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Observations of the use of a nest box by Peregrine Falcons *Falco peregrinus macropus*: Breeding behaviour and parental contribution

Cilla Kinross

Charles Sturt University, Orange, PO 883, Orange, NSW 2800, Australia.
Email: ckinross@csu.edu.au

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Webcams have become an increasingly popular way to learn about birds of prey at natural nests and nest boxes. However, there have been few in-depth published studies of behaviour emanating from these initiatives, despite close observation and around-the-clock data collection capabilities. In Orange, New South Wales, observations have been made of the use of a nest box by Peregrine Falcons, *Falco peregrinus macropus*, between 2008 and 2022, with detailed observations during the breeding seasons of 2012–2017 and 2020. A pair nested annually over the 15 years, during which the male was replaced twice and the female once. There was a hatching success rate of 62%; a fledging success rate based on eggs laid of 57%, and on nestlings hatched of 92%; an overall 87% nest success rate (at least one fledgling produced per attempt); and a mean of 1.7 young fledged per clutch started. The mean clutch size was 2.8. Most eggs were laid in the morning and early afternoon and the mean laying interval was 61 hours. The mean incubation period was 35 days. The female undertook the majority of the incubation, spending up to 54 minutes per hour covering the eggs, depending on the time since laying. Time spent incubating by males varied considerably with individuals. Very little brooding or feeding of nestlings was undertaken by the males. When the nestlings were small, the male did almost all of the hunting but passed his prey to the female to feed the nestlings. Ambient temperature did not affect breeding activities. Lengths of time for incubation coverage and brooding were within normal ranges from other studies of this species. However, the presence of juveniles near the nest was often longer than usually observed: commonly 69–177 days, but with one case of 232 days. A stay of this length is unusual but not unprecedented.

Keywords: Peregrine Falcon; *Falco peregrinus*; webcams; nest boxes; nesting success rates

INTRODUCTION

The Peregrine Falcon *Falco peregrinus* (hereafter referred to as ‘peregrine’) is a global species found on all continents except Antarctica (White *et al.* 2013) with just one resident subspecies, *macropus,* now recognised in Australia (Debus 2022).

There is a large body of research into peregrine breeding behaviour globally, well summarised in books dedicated to falcons (Sale 2016) and peregrines in particular (Ratcliffe 1980; Stirling-Aird 2012; White *et al.* 2013; Sale and Watson 2022). In Australia, of note is the new book on falcons by Debus (2022), a PhD thesis by Hurley (2013), a comprehensive book on raptor ecology by Olsen (1995), and other breeding information is available, e.g. Pruett-Jones *et al*. (1980); Marchant and Higgins (and sources therein) (1993) and Olsen (2014). There is also an excellent photographic description (Hollands 2021) as well as diaries (Tytherleigh 2016) and detailed observations (e.g. Turner *et al.* 1993), so there are some benchmarks against which this study can be measured.

Despite the degree of knowledge already gathered, there are still gaps in our understanding of breeding behaviour. For example, there is little consensus about parental sharing of duties. It is reported that incubation is not shared equally between sexes, with the proportion of male incubation time varying from 12 to 63% of the daylight hours (Sale 2016). In just one region in Alaska, the sharing of parental duties varied considerably between pairs observed (Palmer *et al.* 2001). In Australia, there are few studies on incubation effort by each peregrine sex (Marchant and Higgins 1993), with some exceptions, such as the work by Turner *et al.* (1993) and Olsen and Stevenson (1996).

Most of the literature relates to observations of peregrines in the wild using natural nest sites. Olsen and Olsen (1988) observed that peregrines in Australia preferred nesting on cliffs (81%), with only 11% using stick nests and 8% in hollow trees, and only very rarely using buildings. This is changing, however. Peregrines worldwide are increasingly breeding on human structures such as tall buildings, grain silos, quarries, power poles and mine shafts (White *et al.* 2013). This phenomenon also occurs in Australia, with increasing numbers of nest sites occurring on similar structures (Emison *et al.* 1997; Hurley 2013), including one on a water tower (Hurley unpublished data). Hurley (2013) observed that many of these sites, although attractive to peregrines for breeding, suffered water damage, resulting in poor egg hatch rates.

Nest boxes are growing in popularity but have been used mainly for conservation rather than research (Pagel *et al.* 2018; Macak 2020). Peregrine breeding is adversely affected by the weather, particularly rain (Olsen and Olsen 1989) so the use of nest boxes makes sense in this respect. Hurley’s research in Victoria showed that poorly drained or sheltered sites like quarries and buildings could be significantly improved by installation of nest boxes (Hurley 2013). In another Victorian study in 2010 (Booth *et al.* 2014), six nest boxes were installed, one in a live tree and five on poles in the Gippsland Plains. The ones on poles were unsuccessful, except for one used by a Nankeen Kestrel *Falco cenchroides*, but the one in a live tree was successful.

The only other peregrine nest box in Australia regularly monitored is the one managed by Victor Hurley of the Victoria Peregrine Project in central Melbourne. This nest has successfully raised peregrines since 1992 (Olsen 1995). The one in this present study differs from the Melbourne one, the latter being a gravel-filled wooden tray 100 mm deep, protected on two sides by building walls, whereas the box in Orange has three walls 750 mm high and a complete roof.

The addition of webcams to nest boxes provides education and enjoyment to many. However, to date, webcams have yet to be widely used to collect data for detailed research. They can provide a close and potentially more accurate tool for observation of activities and diet 24 hours a day, 365 days a year, with modest expense and less need for potentially intrusive and uncomfortable field observation, particularly at night (Cogley 1995). They are particularly useful for studies that require exact dates and times of activities such as egg-laying, first feeds or pair-bonding (Dixon 2021), and can help eliminate gaps in the observation periods that could lead to the loss of essential data. Having that close view also makes identification of the sexes, and thus the comparison of male and female behaviour, much easier and more reliable.

