

Year-round courtship and maintenance of pair bonds at a Peregrine Falcon *Falco peregrinus* nest-box

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Abstract. Observations via webcam were made of the year-round pair bond maintenance and mating behaviour of pairs of Peregrine Falcons *Falco peregrinus* sequentially using a nest-box on a water tower at Orange, New South Wales. Between 2012 and 2024, five Peregrines used the site – two females and three males. The courtship and pair bond maintenance behaviour studied included prey delivery, prey-holding (for potential transfer between mates), pair bonding displays and scrape preparation. At least one member of the pair performed all these activities in each month of the year, not just in the pre-breeding season. The delivery and holding of prey increased in July and August (particularly by males), dropped in September during incubation and peaked in October when nestlings were growing. Pair bonding displays and scrape preparation were reasonably constant throughout the year, both peaking in August. Duration of pair bonding varied from less than a minute to over two hours. Scrape preparation dropped in September and showed little difference between the sexes over the year except in August, when the female effort increased fivefold. There was some variability among the behaviour of individuals and pairs in each of these activities. Copulation began over 80 days before egg laying and well before the female's fertile period. Copulation frequency and duration increased until the first egg was laid and ceased shortly after the second egg. The combination of webcam and citizen science provided a chronology and pattern of courtship behaviour that would have been challenging to obtain using traditional field methods.

Keywords: Peregrine Falcon; *Falco peregrinus*; webcams; courtship; pair bonds

INTRODUCTION

The Peregrine Falcon *Falco peregrinus* is a well-studied raptor with many papers and books published on its distribution, diet, biology and behaviour (e.g., Ratcliffe 1980, Sale and Watson 2022, Stirling-Aird 2012). Much of the existing information, however, focuses on its habits and diet during the breeding season.

Information on Peregrine courtship behaviour outside the breeding season is scant (Meier *et al.* 1989; Stirling-Aird 2012), and it is considered likely to be both difficult to obtain and highly variable (Ratcliffe 1980). The breeding season (egg-laying, incubating and brooding) only occupies approximately 15% of the year (Sale and Watson 2022), so being able to report on activities outside this period 24 hours a day can provide helpful insight into year-round behaviour and identify differences between sexes and individuals. Peregrines are highly sexually dimorphic (Stirling-Aird 2012), so differences in courtship behaviour are likely to be marked. Several authors have observed differences between individuals or pairs (Herbert and Herbert 1965; Ratcliffe 1980; Treleaven 1977).

Regarding the chronology of courtship events, Cade (1960) described the sequence of pairing thus: attraction and close roosting; cooperative hunting; courtship flights; display 'familiarities' on the cliff; courtship feeding; copulation and nest scraping. In the current study, pairing had already been established in most years, and cooperative hunting and courtship flights were generally not visible. The courtship and pair bond maintenance behaviours to be discussed here are prey-holding/delivery, pair bonding displays and scrape preparation (all in the

nest-box), as well as copulation (on the water tower that holds the nest-box).

The delivery of prey to transfer from male to female (and occasionally vice versa) is well documented and stated to commence at least six to eight weeks pre-incubation (Fischer 1967 cited in Ratcliffe 1980, Wrege and Cade 1977). The amount of time spent holding prey is not widely reported, however. This behaviour reflects the effort put into the length of time invested in (potentially) waiting for its mate or offspring to take its offering.

Courtship displays are described in detail by Wrege and Cade (1977) and, in the Australian context, by Debus (2022). Wrege and Cade (1977) stated that during the non-breeding season, mates of established pairs in captivity avoid each other, but there is contrary evidence. Some courtship displays (Sale and Watson 2022) and even mating (Meier *et al.* 1989) have been observed outside the breeding season.

