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Breeding biology of the White-headed Pigeon *Columba leucomela* in a modified landscape

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Abstract. Current knowledge of the breeding biology of the White-headed Pigeon *Columba leucomela* is derived mainly from observations of captive birds, with little published data on reproductive behaviour and breeding success in wild populations. Over 10 years (2001–2010), 122 nests were monitored in a rural landscape near Lismore, northern New South Wales. Nests were in a wide variety of trees and shrubs, including ornamentals, mostly <10 years old. Breeding Pigeons tolerated a high level of daily human activity, with many nests close to buildings, and with brooding birds sitting tightly in close proximity to working staff. Nests were re-used in all years, with ~65% of clutches laid in previously used nests. Individual nests were re-used multiple times, both within a season, and over multiple years. Clutches were laid in all months except October and November. Incubation and nestling periods and care are detailed. Body colour of fledglings and juveniles was variable, with the plumage of a minority having a striking resemblance to the Metallic Pigeon *C. vitiensis*. Overall breeding success for nests where the outcome was known was 38.5%. Predation, likely involving a range of taxa, was the largest single cause of nesting failure. White-headed Pigeons using a modified landscape with abundant seasonal fruit and seeds from the introduced tree Camphor Laurel *Cinnamomum camphora* demonstrate traits that facilitate rapid and extended breeding.

Introduction

Once considered an inhabitant of dense wet forests of eastern Australia (Gould 1865; Frith 1952, 1982), the White-headed Pigeon *Columba leucomela* has adapted to changed habitat conditions following the clearing of native forests. In the Richmond River district in north-eastern New South Wales, from about the 1940s, White-headed Pigeon populations increased as the species spread into open country characterised by a mosaic of pastures, regrowth forest, and urban areas, a pattern repeated elsewhere (Frith 1982; Cooper *et al.* 2014; Forshaw & Cooper 2015). Frith (1952, 1982) identified the key role of the fruit of the introduced tree Camphor Laurel *Cinnamomum camphora,* an invasive woody weed, in this process. Recent studies of diet of this species in the Richmond River district (Gosper & Gosper 2008; Gosper 2011) demonstrated that in a heavily modified landscape where Camphor Laurel is abundant, this is their primary food source locally for much of the year. It may be used to some extent year-round, with all reproductive stages of the plant—flowers, green, ripe and fallen fruits and bare seeds—used as food. Fruits are taken from both trees and the ground.

Although now relatively common in parts of its range, and first reported breeding in rural landscapes in the 1970s (Frith 1982, 1983), there have been no major studies of the breeding of the White-headed Pigeon. Basic knowledge of its breeding biology has come mostly from observing captives (Frith 1982; Higgins & Davies 1996; Forshaw & Cooper 2015). Postures and bowing display used in a sexual context have been described by Frith (1977, 1982). There are few or no data on the reproductive behaviour and breeding success of wild populations, in any habitat. I here report the results of 10 years of monitoring of breeding in a rural landscape at Goolmangar (28°42′36″S, 153°13′55″E; ~30 m above sea level), near Lismore, in the Richmond River district.

Study area and methods

The study site comprised 1.7 ha, made up of the grounds of Goolmangar Public School (established in 1929) and my adjoining residence (erected in 1992 in what was then a pasture paddock). The site was essentially like parkland, with buildings and mown playing fields bordered by mostly mature exotic and native trees including Southern Magnolia *Magnolia grandiflora,* Camphor Laurel, Jacaranda *Jacaranda mimosifolia,* paperbarks *Melaleuca* spp., bottlebrushes *Callistemon* spp., Silky Oak *Grevillea robusta* and eucalypts *Eucalyptus* spp. and *Corymbia* spp. Small shrubs and understorey were largely absent. The grounds of the residence consisted of lawns with plots containing native shrubs and trees, primarily local rainforest and eucalypt species, planted in the early 1990s. Additional plantings of native trees were also carried out in the school grounds at this time.

The site was adjacent to two older residences and surrounded by farmland used for cattle grazing (Figure 1). These paddocks comprised a mosaic of pasture and, on steeper slopes, regrowth eucalypt and dry rainforest with extensive areas dominated by the woody weeds Camphor Laurel and Broad-leaved Privet *Ligustrum lucidum.* Tall shrubby weeds, notably Lantana *Lantana camara* and Crofton Weed *Ageratina adenophora*, frequently fringed regrowth forest. Remnant riparian rainforest, also dominated by Camphor Laurel, bordered nearby Goolmangar Creek.

The bird community of the school grounds typically comprised few species. Those present for all or much of the day were Noisy Miner *Manorina melanocephala,* Australasian Figbird *Sphecotheres vieilloti*, Australian Magpie *Gymnorhina tibicen* and Grey Butcherbird *Cracticus torquatus*. Also occurring frequently (and often daily over extended periods) were White-headed Pigeon, Crested Pigeon *Ocyphaps lophotes*, Laughing Kookaburra *Dacelo*

Figure 1. Aerial view of study site and surrounds at Goolmangar, New South Wales.

novaeguineae, Eastern Rosella *Platycercus eximius* and Scaly-breasted Lorikeet *Trichoglossus chlorolepidotus*. Torresian Crows *Corvus orru* visited the grounds regularly, usually when there was little human activity. As plantings around the residence (which was adjacent to older regrowth) matured, additional bird species occurred in that section of the site.

Documentation of birds using the site began in 1990, and from 1994 to 2002 a study of breeding by the Australasian Figbird in the school grounds was conducted (DGG unpubl. data). The first evidence of nesting by White-headed Pigeons was detected in July 1999, when a bird was noted carrying nest material from the school grounds to adjacent roadside vegetation, and in April 2000 a nest was built in a shrub in the residence section of the site. From 2001 to 2010, breeding activity was monitored and documented almost daily except during periods of my absence (3–4 weeks annually in 2001–2007, 6–8 weeks in 2008–2010).

