavity tree each (Table 3).

Disproportionately more cavities (25%) were in trees > 40 cm dbh than trees > 40 cm dbh represented in the ha sample (6%). These large trees were *Teijsmanniodendron bogoriense, Dysoxylum pettigrewianum, Pometia pinnata* and *Dracontomelon dao*. The mean dbh of trees with cavities (25.1 cm) was significantly larger than non-cavity trees (12.48) on the primary plot (t= 5.9068, df = 1355, p<<.01). Eight (38%) cavity trees were small trees (dbh <10 cm).

Twenty trees had cavities on tree boles only; three had cavities on the bole and on a primary branch. Two trees had cavities only on a primary branch, and one tree had a cavity on a secondary branch. Trees with cavities on branches were among the larger cavity trees (dbh >25 cm). Larger cavities were located on larger trees; cavity size was correlated to tree dbh (Spearman rank correlation, r_s = 0.2394, p < 0.01, n = 26 trees).

The largest cavity was 50 cm in greatest diameter, found on the bole of a *Dracontomelon dao* that also had a cavity in a primary branch. The next largest cavities 30 and 25 cm diameter were in *Teijsmanniodendron bogoriense* and *Celtis latifolia*.

Bats flew from the large cavity on felling of the *Dracontomelon dao,* and an unidentified lizard and bats were found in the cavity during cavity assessment of the felled tree. A frog was found in a bole cavity of 9.5 cm diameter, in a *Horsfieldia basifissa.* Ant nests were found in four of the bole cavities. No fauna were found in cavities in branches.

Table 3. Tree species with natural cavities at Wanang. In a comprehensive survey of all trees (N= 1375) felled on a one ha plot of lowland primary forest. Trees are ranked by dominance according to basal area.

Family	Species	No. of cavity trees	Basal area rank /232 spp.	Basal area /ha (cm^2)
Sapindaceae	*Pometia pinnata*	1	1	35332
Verbenaceae	*Teijsmanniodendron bogoriense*	4	2	29396
Rubiaceae	*Mastixiodendron pachyclados*	1	3	19471
Euphorbiaceae	*Pimelodendron amboinicum*	1	4	12469
Myristicaceae	*Horsfieldia basifissa*	2	6	11522
Flacourtiaceae	*Pangium edule*	1	8	7378
Meliaceae	*Dysoxylum pettigrewianum*	1	12	5684
Anacardiaceae	*Dracontomelon dao*	1	14	5301
Ulmaceae	*Celtis latifolia*	1	17	4318
Caesalpinaceae	*Maniltoa psilogyne*	1	19	3703
Meliaceae	*Chisocheton ceramicus*	1	23	3063
Myristicaceae	*Myristica fatua*	1	24	2718
Lauraceae	*Litsea timoriana*	1	25	2623
Flacourtiaceae	*Erythrospermum candidum*	1	32	2200
Gnetaceae	*Gnetum gnemonoides*	1	40	1313
Meliaceae	*Sandoricum koetjape*	1	46	1116
Oleaceae	*Chionanthus ramiflora*	2	57	907
Nyctaginaceae	*Pisonia longilostris*	1	65	734
Lauraceae	*Cryptocarya massoy*	1	90	396
Sapindaceae	*Lepidopetalum comesperma*	1	92	391
Euphorbiaceae	*Bridelia macrocarpa*	1	159	98

Wasu nest box census

Eight months after placing 160 nest boxes, 155 remained; four had fallen, and one was removed by a vandal. Of the remaining boxes: 21 (13.5%) were occupied by mammals and three showed evidence of mammals by tooth and claw marks inside the box. Four had evidence (feathers) of use by birds and 16 (10.3%) had reptiles or evidence of reptiles. Bees occupied 14 (9%) and could not be safely opened, and 21 (13.5%) had some European Honeybees (*Apis mellifera*) or evidence of bee nests present when opened.

Sugar gliders, *Petaurus breviceps*, were the most common vertebrate occupant, found in 18 boxes. Three nest boxes each had a Northern common cuscus, *Phalanger orientalis*. One nest box had a Diehl's little ground snake, *Stegonotus diehli*, and two had lizards that were not identified. Geckos (Boulenger's Bow-fingered Gecko, *Cyrtodactylus loriae,* and *Lepidodactylus sp.*) were found in 11 nest boxes and two boxes had gecko eggs. Most of the boxes had some invertebrates present.