So, although there are now many webcams covering the breeding of peregrines worldwide, published studies using webcams and photography for raptor behavioural research are still rare, although Dixon (2021) provides a useful summary of information from 28 webcams. Of particular interest to this study was one from Albi, France, where a webcam provided detailed information on breeding behaviour from 2008–2012, 24 hours a day (Maurel and Waleau 2010) - similar to what is presented in this study.

The aim of this study was to increase the understanding of peregrine breeding biology in a nest box site in the rural-urban fringe near Orange, New South Wales. In particular, this paper:

- provides key dates of breeding activities 2008–2022
- describes in detail breeding activities in 2012–2017 and 2020 and, in particular,
- reports on the parental effort by male, female and individual peregrines in respect of incubation, brooding and feeding nestling(s)
- compares activities in different periods: years, months or hours of the day as appropriate
- assesses whether ambient temperature in the nest locality has any effect on breeding activities.

BACKGROUND AND STUDY AREA

In 2006, a pair of peregrines was regularly observed roosting on a 35 m water tower at Charles Sturt University, 6 km north of Orange, New South Wales (longitude: 149º 07' 04"; latitude: 33⁰ 14' 50"). The tower, constructed in 1970, still provides water to the university. In 2007, a nest box and two webcams were installed, and the box was used almost immediately to pluck and eat prey and to roost. The birds started to breed in 2008, and a larger model nest box replaced the original a few years later. The nest box is inside and near the top of the water tower (Fig. 1). There is more history and other information about the FalconCam Project on: https://science-health.csu.edu.au/falconcam.

Figure 1. *View of the tower and entrance to the nest box. Inset shows M3 (left) with starling prey and F2 standing over first egg.*
Source: screenshot from webcam 26/08/2022.

The tower is at 900 m a.s.l. in Orange in the Central Tablelands, which, according to the Bureau of Meteorology (2022), has a mean maximum temperature of 18.1º with cold winters (mean minima 2.6, 0.8 and 2.1º C for June, July and August, respectively) usually with a few days of snow, and warm summers (mean maxima of 22.9, 25.3 and 26.3º C in December, January and February respectively). Average rainfall is 870 mm per year relatively evenly spread throughout the year, although thunderstorms are more likely during summer. Conditions during the period of study were drier and warmer than average, particularly during the years 2017–2019. Rainfall in 2019 was only 468 mm with a mean maximum temperature of 20.6. Conversely, rainfall in 2016 was well above average (1345 mm), causing widespread flooding in the district.

The university campus contains a 300 ha farm and there are suburbs within 2 km of the site, so it could be described as rural-urban fringe. The farm has approximately 5% mature tree cover and a few hectares of shelterbelt and creek restoration plantings of mostly local native plants, varying from those 50 years old to those planted as recently as 2023. There is a small remnant of *Eucalyptus dives* woodland below the tower that includes some native shrub planting. In addition, there is a stand of mature live and dead Yellow Box *Eucalyptus melliodora* trees in a paddock about 300 m away. The peregrines roost in both these locations, as well as on the tower itself and occasionally in other sites around the university farm.

Although other unpaired peregrines are occasionally seen, there are few other known breeding pairs of peregrines in the region – one nest site is over 10 km away, and another over 20 km. These are both sites on cliffs in natural bushland. The Orange district lacks suitable peregrine nest sites, and the local peregrines have not been observed nesting in trees.

METHODS

Methods and materials

The box is made of marine ply with a layer of washed river or pea gravel in the base, where the birds can make their scrape (nest). The box is 1.2 m wide, 0.75 m high and 0.65 m deep. It is 35 m from the ground. It can be accessed by a narrow, metal stairway inside the tower, then a ladder.

The two initial cameras were upgraded in 2014 to high definition, with a third installed in 2021, all pointing to the box's nest or ledge. All had sound. This upgrade improved the identification of prey but did not affect the collection of breeding behaviour data. Details of brands and models are available from the author.

Between 2008 and 2012, only basic reproductive events were recorded. These included the dates of egg-laying, egg hatching and fledging. The information was extracted by the author directly from the livestream video. In 2012, systematic data collection began 24 hours a day, 365 days a year as the cameras all had infra-red function at night. Data collection is based on the method used by Maurel and Waleau (2010) and is described below.

The activities monitored during the breeding season included incubation, standing over the egg(s) (not or barely touching), brooding nestling(s), standing over nestling(s) (not or barely touching) and feeding nestling(s). If both adult birds were in the box simultaneously, the activities of both birds were recorded. Other activities, such as pair-bonding, eating, and preparing the scrape, were also recorded but will be reported in a later paper.

Sexing of fledglings was based on comparison with the adults at the time of fledging – the females being larger (Marchant and Higgins 1993). Different individuals were recognised by their distinctive plumages after comparing videos and screenshots, as well as behaviour. Strange falcons arriving in the box lacked the confidence of the residents. They were much more hesitant and curious, carefully inspecting the box if they ventured inside.

The presence of fledged juveniles were noted when they returned to the nest box, but they were not monitored systematically in the field. Some observations were made most days in an area with a radius of approximately 500 m around the water tower and this included checking known roost trees.

Ambient daily temperature data (minimum, maximum and mean) for Orange were obtained from the Bureau of Meteorology (2022).

Surveillance software (Milestone XProtect©) was used to collect the data from 2012–2017. This program recorded the live footage and produced a recording that showed when activity had taken place. The data were extracted daily from these recordings by the author and a few trained volunteers on the rare occasions when the author was away. There was a gap in recording from January 2018 to August 2020 when this equipment failed. The live stream continued to function, so basic information was still collected. In August 2020, a team of volunteers was formed from those who followed the peregrine family's activities on the Internet. This team logged the start and finish of activities on the 'chat' function. These times were then checked and recorded by the author. This was a continuous process, 24 hours a day, 365 days a year as there were many international helpers.