Routine monitoring involved circuits of the site, inspecting trees and shrubs for nests, and noting the movements and behaviour of White-headed Pigeons. Once it became apparent that prospecting for nest-sites had commenced [usually signalled by calling, or nest(s) found], monitoring was increased to twice daily on most days, usually before 0730 h and again after 1630 h. Opportunistic observations were made at any time of day. Limited nest-watch sessions were conducted, mostly on weekends. It became evident early in the monitoring program that pairs of the birds were very wary when prospecting for a nest-site and building, and were prone to abandon the site if approached or disturbed. Therefore, close observation of activity at the actual site of nest prospecting and construction was limited.

Each active nest was allocated a number (e.g. N14/07 representing the 14th clutch located in 2007), with observations logged in diary format. Nest-platforms re-used in the same or subsequent year(s) were cross-referenced to previous breeding event(s) involving that platform. Details recorded included time of day, presence or absence of adult bird(s), sex (where determined), activity (e.g. adding nest material, brooding, brooding changeover), and nest contents (e.g. egg, nestling if visible, fledgling perched close to its nest). Tree species, nest position and (for most nests) height above the ground were also recorded. If a currently active nest was found unattended or empty, the site was scanned briefly for signs of the possible outcome (e.g. fledgling close by, broken eggshell, dead nestling on ground), and for evidence of the cause of failure. If still vacant when next checked, the nest-platform (where accessible), surrounding branches and the ground below within a 5-m radius were closely inspected. Eggshells found were kept for reference purposes.

Unless otherwise stated, all data refer to nests located during 2001 to 2010, and only nests in which laying was confirmed are included in analyses. Breeding season was defined as the month(s) in which clutches were laid. Brooding commenced with laying. The incubation period was calculated using the date that the female went on to the nest around dusk (Day 1) and was relieved by the male the following morning. Fledging was defined as the first day (Day 1) that a nestling moved from the nest-platform (usually to a nearby branch), even if, as often occurred, it subsequently returned to the nest.

Results

White-headed Pigeons nested in each of the 10 years. A total of 122 clutches was located. In a few instances, shell from a freshly hatched egg that could not be accounted for in terms of known nests was found on the ground, suggesting that not all nests were found.

Clutches were laid in all months except October and November, with the majority laid between late January and mid August (Table 1). The seasonally earliest clutch was laid on 25 December, and the latest on *c*. 14 September. Duration of breeding (interval between the laying of the first and last clutches found in a given season) ranged from <1 month to 8 months, with a mean of ~5 months. The number of clutches found in a year varied from one in 2003 to 39 in 2007. The highest number of concurrently active nests recorded was in mid July 2007, when 10 pairs of Pigeons were incubating or feeding nestlings.

Table 1. Number of White-headed Pigeon clutches laid in each month at Goolmangar, New South Wales, during 2001 to 2010.

Year	*Month*												
	Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*Jun.*	*Jul.*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*	*Total*
2001		3	1		1		1	1					7
2002						1	1						2
2003							1						1
2004		1					1						2
2005	1		1	1	1			1					5
2006		1		2	1	1	3		1				9
2007			5	3	7	4	10	7	3				39
2008	6		2	2	3	5	3	5				1	27
2009	3	5	7	3									18
2010	2	3				4	3						12
Total	**12**	**13**	**16**	**11**	**13**	**15**	**23**	**14**	**4**	**0**	**0**	**1**	**122**

Courtship, nest prospecting and copulation

Pre-nesting behaviour of White-headed Pigeons involved increased vocalisation, mainly of the *WHOO-woo* advertising call (Frith 1982, therein described as *oom-coo*), and movement about the site as Pigeons explored shrubs and smaller trees for nest-sites. Males called from prospective sites, including from previously used nests, with the female sometimes close by. A second call, a growl or squawk, probably that described by Hyem (1936), was heard less often, but more specifically when multiple pairs were actively nest prospecting in close proximity. It was sometimes given from a prospective nest-site but also in other contexts (see below).

Nest-site prospecting appeared to be led by the male, with the period of highest activity being mid-to-late morning. Pairs moved from one tree to the next, with the male flying ahead, soon followed by the female. The lead bird moved through the branches until a potentially suitable site was located and was then joined by the female. The pair commonly remained sitting quietly for an extended period, often with the female on the potential nest-site and the male perched within 70 cm. The female sometimes shuffled about and pulled at branchlets. One pair spent 105 minutes in the tree where the birds investigated one potential site and two previously used nests, spending long periods at each site before departing. The following day, a pair was again in the same tree, with the female remaining on one of the previously used nests for almost 4 hours, the male sitting <1 m away throughout. Pigeon pairs, particularly those about to re-nest using a previously used nest, often spent long periods over multiple days on or close to the nest in the prelaying period. Such pairs engaged in mutual preening of the head and neck, and touching of bills, with the partners alternating. The recipient lowered its head while having its crown, face and nape preened. This activity was accompanied by quivering of the tail and wingtips but by which individual was not recorded.

Observed copulations (*n* = 3) took place on exposed branches high in trees or on overhead utilities wires. All were preceded and followed by periods of inactivity and preening, with the members of the pair side by side but >20 cm apart. Pre-copulatory displays involved walking movements initiated by both the male and the female, one toward the other along the perch, one advancing while the other retreated. Sometimes, when still, one or both engaged briefly in what appeared to be displacement preening movements over the shoulder and back to behind the scapulars. The male eventually performed a series of 2–6 bows in front of the female. The female then adopted a crouched horizontal pose and the male mounted and stood briefly on the back of the female before copulation followed. After dismount, both the male and the female performed bobbing movements of the head before settling to preen. In one instance, the pair remained together on the branch for a further 90 minutes, during which the male again performed four bows facing the female, which did not respond. In other displays (not leading to copulation), the male (while performing the bowing display) advanced toward the female with each bow, sometimes accompanied by his growling call. The female usually retreated, but on occasions moved toward the displaying male and pecked at him, which terminated the display.