More nest boxes were used by larger vertebrates (excluding geckos) in the higher elevation (22) than at the lower elevation (9) $\chi^2 = 6.762$, *df* = 1, $p < 0.025$). Bees occupied more nest boxes in the higher elevation (12) than in the lower elevation (2) site $\chi^2 = 5.833$, *df* = 1, $p < 0.025$). There was no significant difference ($p > 0.1$) in the number of nest boxes used by vertebrates between the primary (16) and secondary (15) forest plots or boxes with bees in the primary (4) and secondary plots (10).

Nest box design and placement

Of the 31 nest boxes that were used by larger vertebrates, KP nest boxes were used most (χ^2= 14, *df* = 4, p <.01). The smaller nest boxes, SG and RS, were more commonly overrun by bees than the medium sized RT and larger CC and KP nest boxes. Nest boxes occupied by vertebrates were in larger trees (Mann-Whitney $U = 1988.0$, $p < 0.01$) and higher ($U = 2181.0$, $p < 0.05$) than unoccupied nest boxes.

Gahavasuka nest boxes

Of the 30 boxes, two were stolen and one destroyed by a treefall. Evidence of mammal use (scratch marks, nest material and scat) was found within the first three months and the first occupant (Silky cuscus, *Phalanger sericeus*) found after six months. Occupancy steadily increased after the sixth month through the monitoring period, with 11 boxes occupied by mammals (8 *P. sericeus* and 3 *Petaurus breviceps*) by the end of the study. Of these, ten were consistently occupied by the same species after initial occupation. Seven other boxes had evidence of occasional use by mammals. One box had evidence of use by birds, and four contained bees.

The KP boxes were the most preferred (Table 2). *Phalanger sericeus* were found in at least one census in four of the KP boxes and *P. breviceps* were found in one KP box. *P. breviceps* were also found in two SG boxes, and *P. sericeus* once in CS and RS boxes and twice in RT boxes. Two *P. sericeus* shared a KP box July-December 2010. Numbers of *P. breviceps* sharing a box varied within and among boxes at different censuses.

Discussion

Importance of cavities to the New Guinea vertebrate fauna

Cavity use has been recorded in at least 49 species (23.1%) of 212 terrestrial mammal species resident in New Guinea [37-39] The New Guinea mammalian fauna is most similar to Australia (305 species) where cavity-using mammalian species were estimated at 108 (35.4%) cavity-using species [58]. Among arboreal and scansorial species, 62% use cavities in Australia [59] compared to 44% in New Guinea (Appendix 1). Part of the apparent lower percentages of cavity use in New Guinea is likely due to the poorer information available on denning habits. For 65 New Guinea species, Flannery [38] listed no available data on den use. From what we know of the biology of the species with few data in Flannery, we expect at least another six to regularly use cavities. With these six, cavity use would be about 26%, still considerably less than found in Australia.

Many New Guinea mammals use fallen hollow trees as den sites. When hollow trees fall they create den sites for this additional suite of terrestrial vertebrates. Use of artificial nest boxes would not benefit these taxa but issues of cavity availability and forest management to preserve hollow trees would be relevant to this group of terrestrial mammals.

Nesting habits of many bird species are poorly known-- we could not find nesting descriptions for over 115 species from the region. Comparison with other tropical regions is difficult, because even in the better studied (compared to Papuan) Neotropical rainforests there are few broad surveys of cavity use [11]. But our figures of 17% of the avifauna using cavities and 13% as obligate users are comparable to a study in Mexico that found 17% and 12 % respectively [60]. Figures from temperate regions are usually lower, with less than half the percentage of cavity nesters as tropical communities [7,61]. The absence of primary excavators, the woodpeckers, from the region suggests that cavities might be more limiting than other forests, and competition for nest sites can be intense [15,62]. But most cavity-using bird species in Neotropical forests use natural cavities rather than woodpecker excavations [63].

Availability of cavities in trees and cavity census methods

Ascertaining the availability of possible nest cavities in forests is difficult [17,64]. We found that ground-based determination of what is or is not a cavity is unreliable, missing 75% of cavities found after felling. Furthermore, 37 suspected cavities observed on the two hectares proved not to be habitable cavities. In our study and others [48,58] internal cavity dimensions are not closely correlated to size of external opening. Thus censuses of cavity availability based solely on ground observation are suspect [17,48]. Repeated observations where use by animals can be observed could increase accuracy [19,65], but observing cavity use is difficult and requires substantial effort [20]. It is unlikely that counts of inconspicuous cavities in tropical rainforests can be trusted in absolute terms, but such quantification might still be useful for comparative studies.