There is little information on how much effort is made by each sex to prepare the scrape during the year. In captive Peregrines (housed at Cornell, USA, but from various sources) and Gyrfalcons *Falco rusticolus*, scraping was undertaken by both sexes, starting in January and by the female a few days before laying (Wrege and Cade 1977). Sale (2016) stated that this behaviour is undertaken by the female and comes after the pair bonding displays described above.

Reporting of copulation also shows inconsistencies. Pagel *et al.* (2018), describing Peregrines in United States cities, observed copulation in every month of the year. Others have stated that copulation usually starts a few weeks before egg-

laying – three weeks in the case of captive Peregrines (Wrege and Cade 1977). However, timing and length of the copulation period will vary between resident and migratory Peregrines, the latter having limited time to establish or re-establish bonds before they must reproduce. Olsen (1995) and Wrege and Cade (1977) observed that copulation intensified in both duration and frequency as egg-laying approached.

Despite the widespread use of webcams to observe Peregrines over the last decade, there is little published information on Peregrine behaviour from webcams, a study from a Peregrine family nesting in a cathedral in Albi, France, furnishing a notable exception (Maurel and Waleau 2010). The use of webcams has hugely simplified the study of animal behaviour as it provides easy and comfortable observation of nest sites otherwise often challenging to access; see, for example, Heatherley (1913), Olsen (2014), and Turner *et al.* (1993). Webcams are especially useful for describing activities at night when regular survey techniques cannot be used and for replacing the use of captive birds in the type of behaviour research undertaken by Wrege and Cade (1977).

This study aims to provide information on a species that is well-researched but poorly understood outside the breeding season. The aims are to

- describe year-round courtship activities (pair bonding displays, delivery, holding or caching prey, and scrape preparation) by males, females individuals and pairs
- identify the chronology of courtship activities
- describe the timing, duration and frequency of copulation events
- determine whether there is a relationship between the timing of copulation and prey delivery or pair bonding.

STUDY AREA

The nest-box is inside and near the top of a 35 m water tower at Charles Sturt University, 6 km north of Orange, New South Wales (Fig. 1). It can be accessed by a narrow, metal stairway inside the tower, then a ladder. The tower, constructed in 1970, still provides water to the university.

The tower is at 900 m a.s.l. in the Central Tablelands, which has cold winters, usually with a few days of snow each year, and warm summers. The average rainfall is 870 mm per year (Bureau of Meteorology 2022), which is fairly evenly spread throughout the year, although thunderstorms are more likely during summer.

The tower has various structures, such as a microwave bracket on the western side (Fig. 2), where the falcons were often observed perching. This structure can also be seen on the left-hand side of the tower in Figure 1. There is also a short antenna on the other side of the tower and a hatch where food is often cached.

The university campus contains a 300 ha farm and there are suburbs within 2 km of the site so that it could be described as the 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 September 2024. There is a small remnant of Broad-leaved Peppermint *Eucalyptus dives* woodland below the tower, which includes some native shrub

planting. In addition, there is a stand of mature live and dead Yellow Box *E. melliodora* trees in a paddock about 300 m away. The Peregrines roost in these locations and other sites around the university farm, as well as on the tower itself.

Lone Peregrines are sometimes sighted in the study area. There are few other known breeding pairs of Peregrines in the region. One pair's territory is over 10 km away and another over 20 km.

There is an abundance of prey, such as European Starlings *Sturnus vulgaris*, pigeons, parrots and large honeyeaters (personal observation). The area lacks other suitable Peregrine nest sites, however, and the local Peregrines have not been observed to nest in trees.

BACKGROUND

In 2006, a pair of Peregrines was regularly observed using the water tower as a roost. 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 the box was replaced a few years later with a larger model.

There is more history and other information about the FalconCam Project on the website:
<https://science-health.csu.edu.au/falconcam>

METHODS

Methods and materials

The nest-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). It is 1.2 m wide, 0.75 m high and 0.65 m deep.