Nest-site and construction of nest

Forty-two new nests (in which one or more clutches were subsequently laid) were found. Nests were located throughout the site in 24 individual trees and shrubs of 20 species, both native and exotic. Of the individual nest-trees and shrubs used, 17 had been planted as tube stock after 1990. Multiple nests were built in bottlebrushes *Callistemon* spp., grevilleas *Grevillea* spp. (particularly the cultivar 'Honey Gem'), sheoaks *Allocasuarina* spp., paperbarks Melaleuca spp., lilly pillies *Syzygium* spp.*,* Red Kamala *Mallotus philippensis*, Booyong *Argyrodendron* spp., Tulipwood *Harpullia pendula* and acacias *Acacia* spp.

Nests were typically sited on multiple interlacing branchlets or a multi-branched horizontal (<30°) fork that provided a supporting base for the platform of twigs. These conditions were also created where a bed of leaf-litter had accumulated, where branches had been pruned and multiple shoots had subsequently developed, and in vine tangles in trees. Nests were also constructed in more substantial forks against the trunk, and in shrubs growing against a wall of a building and sheltered below the eaves. Elsewhere locally, a successful nest was constructed on the timber frame of a pergola amongst climbing vines in a house garden (T. Hayes pers. comm.). In 2008, one or both members of a pair regularly occupied an apparently disused possum drey over a 20-day period but laying was not confirmed. Nest-sites were usually well concealed by overhead foliage and placed inside a small tree or shrub. Large trees, whether open-crowned or with denser terminal foliage but bare internal and simple forking branches, were little used: only four nests were found in such trees.

Average height of a nest above the ground (*n* = 31) was 4.5 m (range 2.0–12.5 m). Only three nests were placed higher than 6.5 m. A nest located in 2011 was 1.1 m above the ground in a lilly pilly hedge only 1.5 m from the steps entering a classroom. Nests were usually well distributed across the study site, with a single active nest per tree. Two instances of closer nesting were recorded: once, a second nest was located 2.6 m above another in the same tree and, once, two nests were only 2.4 m apart in interlacing shrubs. In both instances, breeding was asynchronous to the extent that laying by the second pair took place after hatching had occurred in the first pair's nest. In 2007, Crested Pigeons nested successfully in the same tree as a pair of White-headed Pigeons. The nest of the former was 1.4 m directly above the White-headed Pigeon's nest. Again, breeding was asynchronous, with the Crested Pigeon laying during the late nestling stage of the White-headed Pigeon nest. No interactions were observed between any of the pairs involved.

Nest construction was carried out by both the male and female White-headed Pigeons, the male (identified by conspicuously whiter crown, breast and underparts than in females) collecting dead twigs from living trees or shrubs and delivering them to the nest, where the female placed them in the platform. Typically, a male selected a twig by clambering about, mostly among lower branches, before breaking off a potentially suitable stick. He then manipulated the twig in his bill, apparently to determine its suitability. After much manipulation, the twig was either discarded and the search restarted or the male flew with the selected twig to the nest-tree. Delivery to the nest-site was often accompanied by wing-flapping as the male clambered through the branches and foliage with the twig in his bill. The majority of twigs broken off were discarded at the point of selection. Males returned repeatedly to the same tree for material. One male was recorded taking eight twigs to the nest-tree in 17 minutes, another four in 29 minutes. The male stood on the sitting female's back to pass twigs to her but the actual delivery was viewed closely on too few occasions to establish whether this technique was typical. Twigs were collected from a variety of trees but eucalypts were utilised most frequently. Up to three males were noted collecting twigs concurrently from the same tree. Collecting of nest material was observed between 0730 h and 1500 h.

A small sample of nests measured *in situ* (*n* = 5) had diameters of 26–32 cm, with one multi-used nest measuring 41 cm. Re-used nests, particularly those used over more than one season, were often bulkier because of the accumulation of leaf-litter on the platform, together with additional material added at refurbishment. One example measured 14 cm in depth. Old nests re-used at the start of a new season were refurbished but those used again within the same season received minimal or no refurbishment. Nests built on strong underpinnings, such as multi-branched horizontal forks or on a substantial branch against the main trunk, were more durable, with the basic platform lasting >4 years in some instances. Few nests collapsed or were blown down throughout the duration of the study.

Nest-platforms were composed entirely of dead twigs, with longer individual sticks (especially those used in the base of the nest) protruding beyond the rim. Both simple (non-branched) and complex (multi-branched) twigs were used. A single-use nest collected for analysis 8 days after a successful fledging comprised 187 twigs, of which 93 were simple and 94 complex. Twig length was measured in a straight line (with no allowance for curvature), with the shortest twig being 11 cm and the longest 55 cm. The proportion of twigs by length was: 100–199 mm (23.5%), 200–299 mm (45.6%), 300–399 mm (21.9%), 400–499 mm (7.5%) and >500 mm (1.6%). Twigs ranged in thickness from 1.0 mm to 4.5 mm, with the majority being 1.5–2.5 mm.

Laying, clutch-size and incubation

During the interval between the completion of nest construction and laying, the nest was usually unattended for much of the day, particularly from early afternoon onwards, and always vacated overnight. A female moving to and settling on her nest around dusk was a reliable indicator that laying was imminent. Laying was confirmed when the male replaced the female the following morning and incubated throughout the day until relieved by the female again in the evening.

The clutch comprised a single egg on all occasions. Incubation commenced with laying, and the period was determined as 19–20 days (*n* = 7). After hatching, the eggshell was discarded or became crushed and wedged in the nest structure. Many shells were found on the ground below. In two instances, an adult was seen to fly from the nest carrying shell in its bill before dropping this up to 40 m away.