The data were summed into hourly totals – each row representing one hour of activities and absences adding to 60 minutes for each individual bird. Data were then extracted as needed i.e. incubation and brooding data only included the dates when eggs or chicks were present respectively. Most of the analyses used the hourly data i.e. one row per hour, but for 'feeding nestlings' the data were converted to one row per day (daylight hours only) as these activities occurred less frequently than the others. For analysis needing daylight hours only, these were selected as 0500–1900 h. Where appropriate, the day was also divided into six time blocks: 0000–0400 h, 0400–0800 h, 0800–1200 h, 1200–1600 h, 1600–2000 h, 2000–2400 h, based on Palmer (2001), so all dawns were covered by early morning 0400–0800 h, and dusks were covered by the period 1600–2000 h.

The citizen science proved to be a more reliable method of collecting data than the surveillance equipment, which broke down occasionally, leaving gaps in the data. There were no gaps once citizen scientists were used. Average data capture from first egg to last fledge (24 hours a day) was as follows: 2012: 95%; 2013: 88%; 2014: 100%; 2015: 100%; 2016: 95%; 2017: 96%; and 2020: 100%.

Data analysis

Data were analysed using R©, with graphs prepared in Excel©. As there was only one nest site, analysis was, for the most part, restricted to graphical and quantitative descriptive statistics. All errors reported are standard deviations. Changes in incubation and brooding behaviour were analysed in relation to the number of days or weeks after the first egg was laid or hatched. After testing for normality, a t-test (assuming equal variances) was used to test for differences between laying intervals. Spearman's Rank correlation coefficient was used to test for relationships between breeding activities and temperature variables.

In 2014, the eggshell thickness of broken eggs from the 2013 season (an unusual season when all eggs broke) was measured. As the eggs were broken it was not possible to use the more conventional method of estimating thickness using weight, divided by length times breadth (Olsen *et al.* 1993; Ratcliffe 1980). Instead, the fragments were measured directly as per Falk *et al.* (2006) but using Vernier Calipers (20 samples). Fragments were also sent to a laboratory to be tested for the presence of pesticide residue.

RESULTS

There were a few changes to the individual peregrines studied over the 15 years. The original peregrine pair in 2008 (F1 and M1) was replaced in 2015 (F2 and M2), and a third male (M3) replaced the second in 2016. The offspring in that year were sired by M2 but raised by M3. There have been no changes since then, although several visits by unknown falcons have occurred.

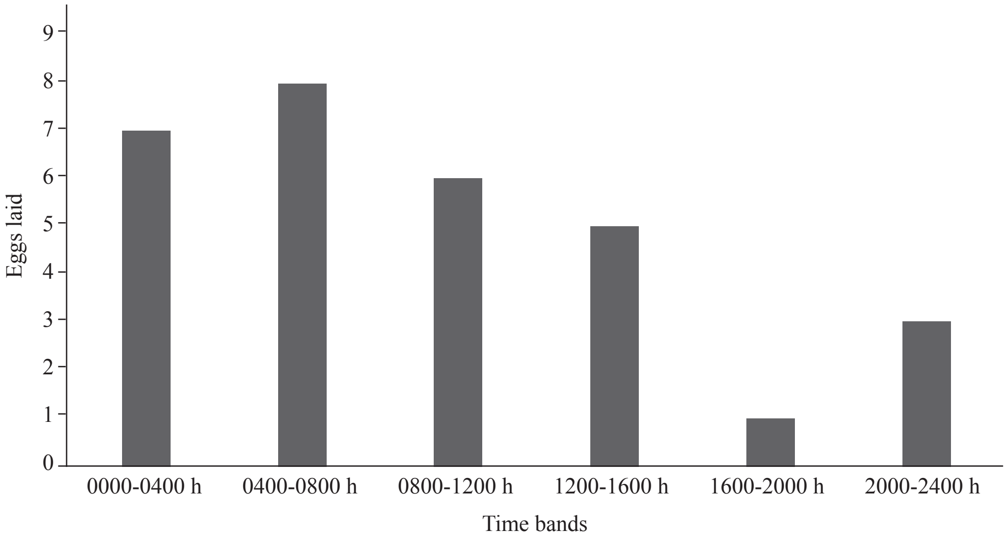

Figure 2. *Counts of eggs (n=30) laid in different periods of the day in the years 2012–17 and 2020.*

Egg-laying

Between 2008 and 2022, the clutch size was three in all years except 2008 (one) and 2012 (two), resulting in 42 eggs over the 15 years and a mean clutch size of 2.8 ± 0.6. The date of the first egg being laid varied from 17 August to 5 September, and 71% were laid between 26 and 31 August. The extremely late date of 23 October in 2008 has been treated as an outlier.

From 2012 to 2022 (when times of day were able to be recorded), the mean laying interval between the first and second eggs was 61.36 hours (n=11; range 58–75) and between the second and third eggs (n=9; range 46–71) was 60.56 hours. There was no significant difference between these means (t-test, t=0.26; p=0.80).

Eggs were laid at all hours, although most were laid in the morning and early afternoon (Fig. 2), with a marked drop in the late afternoon. Not all times of egg-laying were recorded.

Incubation

Incubation was split into two activities: actual ‘incubation’, where the adult was covering and touching the eggs and ‘standing over eggs’, where the adult was not (or was barely) touching the eggs. This section refers to actual incubation.

Between 2008 and 2022, the mean number of days between the first egg being laid and the first egg being hatched was 37.3 ±1.4. (n=14; range 36–40 days). Incubation generally started when the second egg was laid, although in some years, almost immediately after the first, but was not accurately recorded prior to 2012. From that year until 2022, the mean incubation duration until the first hatch was 35 ± 1.5 (n=10; 33–38 days). The eggs were not marked, so it was not possible to give the exact number of days from laying until hatching for each egg.

In the years 2012–17 and 2020, the time the parents spent incubating (incubation constancy) varied according to the length of time since the laying of the first egg. During the first week, female incubation over 24 hours gradually increased from a range of 42.53 ± 39.10% to 84.88 ± 21.98% over five days. It then fluctuated very little between 79.87 ± 32.13% and 89.58 ± 19.05% until day 37, after which it tapered to zero on day 41.