The two initial cameras were upgraded in 2014 to high definition, with a third installed in 2021. All had sound and pointed to either the nest-box's scrape or the ledge. Details of brands and models are available from the author. An external webcam was added in late 2021 and upgraded in 2023.

Between 2008 and 2012, only basic reproductive events were recorded. In 2012, systematic data collection began 24 hours a day throughout the year. At that time, there were few webcams and only one (in Albi, France) where research was being conducted, to my knowledge. No doubt there were others with unpublished data, such as the one in Melbourne's Collins Street (Mirvac 2024); another in London, described by Sale and Watson (2022) as well as some in the U.S.A. e.g. in New Hampshire (NH Audubon 2024). I visited the French site in 2012, and the time activity data collection is based on their method (Maurel and Waleau 2010).

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. After this equipment failed owing to storm activity, there was a gap in recording (January 2018–August 2020), although the live stream continued to function, so basic and prey information could still be 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.



Figure 1. The water tower showing the entrance to the nest-box near the top and a male falcon on the ledge of the nest-box.

Photo: C. Kinross

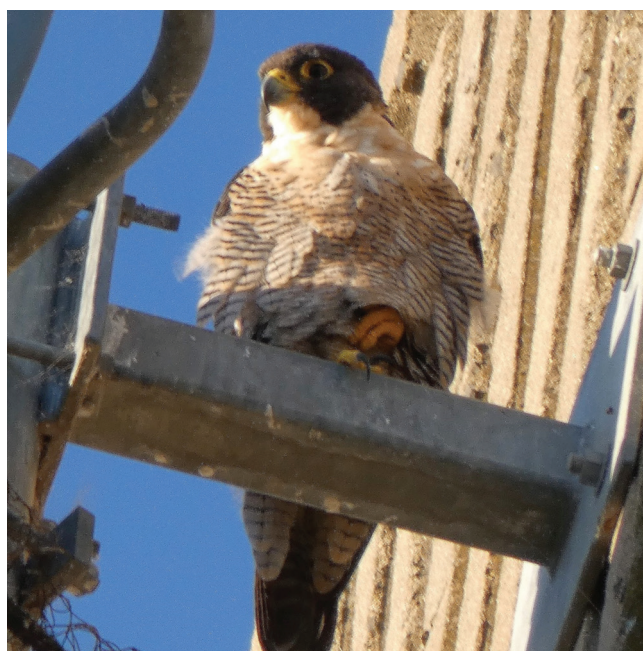


Figure 2. M3 on the bracket of the microwave dish: a favourite place to shelter from the wind and rain and for prey preparation.

Photo: C. Kinross

Table 1

Percentages of observation time of activities and prey delivery via nest cameras by month and year.

Month	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	2024
January		100	88	100	100	100	89	100*	100*	100	0	100*	96*
February		93	99	89	100	99	0	100*	100*	100	0	100*	100*
March		100	100	100	41	100	0	100*	100*	100	0	100*	100*
April		98	100	85	0	100	0	100*	100*	100	0	80*	100*
May		51	64	94	0	100	0	100*	100*	95	0	100*	
June		72	79	100	0	100	0	100*	100*	100	0	100*	
July		100	99	98	100	100	100*	100*	100*	100	100*	100*	
August	22	98	100	100	70	100	100*	100*	32	100	100*	100*	
September	100	100	100	100	94	90	100*	100*	100	3	100*	100*	
October	95	78	100	100	100	100	100*	100*	100	0	100*	100*	
November	100	75	100	100	100	93	100*	100*	100	0	100*	100*	
December	94	89	99	100	100	83	100*	100*	100	0	100*	100*	

*prey delivery only

There were three separate data sets collected: 1) nest-box activities; 2) number of prey items brought to the nest-box; and 3) behaviour relating to mating (also referred to as ‘coupling’ and ‘copulation’). These are described in detail below.