This study confirmed 26 cavity-bearing trees in a hectare of primary forest with none in the secondary forest ha plot. Secondary forests could prove unsuitable for reproduction for cavity-nesting species even if such species forage in secondary forests. Larger trees are more likely to have cavities and have larger cavities, thus some tree taxa that reach large sizes, such as *Teijsmanniodendron bogoriense*, might be particularly important as cavity trees. Some important cavity-bearing species are not necessarily common, such as *Dracontomelon dao*. Size and species, not relative abundance, are usually the main factors associated with cavity formation [48,58]. Some of the small trees (< 10 cm dbh) had hollows 5-8 cm in diameter. Although not suitable for large vertebrates, such hollows could be ideal for some herpetofauna, mice or Microchiroptera whose modal body size is 6-12 g in Papua New Guinea [37]. Additional research in New Guinea is needed to identify whether there are tree species that most commonly have cavities, and if so, this information could help guide forest management that promotes wildlife populations.

By felling and examining all trees on a hectare of primary rainforest we confirmed 26 cavities. Few comparable data exist on cavity availability from other tropical forests, particularly Africa [10]. A site in Costa Rica had 58 cavities/ha [20] and a study in Argentina reported four natural cavities per ha [10]. In Peru, piedmont forests had 4.1 cavities/ha and 3.9/ha in cloud forest [66]. A study in Thailand estimated 407 cavities per ha with 45% of all trees containing cavities [67]. But this study was based on a model of three tree species that most commonly have cavities and applied it to all trees [67], which could substantially inflate the estimate. The closest to our values is a study from two sites on the island of New Britain, just to the north of New Guinea, that estimated 24 and 27 cavities/ha [16]. Estimates of cavity trees in several temperate to subtropical forests of Australia ranged up to 13.2/ha [1]. One should not place too much faith in the actual numbers of different studies (see above), but it seems safe to conclude that tree cavities are fairly scarce relative to the number of taxa that use them. Marsden and Pilgrim found that there were more parrots and hornbills per ha than available cavities [16]; competition for occupancy could be intense given the number of taxa that use such cavities.

Occupancy and use of nest boxes

The Gahavasuka data indicate that occupancy increases with time and was still increasing after two years. Thus the occupancy data from Wasu after eight months were probably not indicative of the proportion of boxes that would be occupied over a longer period of time. Nonetheless it is clear that artificial nest boxes are readily occupied and used by Cuscuses and Sugar Gliders in PNG. At

Gahavasuka, 60% of the boxes either were in use or showed evidence of use by mammals after two years, while the Wasu boxes had 15% use or evidence of use after eight months. It can take years for boxes to be discovered and occupied [24]. We believe that had further monitoring been possible, we would have found higher occupancy at both sites after another year.

Boxes were not checked at night when roosting by diurnal birds would be discovered. The presence of feathers in a few boxes suggests that birds sometimes used the boxes. For birds that might use artificial nest boxes for nesting, the census period at Wasu was probably too short to assess whether birds will utilize such boxes. In the Atlantic forest of Argentina during the breeding season, boxes were occupied within a couple months [65]. There are no data on when breeding peaks at Wasu. The total absence of nesting birds suggests birds might not as readily occupy these boxes as deployed in New Guinea.

Other studies of nest boxes have not reported extensive use by reptiles. The relatively high use of artificial boxes at the lower elevation sites suggests cavities might be an under-recognized resource for rainforest reptiles. We found fairly high numbers of geckos, which are often difficult to locate and census in PNG forests.

Bees occupied a large number of boxes and could exclude use by desired fauna. There has been considerable discussion about how European Honeybees may have altered native pollination systems around the world where they have been introduced and become ubiquitous, but less discussion how these bees might have impacted native vertebrate populations by usurping nest and den cavities, which has occasionally been noted [68,69]. One of us (Mack) has observed bees to take over natural cavities used by Eclectus Parrots (*Eclectus roratus*) and Blyth's Hornbills (*Rhyticeros plicatus*) in PNG. In Australia, bees occupied and excluded mammals from about 10% of boxes [70] and more commonly occupied boxes in young forest [71].