Incubation was shared, the male incubating by day and the female overnight. Brooding birds usually remained on the nest throughout their shift. Individual pairs exhibited relatively consistent changeover timetables. The morning changeover usually occurred 2–3 hours post-sunrise, although changeovers were observed as early as 90 minutes after sunrise during winter and, exceptionally, as late as 4 hours after sunrise in January. Most evening changeovers took place in the 45-minute period from 30 minutes before to 15 minutes after sunset. Changeovers typically occurred earlier (up to 60 minutes before sunset) on overcast or showery afternoons. The longest precisely determined daytime shift by a male was 9 hours 20 minutes. Changeovers were silent, with the arriving bird typically flying in from a perch in a nearby tree and landing elsewhere in the nest-tree before clambering through the branches to the nest. The incubating bird usually departed as the other approached the nest, flying directly away from the vicinity of the nest-tree and out of sight.

In 2005, two nests (one built in late March and the second in a nearby tree in early May) were attended by sitting adults for 23 and 21 days, respectively, but no clutches were laid. More material was added to the second nest in late June. From mid July, it was again occupied for long periods of each day and on at least some nights but without evidence of an egg being laid. From early August, I was absent for a 26-day period. On returning, I found the nest empty but still attended, until it was blown down in a storm on 4 September.

Brooding Pigeons typically sat tightly throughout incubation and the early part of the nestling period. It was unusual to find a nest unattended during the day. Brooding birds tolerated a high level of close human activity, usually remaining on the nest through maintenance of the grounds including ride-on mowers and brushcutters, pruning and lopping, and movements of cars and students. When brooding birds did flush, they usually returned to the nest when human activity ceased. Short-term disturbances resulting from tradesmen working just a few metres from nests were mostly tolerated, but during longer building projects nearby nests suffered high failure levels. Desertion, or loss by predation, was likely linked to extended disturbance.

Nestling stage and parental care

Both adults brooded their young nestling, with the daily timetable similar to that during incubation. Continuous daytime brooding ceased as early as Day 7 in summer and early autumn but extended until Day 14 or 15 in winter. Following the cessation of continuous brooding, the male was often observed on the nest for part of the day (usually during the afternoon), this behaviour being noted up to the day of fledging at some nests. Towards the end of continuous brooding (in the case of older chicks), and the ensuing interval up to fledging, the attending adult sat beside the chick. Nighttime brooding ceased as early as Day 8 in summer and early autumn but continued to Day 14 or 15 in cooler months. One female continued to return to the nest at night up to Day 19 of the nestling period during an extended period of wet weather.

Both the male and female fed the nestling immediately following changeover during the brooding period, but the frequency and intervals between feeding were not determined. When feeding a small nestling, the adult bowed its head, with the bill pointing down in front of its breast, and the nestling reached inside the adult's bill. Typically, by Day 10, begging became proactive, with the nestling 'standing up' in front of the facing adult and plunging its head into the buccal cavity from the side as the adult bobbed its head up and down. During and between bouts of feeding, the nestling flapped its wings but remained silent, with no begging calls heard before Day 14 (see below). The gut contents of three nestlings found dead comprised primarily pigeon milk (Gosper 2011). A milky-looking substance covered the bill of a chick retrieved from the ground but unable to fly that was placed back on a low branch in the natal tree (where it was raised successfully).

Fledging and post-fledging dependence

The mean fledgling period was 22 days (range 18–24 days, *n* = 23). The period of post-fledging dependence was not accurately determined. Feeding of fledglings was noted up to Day 20 post-fledging, and one fledgling remained in the vicinity of the natal tree for at least 24 days and another for 27 days post-fledging. Young Pigeons returned to the nest for parts of the day, typically for 8–12 days post-fledging, but in some instances for up to 22 days. Adults were often perched beside or close by fledglings for extended periods during the middle of the day. Fledglings (and juveniles and adults) also used old nest-platforms in both the natal and nearby trees for daytime loafing.

An instance where two large young were present on the one nest over a 2-day period was thought most likely to involve a recently fledged individual loafing on another (active) nest-platform. However, the possibility that this represented a two-egg clutch could not be ruled out, as a second nestling would have been obscured from most viewpoints and might have been overlooked during routine monitoring.

Overnight roosting was not fully investigated but one fledgling was back on the nest for the night of Day 3 post-fledging. Another spent nights perched as low as 20 cm from the ground in the natal shrub. Young birds were capable of sustained flight at or soon after fledging. One individual was seen to fly 50 m on Day 3 post-fledging.

Both adults fed the fledgling early in the post-fledging period, but frequency and intervals between feeding were not determined. Feeding was noted at various times of day, with the adults sometimes returning together and feeding the fledgling in turn. In the presence of an adult, a hungry fledgling scrambled about making squealing or whistling sounds, accompanied by flapping of wings, and sometimes short flights in pursuit of the adults to nearby trees. This food-begging call is typical of young pigeons (Baptista *et al.* 1997) and is probably that uttered by a nestling when being handled, as described by Hyem (1936).

Plumage development

In advanced embryos examined (*n* = 2) from failed nests, the unhatched chick was covered in orange-yellow down. The partial remains of a predated 5-day-old nestling had orange-yellow down on the head and neck, with emergent dark pin-feathers (up to 22 mm in length) on the wings. At Day 7, a nestling had golden-orange down on the head, neck and mantle, with the rest of the upperparts darker with unopened pin-feathers. At Day 10, down remained on the head, neck and breast, but otherwise the bird appeared blackish with pin-feathers opening and short tail-feathers visible. Chicks retained down throughout the nestling period, with fine yellowish filaments still visible, particularly on the wing-coverts, in the early days post-fledging.