Nest-box activities relating to courtship included pair bonding, holding/caching prey and preparing the scrape (“scraping”). These were recorded for each male and female in minutes to the nearest half minute. At the end of each hour, the minutes for each activity were totalled, so each spreadsheet row represented one hour of activity recorded. The data were then converted to percentages of time per day.

When observing pair bonding, the time spent in display by each of the pair was recorded separately as one of the pair

sometimes stopped displaying. When a bird rested in the scrape without activity, recording of the scraping was paused. If both adult birds were in the box simultaneously, the behaviours of both birds were recorded as they were mutually exclusive. Data collection for these timed activities via the nest cameras commenced on 24 August 2012 and finished on 31 August 2021. Gaps in the observation period are shown in Table 1.

Prey delivery was recorded as the number of items brought to the box per month. This number was calibrated according to the percentage of time monitored in each month. Other data such as species and torso size were also recorded and images stored, and are the subject of a further study. Prey delivery was recorded from 24 August 2012 to 24 April 2024, with a gap from September 2021 to July 2022 (Table 1).

Data collected from the outside cam related only to copulation and included the date of commencement and termination, frequency of events (number per hour and day), and duration (number of seconds). The number of minutes that a mating event occurred before and after bonding displays and prey delivery was also recorded. Data relating to copulation were collected in 2022 (date of commencement and termination, plus some casual observations) and 2023 (all other data). The observation times in 2023 via the tower cam included all hours where there was sufficient light for visibility and there were no gaps.

The total observation period of all activities went from August 2012 to April 2024, and the gaps are shown in Table 1. Gaps in the early part of the study were mainly due to technical failure of the surveillance software. Once citizen science observations commenced in September 2020, there were far fewer gaps.

Data analysis

Data were analysed using R, with graphs prepared in Excel. Analysis was for the most part restricted to graphical measures and descriptive statistics. All error bars are standard deviations. Tests of significance such as *t* tests were avoided due to considerable criticism of this approach (e.g., Cohen 1994), and the nature of the study, i.e. single-site observations inappropriate for hypothesis or significance testing (personal communication, Xie Gang, 20 September 2022). Nakagawa and Cuthill (2007) recommended using effect sizes of the difference between the means with their confidence intervals (95%) as a more effective measure of data relationships for this type of study, so this was the approach taken.

For Cohen's *d* analysis, the activity time data were transformed as there were still many zeroes, even after consolidating the data. Kurtosis and skewness of all the dependent variables were compared after transforming by both log₁₀ (after adding the constant 1) and fourth root (Quinn and Keough 2002) and then compared. Log₁₀ produced the more symmetrical results. Cohen (1988) used the following estimation to gauge the importance of effect sizes: 0.20 = small effect size, 0.50 = medium effect size and 0.80 = large effect size. These have been interpreted on a continuum as 0.20–0.49 = small, 0.50–0.79 = moderate and ≥ 0.80 = large, with the proviso that the confidence intervals did not contain zero as that result indicates that the effect size is unreliable (Nakagawa and Cuthill 2007).

Prey delivery data are presented as the mean number of prey brought in each month, with the standard deviation indicating the variability between each year. Repeat offerings (e.g., Starlings repeatedly brought to the box but ignored by the female) were removed.

To determine whether there was a relationship between copulation events and the delivery of prey or pair bonding, the percentage frequency of gaps between these events were calculated, from 10 minute gaps to up to two hours or over. Frequency and duration of copulation events are presented graphically.

RESULTS

Between August 2012 and April 2024, five individual Peregrines used the box: August 2012–April 2015: F1 and M1; April 2015–October 2016: F2 and M2; and October 2016 to

April 2024: F2 and M3. With the males there was a short gap between one partner disappearing (assumed dead) and another appearing, but F1 shared the box (resting there during the days) for a few days after F2 took up residence. M2 went missing as the eggs were due to hatch. This absence resulted in F2 going for three days without food before leaving to hunt as the first chick hatched, and returning with prey. After a few days, suitors/competitors started arriving. The first two (a juvenile male and a female) were rejected, and the third (an adult male) was accepted. This male, M3, provided for the female and nestlings and all three fledged successfully.