Nest box design and placement

The larger boxes attracted the greatest diversity, being used by large (*Phalanger*) and small (geckos) vertebrates alike. But Sugar gliders were more common in the smaller boxes. With sufficient testing and additional box designs, it might be possible to attract a greater diversity of species to artificial nest boxes of different designs. Clearly "one size does not fit all," and specific management objectives will require different styles of boxes [72]. Our data, however, are sufficient to indicate potential for box use in PNG. Design and testing of new styles are needed specifically for PNG fauna.

Higher placement (>10m) above the ground and in larger trees resulted in higher occupancy and is consistent with other studies [70]. In this study we adhered to a grid for box placement. This sometimes resulted in placement in smaller trees or trees that could not be easily climbed to greater heights. Where nest boxes are being used as a management tool, we believe occupancy would be increased by preferentially selecting the largest trees and ones that can be climbed to a greater height for placement. Occupancy can likely be optimized through strategic placement of boxes.

Implications for conservation

This study indicates natural cavities are important to many vertebrate species, and such cavities are uncommon. Natural cavities are usually in larger trees and often of marketable timber species. Thus, logging in New Guinea is likely to reduce the availability of natural cavities, as found in other tropical forests [11,16,67] and consequently impact populations of cavity-using vertebrates [73]. Hunters in New Guinea often fell den trees to secure prey within cavities [36,74]. This practice also can reduce the availability of natural cavities when rates of cavity formation are slow [15]. Species that forage in regrowth forests might not be able to breed there due to absence of nest cavities [16].

Hunters should be educated not to fell den trees just to secure prey, as this removes a known den cavity. Sustainable logging protocols would ideally include measures to retain both cavity trees and occupied cavity trees [7]. But our study shows it is difficult to identify cavity trees from the ground. As most dens were in large trees, protocols that retain large trees [22], or retain blocks of unlogged forest might be the best hope for retaining trees with natural cavities [10,75]. Additional study is needed in New Guinea to determine the impacts of logging on cavity-using wildlife and possible means to reduce such impacts.

We show that a range of vertebrates, from geckos to large marsupials, readily occupy artificial nest boxes in New Guinea. Supplementing secondary and logged forest sites with nest boxes might help make these forests more suitable for some threatened cavity-using species. But nest boxes can be costly to maintain [71,76], are not always effective conservation tools [77], and early occupancy can be followed by attrition that diminishes any long-term benefits [71]. Additional experimentation and monitoring of nest boxes are recommended. Monitoring over longer census intervals is needed to detect occupants that might be slow to discover and occupy nest boxes, or to detect attrition. New box designs and dimensions could be explored that might be more appropriate to PNG's cavity-using fauna. Nonetheless, this study shows that artificial nest boxes show sufficient promise as a conservation tool to merit more extensive experimentation and monitoring.

Acknowledgements
The staff and colleagues of the PNG Institute of Biological Research helped in the execution and logistics in many ways. Many thanks to Vojtech Novotny and the New Guinea Binatang Research Centre team, particularly John Auga, Markus Manumbor, Martin Mogia and Cliffson Idigel, for their assistance in the tree cavity census at Wanang. The census at Wanang was supported by NSF DEB-0841885. This study was partially funded by a grant from the European Union to the Wildlife Conservation Society – PNG Program (2006 – 2007). Debra D.Wright helped in many ways throughout the study. Katayo Sagata, and Miriam Supuma made helpful comments on earlier drafts of the manuscript. Kristina L. Cockle reviewed and improved the manuscript. Many thanks to the people of Wanang, Wasu, Hongo, Movorong, and Gahavasuka for allowing and facilitating access to their lands, particularly, Hivi Laku (Uncle Kapi) and family, and the Sira families. With great sadness we note the death of Paul Igag before the study was fully completed; he continues to be an inspiration.

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APPENDIX 1. Mammal species recorded as using tree cavities. Data derived from [37-39]. Conservation status from the IUCN Redlist [54]. Taxa endemic to the New Guinea region noted in the Conservation Status column by "E."