At fledging, young birds were fully feathered except for some unopened white pin-feathers on the cheeks, chin and throat, with the latter sometimes still partially bare. The tail was noticeably abbreviated and the wings of juveniles also shorter than in adults (Higgins *et al.* 1996; Gosper & Gosper 2008). All fledged individuals had blackish wings, back and tail, with a blue-green gloss (iridescence) on the mantle. The crown was grey and the cheeks and throat white, but body colour (neck, breast and abdomen) was variable. In most individuals these areas were pale grey, with a pinkish-fawn blush on the breast. In a small minority [five in total, fledged in the 2001, 2003, 2006 and 2007 (2) seasons], the body was a dark grey (vent paler) with a pinkish-brown wash on the breast, and with the pure-white area of the cheeks and throat sharply demarcated from, and contrasting with, the surrounding grey (Figure 2). These individuals were distinct in appearance and bore an unexpected resemblance to the Metallic Pigeon *C. vitiensis* of South Pacific Islands, particularly *C. v. leopoldi* in Vanuatu (Baptista *et al.* 1997; DGG pers. obs.). This form of juvenile plumage appears not to have been previously described or illustrated. It is noteworthy, however, that Goodwin (1970, p. 91) predicted that the juvenile White-headed Pigeon "probably much resembles the juvenile of the very closely related White-throated [Metallic] Pigeon".

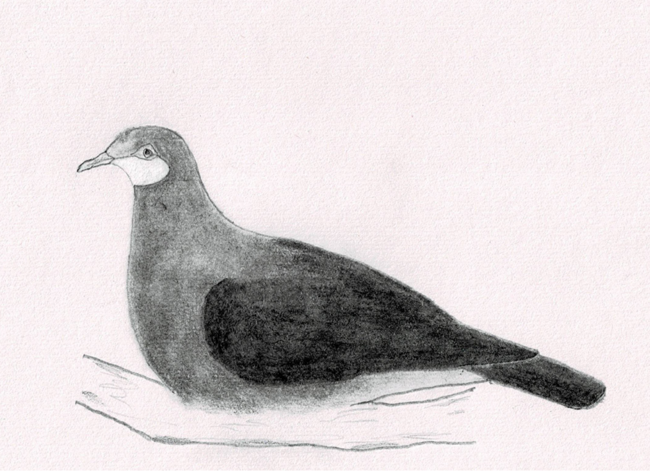

Figure 2. Juvenile White-headed Pigeon (dark form) at *c.* 30–35 days old. Drawing based on sketches and descriptions of individuals made at Goolmangar, New South Wales, on 3 July 2001 and 7 April 2007.

Nest re-use and multiple brooding

Nests were re-used in all years of the study, including those in which only one or two clutches were found. Overall, 64.7% of all clutches found were laid in previously used nests (Figure 3). Most repeat uses occurred within the same or following season but in some instances older platforms were refurbished. Some nest-platforms were used consecutively for up to four seasons. The largest number of new nests was constructed in 2007, coinciding with the beginning of the most intensive period of breeding activity (2007–2009). Over these 3 years, multiple nests were re-used, with the number of clutches laid far outnumbering the number of new nests built. In 2008, 23 of 27 clutches found were laid in previously used nests, with eight nests used more than once, and some up to four times, during the season. In six of 10 years, the first clutch found in the season was laid in an old nest from the previous season.

Nest re-use was apparently associated with both clutch replacements following egg loss, and multiple brooding. The minimum interval between clutch loss and re-laying was 8 days (n = 2). Although thought to involve the same pairs in both instances, this could not be confirmed. Following the successful fledging of young, re-laying sometimes occurred within the apparent post-fledging dependency period. At several nests, the female was again spending time on the nest from as early as Day 9 post-fledging, with laying taking place between 13 and 17 days after fledging. Some dependant young loafed on the nest during the middle of the day right up to the day before the laying of the next clutch, and subsequently close by (sometimes within 50 cm), sometimes together with one adult, while the other brooded. Females appeared to cease to feed the fledgling when re-nesting was imminent. In one instance, a female that had been noted sitting beside her fledgling, on or near the nest, in preceding days, was alone on the nest, with

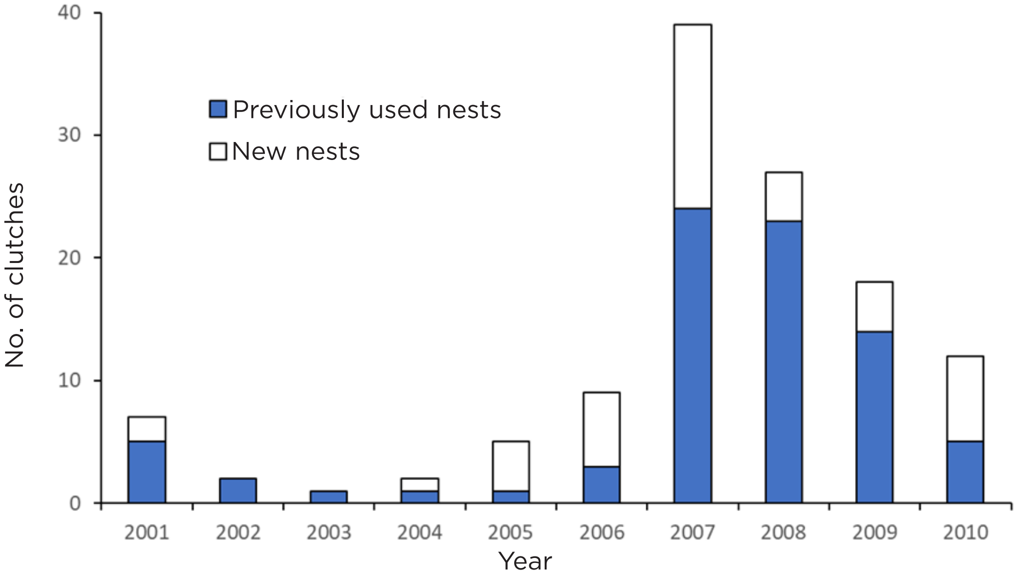

Figure 3. White-headed Pigeon clutches: number of clutches laid in newly constructed nests and previously used nests per year at Goolmangar, New South Wales, during 2001 to 2010.

the fledgling (Day 13 post-fledging) perched elsewhere in the tree. At 0815 h, the fledgling, begging vigorously, approached the sitting female but the female departed to the other side of the tree. When next checked at 1300 h, the female was again on the nest, with the fledgling elsewhere in the tree. Incubation of a new clutch commenced by Day 15, with the fledgling still present in the natal tree. Multiple brooding, inferred from the repeat use of nests and re-nesting with a dependant fledgling, occurred in most years of the study period.