Prey delivery

A total of 3,880 vertebrate prey (all birds, bar four microbats) and 442 invertebrate prey (mostly cicadas) were observed being brought to the box from August 2012 to April 2024. The number of vertebrate prey items varied considerably over the season (Fig. 3). After a quiet start to the year, during which prey was brought occasionally by both sexes, there was a rapid increase in prey delivery during July and August.

Figure 3 shows the average number of prey items taken each month by each falcon and brought to the nestbox. Males are shown in brown, females in green, and unknown adults in grey. The latter represent prey (prepared) brought to the box by the female but there was some uncertainty over which adult actually caught the prey due to the length of time the female was absent from the box. There were few prey from December to June, so the those for these months were totalled.

Cohen's *d* effect sizes and confidence intervals are shown in Table 2. Insects were not included in this count, being small and highly seasonal. It is worth noting that they were caught by all adults, particularly F1 in her last year when she was quite lame, and they were often the first prey caught by juveniles after fledging.

Holding or caching prey

After the adult landed with prey, it often waited several minutes on the ledge. If the mate did not arrive, the bird cached the prey in the box, ate it or flew away with it. The assumption had been made, incorrectly, that it would primarily be the male role to hold prey as a gift for the female, at least during winter. In fact, the female often held the prey on the ledge too. She was not observed giving it to the male, although he was frequently seen helping himself to cached prey.

Caching was also observed outside in trees and on the tower: by a hatch and on the microwave dish. Occasionally, the caching took some time as the bird (usually the male) kept returning to the prey, picking it up and holding it again before finally caching, eating or flying away with it.

The percentage of time in each month spent holding prey within the box ranged from 0 % (females in January and males in February) to 0.25 % (± 0.19) (males in August) (Fig. 4). Both males and females held/cached prey in almost all months, with little difference between the sexes apart from in late winter, when male activity was considerably higher. Table 3 shows the effect sizes of the differences between the sexes, as well as those between individuals.