Male incubation followed a similar pattern at a much lower constancy, increasing from 1.42 ± 4.68% on day one to 7.47 ± 19.10% on day four, after which it fluctuated between 6.92 ± 17.80% and 17.30 ± 32.17% and then, as for the female incubation, it tapered from day 37 to zero on day 41.

Incubation rates during the day versus the night varied considerably between males and females, with males rarely incubating between the hours of 1900–0500. During the day, the male contribution was generally less than half the rate of females, but differences due to time of day were not evident.

Variation in individual parental incubation effort is illustrated in Fig. 3. The mean for the male during daylight hours was 18.98%, and the female 73.75%. The male share of incubation from 2012–2014 appears to be considerably lower than in 2015–2016, with a concomitant increase in effort by the female. This graph shows that the difference between years for female incubation is not high, but that the individual male contribution was quite variable, with male M1 doing much less incubation than either M2 or M3 (Fig. 4).

Standing over eggs

There was a small amount of time spent by each bird (mainly the female) standing over the egg (not or barely touching), either prior to actual incubation or at other times. The time spent by the female each year (2012–2017 and 2020) ranged from 0.82 ± 2.25% to 3.82 ± 4.67%, and by males, from 0 (in 2014) to 0.9 ± 2.22%. As the standard deviations were extremely high and time spent in this activity was relatively low overall, especially by males, it was not pursued further, apart from reporting on whether it was affected by temperature (see below).

Hatching

The number of hatches ranged from zero (in 2013, when all eggs broke) to three in 2011, 2015 and 2016 (the latter two years representing the ones after F2 had taken over the nest

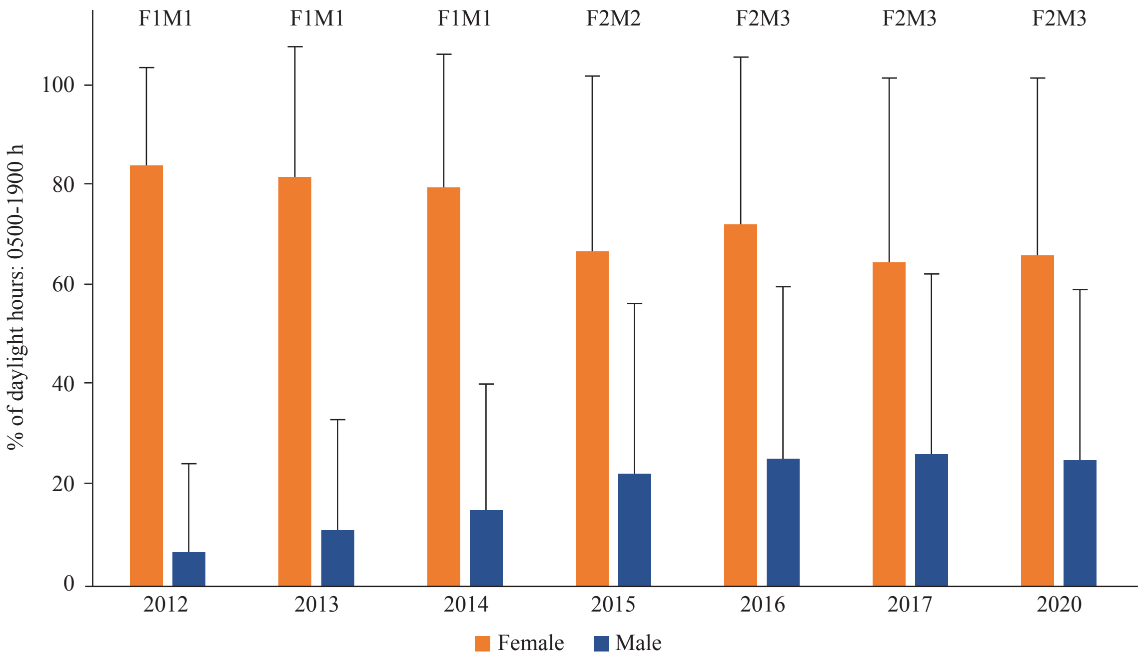

Figure 3. *Average incubation constancy of male and female peregrines during daylight hours (0500–1900 h) by year 2012–17 and 2020. Each year there were three eggs except for 2012 (two).*

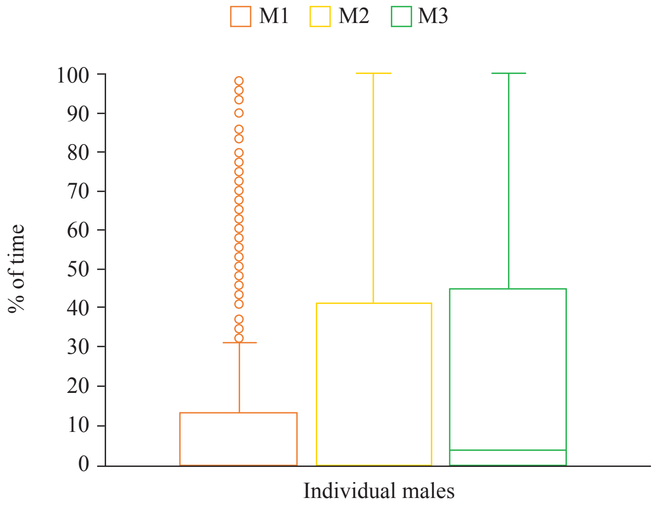

Figure 4. *Distribution of percentage of incubation time during daylight hours (0500–1900 h) by three male peregrines 2012–17 and 2020. The median is the lower horizontal bar, only showing on M3 as other medians are zero. The box (the interquartile range) contains 50% of the data. The 'whisker' extends to the furthest data point in each wing that is within 1.5 times the interquartile range. The dots indicate outliers.*

box). The results from the pesticide residue tests on the broken eggs from 2013 were inconclusive. Residue from an unspecified organochlorine pesticide was detected, but not of sufficient quantity to determine that it had caused the breakage. Eggshell thickness was estimated at 0.31 mm.