Failure because of predation usually resulted in nests remaining vacant in the period immediately following. However, some were used again ≥4 months later in the same season, or in the following season(s). An exception was Nest 34/07 (used successfully earlier in the season in March and June of 2007), in which a third clutch was laid on 10 August. The nest was empty at 0720 h on 23 August (an adult was incubating on the nest at 1600 h the previous day), and the egg on the lawn 20 m away under the nearest tree, with a single hole in the shell. The next morning a pair of White-headed Pigeons was in the nest-tree at 0855 h, with the female on the nest and male close by. The pair spent the next 100 minutes in the tree, with the female on the nest most of that time. The male appeared to investigate other locations within the tree and was joined at one of these by the female for a period. Both then returned to the nest, sitting together and engaging in mutual preening. The male twice repelled another White-headed Pigeon that had entered the tree. In the following days, the pair continued to attend the nest, with the male seen collecting and delivering twigs to the female on the nest. On the morning of 2 September, many body feathers were noted on the nest, foliage and ground below, suggesting that the bird had been attacked or disturbed while on the nest. The nest was subsequently abandoned.

Several pigeon species breeding at the study site (house garden section only) re-used nests built by other species. In 2002, Bar-shouldered Doves *Geopelia humeralis* laid successful clutches in October and December in a nest twice used unsuccessfully by White-headed Pigeons earlier in the year. A nesting attempt by Bar-shouldered Doves in October 2004, again in a former White-headed Pigeon nest, was abandoned with an incomplete clutch, probably because of repeated human disturbance. Brown Cuckoo-Doves *Macropygia phasianella* bred in the study area from 2005 and Brown-capped Emerald-Doves *Chalcophaps longirostris* from 2007. In 2005, a White-headed Pigeon nest (March clutch; predated at nestling stage) was subsequently occupied by Brown Cuckoo-Doves, the latter laying in May (failed at nestling stage) and July (predated during incubation). This nest was in turn again used by White-headed Pigeons in August (predated during incubation). In following seasons, old nests of both White-headed Pigeons and Brown-capped Emerald-Doves were used by Brown Cuckoo-Doves. In 2007, a breeding attempt by Brown-capped Emerald-Doves, using a White-headed Pigeon nest built earlier in the year, failed at the nestling stage. All three species also constructed their own nests in or immediately adjacent to the site. One Brown Cuckoo-Dove nest was placed on leaf-litter, sheltered under tree-fern *Cyathea* sp. fronds, on the metal roof of a garage. The use of old nest-platforms, including those of other species of birds, has been reported to occur in many species of pigeons that build nests in trees and shrubs (Goodwin 1970).

Nest-defence

Defence strategies, other than that of sitting closely during the incubation and early nestling stages, were not evident. The use of explosive wing-claps by White-headed Pigeons to deter a potential predator was observed in Nightcap National Park on 12 December 1993. On hearing what sounded like periodic loud claps, I located two Pied Currawongs *Strepera graculina* moving about just below the canopy. They were circling and peering at a White-headed Pigeon on a nest, and the brooding bird was responding with periodic explosive wing-claps. The Pigeon continued to sit tightly and eventually the Currawongs departed.The use of wing-claps was recorded once during the present study, but the circumstances and function were unclear. In this instance, I was alerted by the alarm calls of Noisy Miners, followed by 4–5 loud wing-claps. I arrived to see two White-headed Pigeons burst out of the foliage and, as I approached the clump of trees containing the nest, two Pied Currawongs exited from the opposite side. The nest, which had earlier in the day contained a large nestling, was empty. A brief search for the nestling was inconclusive. Hyem (1936) stated that a White-headed Pigeon flushed from a nest will land some distance away and flap its wings vigorously, and suggested that this behaviour serves to attract attention away from the nest. Distraction displays involving violent wing-flapping, is said to be common in pigeons of many species when flushed from the nest (Goodwin 1970).

Intra- and interspecific interactions

Intraspecific aggression was evident during periods when there was apparent competition for nest-sites involving multiple pairs of White-headed Pigeons in close proximity but was rarely noted outside these times. The ’growl’ call was most often heard during these interactions, possibly given by the male, in the presence of an intruder. However, its function remained unclear. Most interactions were brief and involved pairs engaged in nest prospecting where a second male, or pair, entered an already occupied tree. The first male usually responded by flying towards the intruder and causing it to take flight. In an instance of more extended aggression, a male, returning to its nest for the morning changeover, chased another male that had perched on wires above the nest-tree. The two subsequently landed close together and facing, further along the wire, whereupon a brief alternating pecking exchange directed at the head followed. Both flew again and the sequence was repeated until the ‘intruder’ left. The first male then moved to the nest. Occasionally, a male drove off another male when both were collecting nest material from the same tree.

A female was seen to engage in similar behaviour towards another female when the latter individual landed on a powerline ~8 m from a pair that had been seen to copulate *c.* 5 minutes earlier. Both the pair and the recently arrived female then worked their way along the wire towards each other before the females engaged in a short pecking exchange. All three subsequently settled and preened. In all instances, physical contact, if any, appeared light.

Table 2. Breeding success (young fledged from clutches where outcome was known) of White-headed Pigeons at Goolmangar, New South Wales, during 2001 to 2010.

Year	*No. clutches*	*Failed (incubation)*	*Failed (nestling)*	*Outcomes*		
				Unknown	*Fledged*	*Success (%)*
2001	7	3	2	1	1	16.7
2002	2	2	0	0	0	0
2003	1	0	0	0	1	100
2004	2	1	0	0	1	50
2005	5	3	1	0	1*	20
2006	9	2	1	1	5	62.5
2007	39	18	2	1	18	47.4
2008	27	5	4	8	10	52.6
2009	18	9	3	6	0	0
2010	12	6	2	1	3	27.3
Total	**122**	**49**	**15**	**18**	**40**	**38.5**

*Predated soon after fledging

Few interspecific interactions were seen (but see also Causes of nesting failure). Grey Butcherbirds, particularly immatures, made occasional brief passes at adult White-headed Pigeons. When mobbed by Noisy Miners, fledgling White-headed Pigeons responded by crouching, spreading the tail and holding the wings up in 'angel' position.