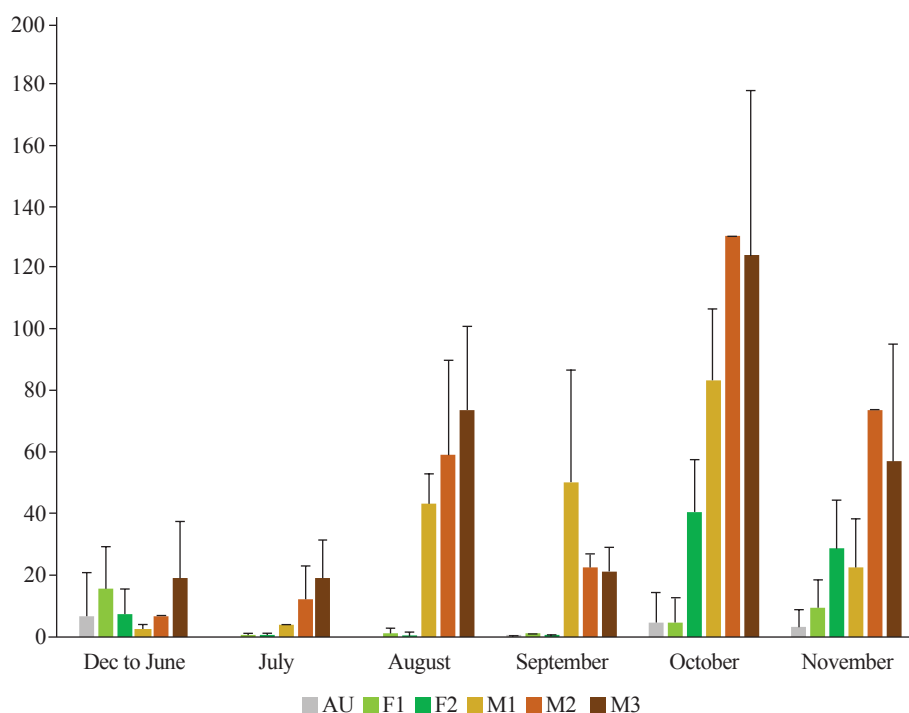


Figure 3. The mean number of vertebrate prey items brought to the box (and assumed caught) by males, females and adults (unknown) in each month, August 2012 to August 2021 plus August 2022 to April 2024. AU = Adult unknown, all years; F1 = 2012–2015; F2 = 2015–2024; M1 = 2012–15; M2 = 2015–16; M3 = 2016–24.

Table 2

Cohen's *d* effect sizes with confidence intervals for the difference between the number of prey items brought to the nest-box by males, females and individuals. Small effect = 0.20–0.49; medium = 0.50–0.79; ≥ 0.80 = large. Where CIs include zero, the result is left unshaded. NA indicates that there were insufficient data to undertake the analysis.

	M>F [F>M]	F2>F1 [F1>F2]	M2>M1 [M1>M2]	M3>M1 [M1>M3]	M3>M2 [M2>M1]
Dec to June	0.05 (-0.75, 0.85)	[0.68 (-0.67, 2.01)]	0.51 (-1.36, 2.3)	2.15 (0.33, 3.87)	1.45 (-0.16, 2.98)
July	1.85 (0.82, 2.85)	[0.06 (-1.48, 1.59)]	1.63 (-0.93, 3.99)	1.58 (-0.23, 3.3)	0.84 (-0.82, 2.44)
August	4.01 (2.5, 5.48)	[1.48 (-0.23, 3.12)]	0.94 (-1.28, 3.00)	1.14 (-0.57, 2.87)	0.74 (-0.9, 2.33)
September	0.89 (1.93, 2.94)	[2.03 (0.38, 3.61)]	[1.67 (-0.61, 3.78)]	[1.58 (-0.07, 3.15)]	0.24 (-1.38, 1.84)
October	2.52 (1.36, 3.64)	2.53 (0.73, 4.24)	NA	0.94 (-0.51, 2.34)	NA
November	0.28 (1.20, 2.10)	1.37 (-0.12, 2.81)	NA	1.12 (-0.36, 2.55)	NA
Year- round	0.71 (0.45, 0.96)	0.25 (-0.16, 0.25)	0.26 (-0.36, 0.88)	0.24 (-0.18, 0.66)	0.11 (-0.44, 0.67)

The differences between the time spent holding prey by individuals were not generally substantial. Table 3 shows, however, that M2 and M3 both held prey longer than M1 in five and seven months respectively, including during the pre-breeding period of interest.

At the beginning of each season, the male, particularly M3, was often observed to be reluctant to let the prey go, resulting in tugs of war. But after a week or two, he would generally be less protective of his catch. On occasion, the male arrived with prey

and the female rejected it, either flying off without the prey or refusing to take it.

Pair bonding

Pair bonding displays within the box continued evenly all year with a range of 0.05 to 0.09% of daily time in most months, with a slight increase in July and November (0.11%) and a more than doubling in August (female $0.24 \pm 0.10\%$; male $0.35 \pm 0.31\%$) (Fig. 5).