In the other years, the eggs did not hatch either because they were infertile (after inspection through candling) or not fully developed. In one year (2012), the male flew off with an egg stuck to his feathers after incubation. Over the 15 years, the hatch rate was 26 hatched from 42 eggs (1.7 young ± 0.9 per annum; 62% hatch rate overall).

The hours (when known) between the hatching of the first and second eggs ranged from 1 to 108 (n=8), with a mean of 27.1 ± 36.1 and between the second and third eggs, from 12 to 49 (n=3), with a mean of 35.0 ± 20.1. The sample was too small and variable to provide robust figures but does highlight the unpredictability of this duration.

Brooding

This activity was divided into true 'brooding', where the bird was covering and touching the nestling(s) and 'standing over nestling(s)', where the bird covered the nestling(s) but was not (or was barely) touching. These analyses refer to the years 2012–17 and 2020.

After hatching, true brooding constancy decreased daily, excluding the first two or three days when eggs were often still present. The difference between male and female parental effort here was stark. During the first week, on average, the females brooded for 70.27 ± 35.57% of the time compared to the males' 0.30 ± 1.90%, and the females 'stood over the nestling(s)' for 7.22 ± 14.82% of the time *versus* the males' 0.22 ± 1.08%. The combined mean time percentages and standard deviations of the females' brooding and standing over nestlings in the weeks after hatching are shown in Fig. 5.

In 2016 no brooding was undertaken by the male (M3). M2 went missing just as the eggs were hatching. F2 went three days without food before she finally went hunting. Over the next few days, an adult female and a subadult male presented, and both were chased off. After a week, M3 appeared, and his first act was to steal the nestlings' food. He was accepted, however, and provided for the family for the season, despite avoiding contact with the nestlings until they were ready to fledge. He remained at the site and took up full-time parental care in the following years.

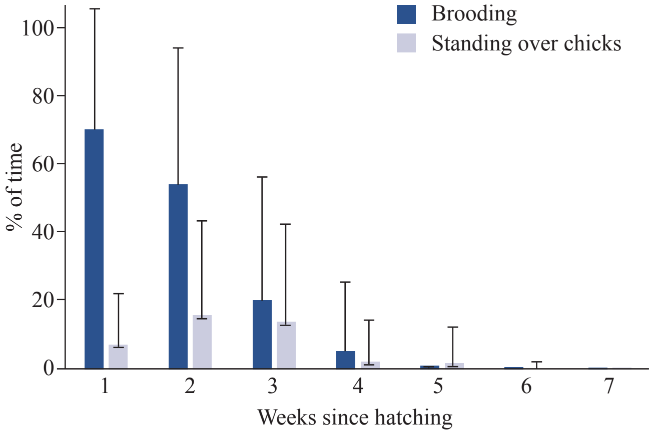

Figure 5. *Time spent by the female brooding or standing over nestlings in the weeks after hatching (all hours included), in the years 2012–2017 and 2020.*

Figure 6. *Male peregrine (M3) about to brood three-day-old nestling 12/10/21. The two eggs shown did not hatch.*

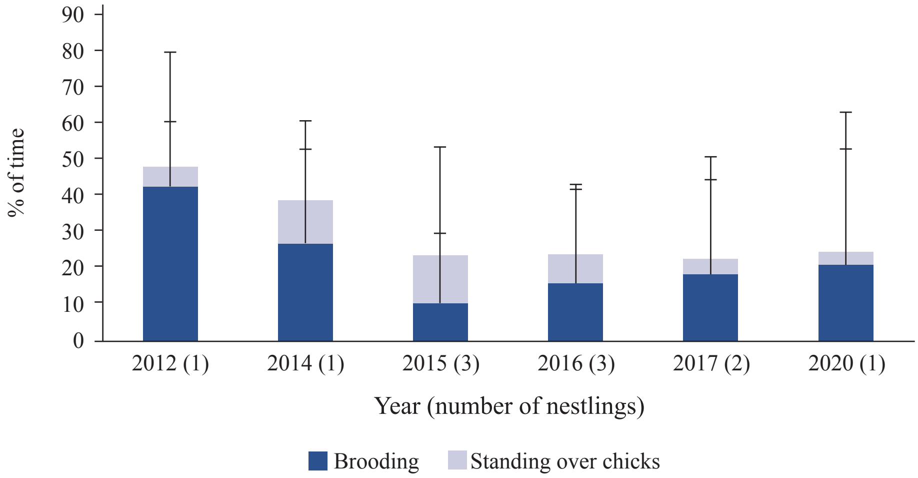

Figure 7. *Relationship between years (2012–17 and 2020) (and the number of nestlings) and the time spent brooding and standing over nestlings by females, with standard deviations shown for both categories.*

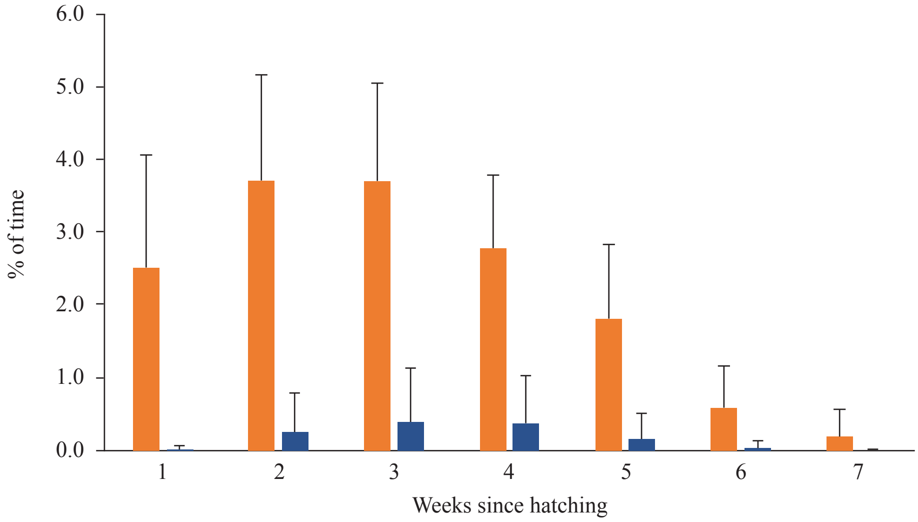

Figure 8. *Average percentage of time per day spent feeding nestlings in the weeks after hatching in the years 2012–2017 and 2020 (daylight hours only 0500-1900).*

Table 1

Calendar of peregrine fledging dates and the days post-fledging until the last sighting of each fledgling.