Breeding success

Forty young White-headed Pigeons fledged from 104 nests (where the outcome was known), giving an overall success rate of eggs laid of 38.5%. Young fledged from eggs laid in all months from January to August. The proportion of successful clutches was highest from April to July, peaking in May–June (>70%). Breeding success fluctuated widely between years (Table 2). There was no apparent difference between the success rates of clutches laid in new nests and those laid in previously used nests, with 15 young fledging from 39 new nests and 25 from 65 clutches in re-used nests. Nest position appeared unrelated to breeding success, and there was no consistency in outcomes at individual nests when used more than once.

Causes of nesting failure

Of 64 nests that were known to have failed, 49 were lost during incubation and 15 during the nestling stage (Table 2).

Failed clutches were categorised as follows (number of clutches in parentheses):

1. egg infertile (1)
2. clutch deserted (2)
3. egg/small nestling fallen from nest (apparently dislodged by adult, winds and/or nest collapse) (6)
4. nest found empty with fragments of shell below (indeterminate) (3)
5. egg predated (shell remains usually on ground with characteristics indicative of attack; body feathers on/around nine nests was deemed indicative of predation while an adult was on the nest) (28)
6. nestling predated (remains of partly eaten nestling on ground; nestling pin-feathers strewn on branches and ground below nest; at one nest, many body feathers on/around nest were indicative of predation while an adult was on the nest) (9)
7. nest contents disappeared during incubation/early nestling stage (unexplained) (15).

Thirty-seven failures (57.8%) were attributed to predation. It is probable that predation was involved in an unknown number of a further 15 nests from which the egg or nestling disappeared. Therefore, the proportion of failures because of predation was potentially higher (>80%).

No acts of predation were witnessed. However, physical evidence from nest-sites, incidental observations of known nest-predators at pigeon nests and a report from a local resident implicate a range of taxa. The majority of instances of suspected predation were discovered during the morning round of monitoring, indicating that attacks most often occurred between late afternoon and early morning (1630–0730 h). At one nest in which laying was imminent, the sound of wings flapping was noted at *c.* 0200 h. A mass of body feathers was found on the nest-platform during daylight of that morning, and no further activity occurred at the site.

In the 2005 season, following the abandonment of a nest (laying imminent but not confirmed), clumps of white hair from a Cat *Felis catus* were found on nest twigs and on two lower branches in the shrub. In the preceding 30 days, two young White-headed Pigeons, one a fledgling (Day 3) and the other a nestling, had been found dead on the ground. Both had parts eaten, with the bones of one wing of the fledgling chewed through. In the 2007 and 2008 seasons, a further three partially eaten nestlings, each appearing to have been chewed, were found on the ground under nest-trees. In one, about a third of the body (including the legs and a wing) of a 5-day-old nestling was eaten. As in the earlier deaths, the body cavity had been exposed and entrails uneaten. While suggestive of predation by Cats, evidence was inconclusive.

On 5 April 2007 at 1710 h, a 1.7-m-long Carpet Python *Morelia spilota* was coiled in a shrub ~1 m directly above White-headed Pigeon nest N5/07, which was empty but with a few feathers scattered in and below the nest structure. Incubation at this nest had occurred for at least 6 days, and the female Pigeon was on the nest at 0800 h that day. When I returned at 1720 h, a female Pigeon was in the outer branches <2 m away at nest level, peering at the nest and python. The female remained in this position for almost 15 minutes, during which she repeatedly raised her left wing without fully opening it. She then left for a nearby tree. A reported instance of predation by a Carpet Python locally (S. Jones pers. comm.) involving either a brooding adult or possibly a recent fledgling took place toward dusk on 1 May 2008 at a nest in a home garden; the observers were alerted by the sound of wings flapping, and found the snake coiled around the pigeon, which it subsequently swallowed.

Shells of freshly predated eggs were usually found on the ground within 2 m of a nest, but sometimes under an adjacent tree up to 20 m away. Characteristics of most shells fell into one of two categories, both clearly different from the appearance of shells from successfully hatched eggs, which were typically neatly cracked and often found with one half of the shell inside the other. Many featured a single puncture-like opening (15 x 15 to 26 x 18 mm) with ragged edges, suggestive of being pecked open. A few had the appearance of being crushed, with large pieces of shell being fractured all over and with the edges bent inward, but held together by the shell membrane.

A feature of 14 failed White-headed Pigeon nests (most during incubation), and of at least one Crested Pigeon nest, was the presence of a mass of pigeon body feathers left on and under the nest. This was taken as indicative of the brooding adult having been attacked or startled in such a way as to cause it to shed feathers in its haste to escape. No injured adults were found, suggesting that most escaped, although the frequency of brooding birds being taken by Carpet Pythons was unknown. Disturbance in this way was probably responsible for some instances of dislodgement of nest contents (e.g. broken egg below, with contents uneaten) and desertions.

Grey Butcherbirds, Australian Magpies, Torresian Crows and Pied Currawongs, all potential predators (cf. Higgins *et al*. 2006), were disturbed when apparently investigating pigeon nests or attacking brooding birds. In four instances, all involving Crows or Currawongs at White-headed Pigeon nests, evidence of predation was found, either immediately after the disturbance or in the days following. Two others involved attacks by a Grey Butcherbird and an Australian Magpie, respectively, on brooding Crested Pigeons. In the first, the attacker was successfully repelled by the Crested Pigeon, which pursued the Butcherbird through the foliage as it circled the nest, until it retreated. In the second, the Pigeon was driven from the nest by the attacker, which then hopped onto the nest briefly before flying off. An immediate check revealed a warm, broken egg below. The outcome of the remaining instances was inconclusive. One involved a Butcherbird at an unattended White-headed Pigeon nest containing an egg that subsequently disappeared. In the second, a large White-headed Pigeon nestling could not be located following a disturbance involving Currawongs in the vicinity of the nest (see Nest defence above).