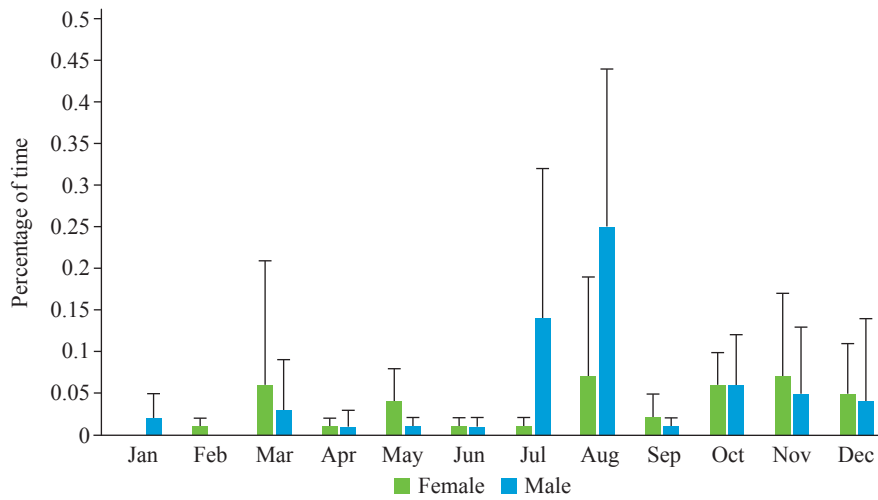


Figure 4. Percentage of time spent holding prey in the box in different months, August 2012 to January 2018 plus August 2020 to August 2021.

Table 3

Cohen’s *d* effect sizes, with confidence intervals for the difference between the time spent holding or caching prey by males, females and individuals. Small effect = 0.20–0.49; medium = 0.50–0.79; ≥ 0.80 = large. Where CIs include zero, the result is left unshaded.

Month	M>F [F>M]	F2>F1 [F1>F2]	M2>M1 [M1>M2]	M3>M1 [M1>M3]	M3>M2 [M2>M3]
January	0.12 (-0.07, 0.30)	0.06 (-0.21, 0.33)	0.37 (-0.04, 0.77)	0.29 (0.00, 0.58)	0.17 (-0.23, 0.58)
February	[0.17 (0.04, 0.39)]	0.19 (-0.11, 0.50)	[0.13 (-0.29, 0.55)]	0.05 (-0.29, 0.39)	0.17 (-0.28, 0.61)
March	0.03 (-0.18, 0.25)	[0.15 (-0.15, 0.46)]	0 (0, 0)	0.43 (0.11, 0.76)	0.30 (-0.30, 0.90)
April	[0.03 (-0.20, 0.25)]	0.28 (-0.05, 0.61)	0 (0, 0)	0.25 (-0.10, 0.60)	0.20 (-0.29, 0.69)
May	[0.18 (-0.06, 0.43)]	[0.02 (-0.36, 0.39)]	0 (0, 0)	0.30 (-0.10, 0.70)	0.29 (-0.15, 0.72)
June	0.04 (-0.20, 0.28)	0.23 (-0.12, 0.58)	0.43 (0.03, 0.89)	0.46 (0.07, 0.84)	0.38 (-0.07, 0.82)
July	0.44 (0.20, 0.61)	0.20 (-0.11, 0.51)	0.41 (0.06, 0.77)	0.63 (0.27, 0.99)	0.36 (0.01, 0.72)
August	0.49 (0.29, 0.69)	0.12 (-0.17, 0.41)	0.84 (0.47, 1.21)	0.88 (0.54, 1.23)	0.22 (-0.13, 0.57)
September	[0.15 (0.04, 0.34)]	[0.45 (0.17, 0.73)]	[0.13 (0.2, 0.46)]	0.21 (-0.12, 0.54)	[0.17 (-0.19, 0.53)]
October	[0.08 (-0.11, 0.27)]	0.35 (0.08, 0.63)	0.93 (0.51, 1.36)	0.97 (0.66, 1.29)	0.57 (0.16, 0.99)
November	[0.03 (-0.17, 0.22)]	0.27 (-0.01, 0.55)	0.59 (0.16, 1.01)	0.35 (0.05, 0.64)	0.23 (-0.18, 0.65)
December	[0.04 (-0.15, 0.23)]	0.11 (-0.16, 0.39)	[0.12 (-0.29, 0.53)]	0.34 (0.04, 0.63)	0.28 (-0.13, 0.69)
Year-round	0.10 (0.04, 0.16)	[0.08 (-0.01, 0.16)]	0.41 (0.29, 0.53)	0.42 (0.34, 0.63)	0.16 (0.04, 0.27)

The frequency of bonding sessions varied from zero to five times per day, each lasting less than half a minute to over two hours. On occasion, one bird displayed whilst the other did not; one bird (generally the female) would sometimes stand upright and look away or turn her/its back. For this reason, times were recorded for individuals separately, resulting in different times for males and females.