Year	Pair	No. fledglings	November 5	11	12	13	14	16	17	18	19	20	22	Days to last sighting
2011	F1M1	3					M	FF						8
2012	F1M1	1	M											71
2015	F2M2	3						M	F		F			10/88
2016	F2M2	3						F	M	F				7/76
2017	F2M3	2			M	F								4/69
2018	F2M3	2	MF											110/117
2019	F2M3	2					M	F						132
2020	F2M3	1									M			232
2021	F2M3	1											M	7
2022	F2M3	2		M								M		9/126

So, apart from M3 in 2016, most males did some brooding in daylight hours (0.08 ± 0.97% of the time) and standing over nestling(s) (0.08 ± 0.72%), especially when the nestlings were under two weeks old (see Fig. 6 for example). However, as the male contribution is minimal (<1%) and highly variable, it is not considered further.

Regarding the variation in brooding over the different years, Fig. 7 shows the combined female brooding and standing over nestling times (using all hours). There were considerable differences between years. These differences probably have less to do with the individual female and more with the number of nestlings to be brooded, with higher brooding rates in years with fewer nestlings.

It was expected that temperature would affect incubation and brooding, but this was not the case. Mean daily temperature during the breeding period ranged from 2.3º to 19.2º C. Daily minima ranged from -5.8º to 11.5º C and maxima 6.5º to 27.7º C.

Time spent by males and females (as well as individuals) in incubation, standing over eggs, brooding and standing over nestlings were all tested for correlation relationships with mean, minimum and maximum daily temperature, using a 95% confidence level. No significant relationships were found between any of these variables. Correlations ranged from 0.00–0.11.

Feeding nestlings

During the early part of this period, when the nestlings were small, almost all the hunting was undertaken by the male, which gave the prey to the female to feed the nestlings. When the female was still brooding young nestlings, she often left the nest box at the approach of the male with prey (even when he appeared to be out of sight or hearing range), then turned and followed him in, grabbing the prey to prepare it or feed it to the nestlings. Once the nestlings were old enough to be left alone, she hunted regularly but still did most of the feeding.

The time spent feeding the nestlings bill to bill after hatching followed a similar pattern with both sexes: a rapid increase to three weeks, followed by a slow decrease (Fig. 8). To reduce the standard deviations, the calculations for this graph are based on minutes per day (daylight hours 0500–1900 h), rather than minutes per hour, reflecting the lower proportion of time spent on this activity.

Fledging and dispersal

A calendar of fledging dates (Table 1) shows the dates of fledging by males and females and the days to the last sighting post-fledging. In years where there were both a male and a female nestling, the male fledged first in four out of six cases. In 2016 the male fledged second out of three juveniles, and in 2018 both left on the same day (in fact, within the same hour). The number of days from the first hatch to the first fledge ranged from 40 to 45, with a mean of 42.0 ± 1.4. (n=12). The nestlings were not marked, so it was not possible to compare the time from hatch to fledge of each individual.

Between 2008 and 2022 there were 24 nestlings fledged (range 0–3), so fledging success based on eggs laid was 57%. From nestlings hatched, it was 92%, with two nestling losses: in 2014 one nestling was blown out of the box during a storm the week before fledging, and in 2020, one nestling died within two days of hatching (reason unknown). Out of the 15 years, there were 13 years with at least one successful fledging, i.e. an overall nest success rate of 87%.

The number of days between fledging and the last sighting in the area was highly variable, ranging from seven days when the juvenile disappeared after severe thunderstorms and 232 days. Some periods seem very short, but these do not necessarily indicate death, but rather the absence or lack of information: either they did not return to the box or were not observed in the field.

Until 2014, the juveniles reunited after fledging with their parents in a group of old *Pinus radiata* trees in the centre of a small *Eucalyptus dives* woodland about 75 m from the nest. After the pines were felled, the family used a copse of mature and dying *Eucalyptus melliodora* trees in a paddock about 300 m from the nest. Since 2020, they have started reuniting again in the first woodland, using the remnant eucalypts. They also use the tower roof and various protruding structures as a roost.

Most fledglings found their way to the roost trees or the tower within days. Several juveniles managed to return to the nest box shortly after. Finding the small ledge in the 35 m tower involves considerable flying skills.

Generally, the juveniles were observed daily until their departure as they used regular roost trees or the tower itself and their hunting activity was also witnessed within a few hundred metres of the tower. Solitary fledglings interacted with their parents more than fledglings with siblings (personal observation). On three occasions, the adult female was observed blocking the nest box entrance to juveniles (a female on 1/2/2016; two males on 16/7/2021 and 18/3/2023), shortly after which the youngsters dispersed.

DISCUSSION

Clutches and egg-laying

The average clutch size at this site was 2.8 over the 15 years. This is low compared to other nest box studies e.g. Albi, France (4.0 over four years) (Maurel and Waleau 2010), and Melbourne (3.2 over 26 clutches) (Victor Hurley personal communication 7/9/22). It is well within normal boundaries for the Australian subspecies of peregrine, however, which ranges from 2.4 (over 55 events) in the Snowy Mountains (T. Stubbs, cited in Debus 2022) to 3.1 (over 13 events) in south-eastern Australia (Olsen *et al.* 1998) with other clutch sizes falling in between (e.g. Pruett-Jones *et al.* 1980; Hurley 2013).

The egg-laying dates were predictable, with a few exceptions, with the majority being within five days of each other. This consistency is supported by evidence from studies showing that some females lay on the same date year after year (Sale and Watson 2022).