Species	**English name**	**Conservation status**
Dasyuridae		E
Murexia longicaudata	Short-furred Dasyure	
Phalangeridae		E
Phalanger carmelitae	Mountain Cuscus	
Phalanger orientalis	Northern Common Cuscus	E
Phalanger sericeus	Silky Cuscus	E
Phalanger vestitus	Stein's Cuscus	E
Acrobatidae		E
Distoechurus pennatus	Feather--tailed Possum	
Burramyidae		
Cercartetus caudatus	Long-tailed Pygmy-possum	
Petauridae		E
Dactylopsila palpator	Long-fingered Triok	
Dactylopsila trivirgata	Striped Possum	
Petaurus abidi	Northern Glider	critically endangered E
Petaurus breviceps	Sugar Glider	
Pseudocheiridae		near threatened E
Pseudochirops corinnae	Plush-coated Ringtail	
Pseudochirops coronatus	Reclusive Ringtail	vulnerable E
Pseudochirops cupreus	Coppery Ringtail	E
Pseudochirulus canescens	Lowland Ringtail	E
Pseudochirulus forbesi	Painted Ringtail	E
Muridae		near-threatened
Conilurus penicillatus	Brush-tailed Rabbit-rat	
Abeomelomys sevia	Menzies' Mouse	near-threatened E
Chiruromys forbesi	Forbes' Tree-mouse	E
Chiruromys lamia	Broad-headed Tree-mouse	E
Chiruromys vates	Lesser Tree-mouse	E
Mallomys rothschildi	Rothschild's Woolly-rat	E
Pogonomelomys bruijni	Large Pogonomelomys	near-threatened E
Pogonomelomys mayeri	Shaw Mayer's Pogonomelomys	E
Uromys anak	Black-tailed Giant-rat	E
Uromys caudimaculatus	Mottled-tailed Giant-rat	
Rattus steini	Small Spiny Rat	E
Pteropodidae	Great Bare-backed Fruit Bat	
Dobsonia moluccensis		
Dobsonia pannietensis	Panaeati Bare-backed Bat	near-threatened E
Emballonuridae	Naked-rumped Sheath-tailed Bat	
Saccolaimus saccolaimus		
Saccolaimus flaviventris	Yellow-bellied Sheath-tailed Bat	
Hipposideridae	Dusky Horseshoe Bat	
Hipposideros ater		
Hipposideros diadema	Diadem Leaf-nosed Bat	
Hipposideros maggietaylorae	Maggie Taylor's Horseshoe Bat	E
Hipposideros muscinus	Fly River Leaf-nosed Bat	data deficient E
Hipposideros semoni	Greater Wart-nosed Bat	data deficient
Vespertilionidae	Hoary Bat	
Chalinolobus nigrogriseus		

Kerivoula muscina	Fly River Trumpet-eared Bat	E
Nyctophilus bifax	North Queensland Nyctophilus	
Nyctophilus timoriensis	Greater Nyctophilus	data deficient
Philetor brachypterus	Rohu's Bat	
Pipistrellus collinus	Mountain Pipistrelle	E
Pipistrellus papuanus	Papuan Pipistrelle	
Scotorepens sanborni	Sanborn's Broad-nosed Bat	
Miniopterus australis	Little Bent-winged Bat	
Molossidae *Mormopterus beccarii*	Beccari's Mastiff Bat	
Mormopterus loriae	Little Northern Mastiff Bat	
Otomops papuensis	Papua Mastiff Bat	data deficient E
Tadarida kuboriensis	New Guinea Mastiff Bat	least concern E
Tadarida jobensis	Northern Mastiff Bat	E

Appendix 2. Bird species recorded as nesting or roosting in cavities. Data primarily derived from [41-43,78]. Conservation status from the IUCN redlist [54]. Taxa endemic to the New Guinea region noted in the Conservation Status column by "E."