Discussion

The results of this study of a wild population of the White-headed Pigeon are consistent with the limited published accounts of its life history, derived mainly from captive breeding, and are typical of pigeons generally (e.g. Goodwin 1970; Westmoreland *et al.* 1986; Higgins & Davies 1996).

Active White-headed Pigeon nests have been reported from all months of the year (Higgins & Davies 1996; Cooper *et al*. 2014). Although standard references (Beruldsen 1980; Frith 1982; Higgins & Davies 1996; Cooper *et al.* 2014; Forshaw & Cooper 2015) list the main nesting period as being between August and January, which contrasts with the pattern reported here, the species is clearly able to breed at any time of year if conditions are suitable. Such variation is likely linked to when food is most abundant locally, food availability being the dominant factor regulating breeding (Frith 1982; Baptista *et al.* 1997). At Goolmangar, parallel studies of diet (Gosper & Gosper 2008; Gosper 2011) and the correlation between breeding season and fruiting of Camphor Laurel confirm that the annual breeding cycle of White-headed Pigeons locally is dependent on the Camphor Laurel fruit crop, and its length is linked to the duration of fruiting. Camphor Laurel fruits ripened from late February and typically remained abundant at least until July. However, the duration of the crop (when trees carried ripe fruit) varied greatly between years, ranging from four to almost eight months. In some years, fruiting had finished by mid June (2009) whereas in 2008 some trees were still carrying fruit on 11 October. In 1994, analyses of faeces of Australasian Figbird nestlings showed that ripe Camphor Laurel fruits were being fed to the young from as early as 23 February, with fruit still present on trees, and being consumed by Figbirds, at least to 7 October in that year (unpubl. data).

White-headed Pigeons in the partially wooded landscape of the present study nested in relatively exposed locations, used ornamental trees and shrubs, and pairs tolerated close intraspecific nesting and proximity of human traffic. Nests were built in trees and shrubs bordering playing fields and lawns, along fence-lines and against buildings, and in isolated feature trees. Although the nest itself was usually at least partially concealed, adult birds approached and exited the nest-tree by direct flight. Crome & Shields (1992) stated that the White-headed Pigeon is a solitary breeder in rainforests, although there appear to be no published measures of nesting density. In the present study, multiple pairs bred concurrently within the 1.7-ha site in seven of 10 years, with nesting density peaking at 5.9 pairs per hectare in July 2007. Close nesting has been achieved in aviculture with the successful breeding of four pairs in the same aviary (Frith & Rushton 1982).

Contrary to Frith (1982), aerial display flights by male White-headed Pigeons, said to be performed over forest and sometimes when flying across open country to and from feeding places, were not observed. The reason for this, and whether the absence of this behaviour is linked to the Pigeon's adaptation to open habitats, is unclear.

White-headed Pigeons probably form monogamous pair-bonds, at least for the duration of a season, as is typical in the Columbidae (Baptista *et al.* 1997). As evidenced in the present study, multiple pairs may nest in close proximity in 'islands' of trees and shrubs in open country where there is an abundant seasonal food supply. As most White-headed Pigeons dispersed or left the immediate area following breeding and/or when Camphor Laurel fruit and seed were exhausted, and reappeared the next year when fruiting commenced again, Pigeons moving to these sites to breed may already be paired. Further investigation, involving marked birds, is needed to determine the duration of pair-bonds, and to establish whether individual pairs return to a site to breed over multiple seasons, and whether they re-occupy the same nest-sites.

Predation was the largest single factor influencing the outcome of breeding attempts. Fluctuations in breeding success between years, together with physical evidence of predation found at nests, suggest that a suite of taxa was involved (cf. Guppy *et al.* 2014) but the identification and impact of individual predator species are unknown. Although not directly implicated, other potential nest-predators found at the study site were rats *Rattus* spp., Mountain Brushtail Possum *Trichosurus caninus* and Lace Monitor *Varanus varius.* The first two were regularly present but the third was infrequently recorded in or close to the study site and, although once observed preying on Australasian Figbird nestlings (unpubl. data), was thought not to be a significant predator. Rats are well known as nest-predators but the potential role of the larger possums in the depredation of pigeon nests at this site should not be overlooked. The Common Brushtail Possum *T. vulpecula* has been implicated in the predation of birds' eggs and nestlings (e.g. Garnett *et al.* 1999; Matthews *et al.* 1999; Zanette 2002; Olsen & Trost 2009), although it is unclear whether it is a significant nest-predator (Fulton 2018). In New Zealand, the introduced Common Brushtail Possum has been identified as an important predator of eggs and chicks (Brown *et al.* 1993; Moorhouse *et al.* 2003). Furthermore, there appear to be similarities (overall fracturing of the shell, which remained held together as large pieces by the membrane) between the shell characteristics of eggs consumed by possums, as described by Brown *et al*. (1996), and the remains of some predated eggs found in the present study (see Causes of nesting failure above).

Multiple brooding and nest re-use have been reported in many pigeon species, including Australian species (Crome 1975; Frith 1982; Gosper 1996). Although White-headed Pigeons in the present study were generally not recognisable individually, multiple brooding was strongly inferred from the pattern of extended breeding, involving the high proportion of clutches laid in previously used nests, the multiple re-use of individual nests and timing of same, and apparent re-nesting with dependant fledgling. Such a suite of reproductive traits, found in many pigeons (Westmoreland *et al.* 1986), enables rapid breeding while there is abundant food. These attributes, in conjunction with other flexible behaviours pertaining to the ability to adapt to open and altered habitats, to exploit new food sources and tolerate human presence (Gosper 2011), have contributed to the White-headed Pigeon's successful occupation of modified landscapes in northern New South Wales.

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