Regarding the time of day and intervals between egg-laying, Marchant and Higgins (1993) state that eggs are typically laid in the early morning at intervals of 48 hours, with Olsen (1995) providing a figure of 52 hours. Our egg-laying intervals ranged from 52 to 75 hours, with a mean of 61 for both intervals. These are closer to those cited by Sale (2016), i.e. 48–72 hours. The eggs at this site were laid mainly in the morning and early afternoon but were more spread out than expected.

Incubation

The length of incubation was relatively consistent (36–40 days) at the Orange site but was more extended than observed at other sites globally e.g. 29–35 days (Sale 2016). In Australia, Pruett-Jones *et al.* (1980) cites a mean of 33 days in a Victoria study. Incubation usually starts after the penultimate egg is laid (Olsen 2014), typically the second egg at this site. However, it was observed that sometimes incubation started earlier here, perhaps due to the colder temperatures, which may explain the extended period.

In respect of incubation rates in the period after egg-laying, males and females at this site followed a similar pattern of an increase in the first week and tapering off in the last. This pattern is partly supported by studies from northern Spain, where the males, at least, incubated slightly less during the first and last weeks (Zuberogoitia *et al.* 2017) and in Alaska, where it was observed that male incubation generally decreased to 25% as hatching approached (Enderson *et al.* 1973). In respect of incubation generally, these authors found that inattentive periods during incubation in Alaska decreased as hatching approached but admitted that this may have been partly caused by the authors' maintenance visits.

Sale and Watson (2022) provide comprehensive, up-to-date data on male incubation effort, as well as its timing, and their review supports the evidence from this study that the female contributes the majority of the incubation, but that the male contribution varies considerably from individual to individual. In Alaska, as well as high male variability in effort, there were even observations of males incubating at night (Enderson *et al.* 1973).

Male incubation rate at this site was 19% of daylight hours, albeit with considerable variability. This is much lower than the male effort in the nest box at Albi, France (48–53%) (Maurel and Waleau 2010) and in Australia (normally 20–30% of daylight hours, but ranging from 0–50%) (Olsen 1995). The only Australian (open) nest box comparison is in Melbourne, where the male peregrine (7+ years old) in 2021 incubated for 51% of daylight hours (personal communication Victor Hurley 7/9/22).

Female peregrines are generally 15% larger than males (Stirling-Aird 2012) so this sexual dimorphism may account for the males' reduced incubation effort. It was noticeable that, when there were three eggs, some of the males at Orange found it difficult to adequately cover the whole clutch. Furthermore, it is known that, although both sexes may have brood patches, the ones in males can be rudimentary or completely absent, so male incubation is likely to be less efficient in transferring body heat (Sale and Watson 2022). Poorly developed brood patches could be a factor in reduced male incubation time in Orange, especially in cold weather (Zuberogoitia *et al.* 2017).

Inadequate brood patches may explain lower male effort, but not such marked variability. A possible contributing factor might simply be individual character differences. M1 would frequently get up off the eggs and stand on the ledge until the female returned. With the other males, the female would usually have to nudge him off the eggs unless she had been away for several hours, when he would usually leave without prompting, a finding supported by the observation from Canberra that the male was often reluctant to leave (Olsen and Stevenson 1996). As the overall incubation rate remained stable over the years and between pairs in this study as elsewhere, one could surmise that individual behaviours were probably the main factor.

Unlike Zuberogoitia *et al.* (2017), no relationship was found between incubation or brooding and temperature. This result may be due to the shelter that the box provides from temperature extremes and is consistent with results from the French nest box study, where Maurel and Waleau (2010) also found no relationship between incubation and weather. As the box at Orange was weatherproof, rainfall was not measured.

Brooding

There was a substantial variation in brooding rates in different years, with generally lower rates in years with two or three nestlings. Three nestlings soon become a large bundle to tuck under the body or to stand over (especially for the smaller male). Moreover, two or three nestlings can keep each other warm to a certain extent, so there is less need for brooding. Others' findings support this observation, e.g. Henderson (2016), who observed little brooding after three weeks in a cliff nest site in the Australian Capital Territory.

The males at this site undertook very little brooding (just under <1%), and this is consistent with studies from Alaska (Enderson *et al.* 1973; Palmer 1998), UK (Treleaven 1977) and Australia (Olsen and Stevenson 1996) and reviews by Ratcliffe (1980) and Stirling-Aird (2012). It has been argued that males can only brood when the nestlings are very small (Sale 2016) due to the males' smaller size. However, other studies have shown that males tend not to brood during the early nestling period (Palmer *et al.* 2001), possibly due to a desire by the females to keep males away from tiny nestlings (Carlier and Gallo 1995). Unfortunately, the males at the Orange site did not brood sufficiently to provide enough data to support either suggestion.

Feeding nestlings

In the week after hatching, minimal feeding of nestlings was undertaken by the males. This lack of effort might be simply because males were not trusted to prepare the food properly, so were discouraged by the females. At this site, one of the males (M3) tried twice (30/8/2017 and 1/9/2022) to feed recently laid eggs. Males were also frequently observed trying to feed nestlings with morsels too large for their beaks. M3 in 2016 did not feed the nestlings at all, perhaps due to inexperience or because they were not his offspring.

The males seemed to actively avoid feeding older nestlings, especially in the weeks leading up to fledging, as the older nestlings could be aggressive. The males dropped the prey, which was grabbed by one of the nestlings, and then quickly left the nest. The females, conversely, were more likely to keep the prey (or take it back from the nestling) and would tolerate the kicks and bites to ensure the prey was prepared and eaten.

The decline in feeding time after week three and the overall low effort made by the male, apart from doing almost all of the hunting when the nestlings are small, is also supported by the literature, e.g. Sale (2016). However, it has been observed that the male will make more of an effort to feed nestlings where there is more than one, and that different individuals have varying feeding strategies (Turner *et al.* 1993). Enderson *et al.* (1973) found that some males did no feeding of nestlings, and Cameron and Olsen (1993) observed the male feeding nestlings only four times when the nestlings were seven days old to fledging age.