Species	English Name	Cavity Use	Conservation status
Bucerotidae *Aceros plicatus*	Blyth's Hornbill	obligate	
Coraciidae *Eurystomus orientalis*	Dollarbird	obligate	
Alcedinidae *Alcedo pusilla*	Little Kingfisher	opportunistic	
Ceyx lepidus	Dwarf Kingfisher	opportunistic	
Dacelonidae *Dacelo leachii*	Blue-winged Kookaburra	opportunistic	
Dacelo tyro	Spangled Kookaburra	opportunistic	E
Dacelo gaudichaud	Rufous-bellied Kookaburra	opportunistic	E
Clytoceyx rex	Shovel-billed Kingfisher	presumed obligate	data deficient E
Todiramphus nigrocyaneus	Blue-black Kingfisher	presumed opportunistic	near-threatened E
Todiramphus macleayii	Forest Kingfisher	presumed opportunistic	
Todiramphus albonotatus	New Britain Kingfisher	presumed opportunistic	near-threatened E
Todiramphus leucopygius	Ultramarine Kingfisher	presumed opportunistic	
Todiramphus chloris	Collared Kingfisher	opportunistic	
Todiramphus saurophaga	Beach Kingfisher	obligate	
Melidora macrorrhina	Hook-billed Kingfisher	presumed opportunistic	E
Actenoides bougainvillei	Moustached Kingfisher	presumed opportunistic	vulnerable E
Syma torotoro	Yellow-billed Kingfisher	opportunistic	
Syma megarhyncha	Mountain Kingfisher	opportunistic	E
Tanysiptera hydrocharis	Little Paradise-Kingfisher	presumed opportunistic	data deficient E
Tanysiptera galatea	Common Paradise-Kingfisher	presumed opportunistic	
Tanysiptera ellioti	Kofiau Paradise Kingfisher	presumed opportunistic	data deficient E
Tanysiptera riedelii	Biak Paradise Kingfisher	presumed opportunistic	near-threatened E
Tanysiptera carolinae	Numfor Paradise-Kingfisher	presumed opportunistic	near-threatened E
Tanysiptera nympha	Red-breasted Paradise-Kingfisher	presumed opportunistic	E
Tanysiptera danae	Brown-headed Paradise-Kingfisher	presumed opportunistic	E
Tanysiptera sylvia	Australian Paradise-Kingfish	presumed opportunistic	
Centropodidae *Centropus ateralbus*	Pied Coucal	opportunistic	E
Psittacidae *Chalcopsitta duivenbodei*	Brown Lory	presumed obligate	E
Chalcopsitta sintillata	Greater Streaked Lory	presumed obligate	E

Chalcopsitta cardinalis	Cardinal Lory	presumed obligate	E
Eos squamata	Moluccan Red Lory	obligate	
Eos cyanogenia	Biak Red Lory	obligate	vulnerable E
Pseudeos fuscata	Dusky Lory	obligate	E
Trichoglossus haematodus	Rainbow Lorikeet	obligate	
Psitteuteles goldei	Goldie's Lorikeet	obligate	E
Lorius lory	Western Black-capped Lory	obligate	E
Lorius hypoinochrous	Eastern Black-capped Lory	presumed obligate	E
Lorius albidinucha	White-naped Lory	presumed obligate	near-threatened E
Charmosyna rubrigularis	Red-chinned Lorikeet	presumed obligate	E
Charmosyna meeki	Meek's Lorikeet	obligate	near-threatened E
Charmosyna multistriata	Streaked Lorikeet	presumed obligate	near-threatened E
Charmosyna wilhelminae	Pygmy Lorikeet	presumed obligate	E
Charmosyna rubronotata	Red-fronted Lorikeet	presumed obligate	E
Charmosyna placentis	Red-Flanked Lorikeet	presumed obligate	
Charmosyna margarethae	Duchess Lorikeet	presumed obligate	near-threatened E
Charmosyna pulchella	Little Red Lorikeet	obligate	E
Charmosyna josefinae	Josephine's Lorikeet	presumed obligate	E
Charmosyna papou	Papuan Lorikeet	presumed obligate	E
Oreopsittacus arfaki	Plum-faced Lorikeet	presumed obligate	E
Neopsittacus musschenbroekii	Yellow-billed Lorikeet	obligate	E
Neopsittacus pullicauda	Orange-billed Lorikeet	presumed obligate	E
Probosciger aterrimus	Palm Cockatoo	obligate	near-threatened
Cacatua galerita	Sulphur-crested Cockatoo	obligate	
Cacatua ophthalmica	Blue-eyed Cockatoo	presumed obligate	E
Micropsitta keiensis	Yellow-capped Pygmy-Parrot	obligate	E
Micropsitta geelvinkiana	Geelvink Pygmy-Parrot	presumed obligate	near-threatened E
Micropsitta pusio	Buff-faced Pygmy-Parrot	obligate	E
Micropsitta meeki	Meek's Pygmy-Parrot	obligate	E
Micropsitta finschii	Finsch's Pygmy-Parrot	obligate	E
Micropsitta bruijnii	Red-breasted Pygmy-Parrot	obligate	
Cyclopsitta gulielmitertii	Orange-breasted Fig-Parrot	obligate	E
Cyclopsitta diophthalma	Double-eyed Fig-Parrot	obligate	
Psittaculirostris desmarestii	Large Fig-Parrot	obligate	E
Psittaculirostris edwardsii	Edwards' Fig-Parrot	obligate	E
Psittaculirostris salvadorii	Salvadori's Fig-Parrot	obligate	vulnerable E
Psittacella brehmii	Brehm's Tiger-Parrot	presumed obligate	E

Psittacella picta	Painted Tiger-Parrot	presumed obligate	E
Psittacella modesta	Modest Tiger-Parrot	presumed obligate	E
Psittacella madaraszi	Madarasz's Tiger-Parrot	presumed obligate	E
Geoffroyus geoffroyi	Red-cheeked Parrot	obligate	
Geoffroyus simplex	Blue-collared Parrot	obligate	E
Geoffroyus heteroclitus	Singing Parrot	obligate	
Tanygnathus megalorynchos	Great-billed Parrot	presumed obligate	
Eclectus roratus	Eclectus Parrot	obligate	
Psittrichas fulgidus	Vulturine Parrot	obligate	vulnerable E
Alisterus amboinensis	Moluccan King-Parrot	presumed obligate	near-threatened
Aprosmictus erythropterus	Red-winged Parrot	obligate	
Alisterus chloropterus	Papuan King-Parrot	presumed obligate	E
Loriculus aurantiifrons	Papuan Hanging-parrot	obligate	E
Loriculus tener	Green-fronted Hanging-parrot	presumed obligate	near-threatened E
Apodidae *Mearnsia novaeguineae*	Papuan Spine-Tailed Swift	obligate	E
Tytonidae *Tyto multipunctata*	Sooty Owl	obligate	
Tyto manusi	Manus Masked Owl	presumed obligate	vulnerable E
Tyto aurantia	Golden Masked Owl	presumed obligate	vulnerable E
Tyto novaehollandiae	Masked Owl	obligate	
Tyto alba	Barn Owl	obligate	
Tyto longimembris	Grass Owl	presumed obligate	E
Strigidae *Otus magicus*	Moluccan Scops-Owl	obligate	endangered
Ninox rufa	Rufous Owl	obligate	
Ninox connivens	Barking Owl	obligate	
Ninox novaeseelandiae	Southern Boobook	obligate	
Ninox theomacha	Papuan Boobook	obligate	E
Ninox meeki	Manus Hawk-Owl	presumed obligate	E
Ninox variegata	Bismarck Hawk-Owl	presumed obligate	E
Ninox odiosa	New Britain Hawk-Owl	presumed obligate	E
Ninox jacquinoti	Solomons Hawk-Owl	obligate	
Nesasio solomonensis	Fearful Owl	presumed obligate	vulnerable
Uroglaux dimorpha	Papuan Hawk-Owl	presumed obligate	data deficient E
Aegothelidae *Aegotheles insignis*	Feline Owlet-Nightjar	obligate	E
Aegotheles cristatus	Australian Owlet-Nightjar	obligate	E
Aegotheles bennetti	Barred Owlet-Nightjar	presumed obligate	E

Aegotheles wallacii	Wallace's Owlet-Nightjar	obligate	data deficient E
Aegotheles albertisi	Mountain Owlet-Nightjar	obligate	E
Aegotheles archboldi	Archbold's Owlet-Nightjar	presumed obligate	E
Falconidae *Falco severus*	Oriental Hobby	opportunistic	
Falco peregrinus	Peregrine Falcon	opportunistic	
Climacteridae *Cormobates placens*	Papuan Treecreeper	presumed obligate	E
Maluridae *Malurus grayi*	Broad-Billed Fairy-Wren	presumed opportunistic	near-threatened E
Eopsaltriidae *Amalocichla incerta*	Lesser Ground-Robin	opportunistic	E
Petroica multicolor	Pacific Robin	presumed opportunistic	
Corvidae *Ptilorrhoa leucosticta*	Spotted Jewel-Babbler	opportunistic	E
Cicinnurus regius	King Bird of Paradise	obligate	E
Sturnidae *Aplonis cantoroides*	Singing Starling	obligate	
Aplonis feadensis	Atoll Starling	obligate	vulnerable
Aplonis grandis	Brown-winged Starling	opportunistic	
Acridotheres tristis	Common myna	obligate	
Mino anais	Golden Myna	obligate	E
Mino dumontii	Yellow-faced Myna	obligate	