The decline in feeding time as the fledging day nears is mainly due to the growing ability of nestlings to pluck and eat their own prey at that age, although this behaviour is not predictable – for example, very little self-feeding was observed in one Alaskan study (Enderson *et al.* 1973). During the last week there was a reduction in prey delivery with a concomitant occurrence of adults flying past the box with prey (personal observation). This could be a potential means of luring the nestling out of the box when the parents deem it ready and may also be a contributing factor.

There was little apparent aggression between the siblings, apart from some pecking, jostling for position and 'tugs-of-war'. Occasionally, the smallest nestling would miss out, but this was not commonly observed. Usually, there was plenty of prey to go around, so the smallest nestling would eventually be fed when the older ones were full or would sneak in front of its siblings and reach up for food. This lack of sibling aggression is consistent with other findings, such as those of Turner *et al.* (1993) and Debus (2022). There were no nestlings lost to starvation in this study.

Fledging

There were only two years with no fledges: 2013, when all the eggs broke; and 2014, when the single nestling was blown out of the nest box during a thunderstorm a week before it was due to fledge. At 0.31 mm, the broken eggs from 2013 had slightly thinner eggshells than normal, estimated to be 0.35–0.36 mm (Golden *et al.* 1998), but was well above the 0.28 mm threshold for population declines due to pesticide residue (Falk *et al.* 2006).

The age of juveniles worldwide at fledging is quite variable, averaging, globally, 39–44 days (Sale 2016) and in Australia (38–45) (Olsen 2014). Males usually fledge a day or two earlier than females (Ratcliffe 1980). The data from this site (40–46 days) fall into these ranges. At Orange, the males generally fledged before the females, but the number of days from hatching to fledging for each nestling was unknown, so precise comparisons between the sexes cannot be drawn.

After fledging, some juveniles disappeared after a few weeks, but others, particularly lone male nestlings, stayed over 100 days and, in one case (2020–21), for 232 days. The parents were never seen to be physically aggressive toward the juveniles, apart from the blocking of the nest-box entrance. This lack of aggression is consistent with recent literature (Debus 2022). The male that stayed until August 2021 (having fledged in November 2020) had shown some aggression toward his father and suggestive courtship behaviour towards his mother.

It is known that, in general, non-migratory juveniles stay in their natal area, becoming less and less dependent on the adults, for about eight or nine weeks (Stirling-Aird 2012; Sale 2016) and in Australia, usually up to six or seven weeks, but the period can be considerably longer, even up to eight months (Marchant and Higgins 1993). This demonstrates that a stay of 232 days, although unusual, is not unprecedented.

Nest boxes and reproduction

In nature, poor weather, especially the number of rain days, is likely to lower reproductive success due to flooding, as are extreme temperatures (Olsen and Olsen 1989). Sheltered cliff sites lead to improved outcomes (Olsen 2014) as do nest boxes (Pagel *et al.* 2018; Hurley 2013). Hatching success at 62% at this site, however, is lower than observed in other studies. Stubbs (cited in Debus 2022) recorded 84% from the Snowy Mountains, and Hurley (2013) achieved 77% at 18 sites after installing nest boxes in Victoria.

It is impossible to say how old the first adults were when they arrived at the box in 2007. However, the low hatching success in some years in Orange may be due to the assumed older age of the first pair of peregrines rather than the quality of the nest box site itself, as success increased noticeably when the new pair took up residency in 2015. In her final years of residency, F1 was limping and often lay down in the box for hours at a time, indicating an older bird and possibly suggesting difficulty in mating. It is hard to be conclusive as Zabala and Zuberogoitia (2015) found no age-related lack of reproductive success in peregrines in north-western Spain. It was not clear, however, whether this was due to the experience and skills of older birds or because younger ones replaced older birds (> 14 years) before senescence became an issue.

Where reproductive success has been improved with nest box installation, it has been suggested that juvenile survival to breeding age may not be improved (Altwegg *et al.* 2014). There are two areas of concern: juveniles raised in nest boxes may not recognise natural nest sites; and birds raised at natural sites may not recognise nest boxes as suitable. This study indicates that the latter concern at least is not an issue, as the original Orange parents were almost certainly raised on cliffs. Brown and Collopy (2013) found that neither of these issues was a problem for American Kestrels *Falco sparverius paulus*. Furthermore, Olsen (2006) describes a case where a cliff-nest-raised male peregrine took over the nest of an Australian Hobby *Falco longipennis* and bred successfully, countering the traditional notion that peregrines only nest in sites similar to their natal nest site.

The Orange site had an 87% nest success rate, and this compares to a rate of 43% in 21 cliff sites in high-altitude areas of the Australian Capital Territory (Olsen *et al.* 2004) and 60% in Victoria (Pruett-Jones *et al.* 1980). Fledging success (from eggs) was 57%, falling between other studies, e.g. 94% and 43%, both from south-eastern Australia (Olsen *et al.* 1998). The overall reproductive rate (1.6 fledged young per pair per year) was similar to that found in natural sites in Australia, e.g. 1.2–1.6 young per pair (Marchant and Higgins 1993), 1.8 in high altitude areas (Olsen *et al.* 2004), but lower than a reported 2.0 in Victoria (Pruett-Jones *et al.* 1980).

Being close to a large rural centre is unlikely to have adversely affected reproductive success. Urbanisation may improve fertility rates given sufficient prey, such as Rock Dove *Columba livia* (Kettel *et al.* 2018), although there are increased hazards, such as windows and vehicles. At this site, there never seemed to be a shortage of prey. European Starling *Sturnus vulgaris* was the prey most often taken and pigeons (native and introduced), as well as several species of parrots and large honeyeaters, also featured prominently. The timing of breeding is likely to coincide with plentiful and unwary prey offspring when the juvenile peregrines are learning to hunt (Olsen 2014). Comparison between the behaviour, reproductive success and diet of nest box-using urban, natural and semi-rural peregrines is a potential source of future research.

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