Over the whole year F2M2 spent more time pair bonding than the other two pairs, although the difference among the three pairs was relatively low (Fig. 6).

The percentage of time spent bonding by the individual pairs varied considerably month by month, especially from April to August. The Cohen’s *d* and the confidence intervals are shown in Table 4.

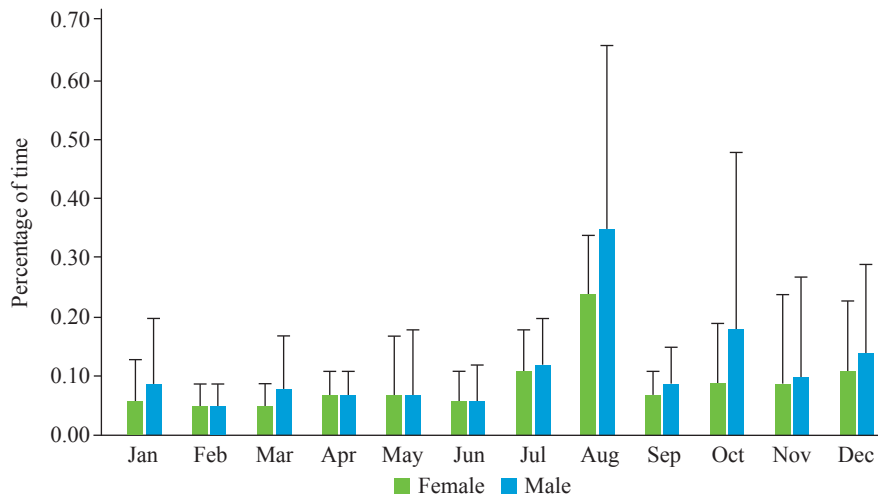


Figure 5. Percentage of time spent in pair bonding display each month, August 2012 to January 2018 plus August 2020 to August 2021.

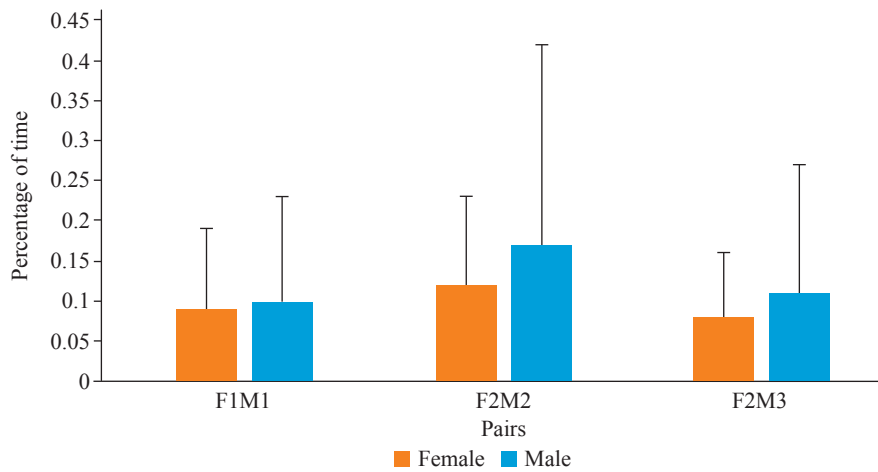


Figure 6. Percentage of time in pair bonding display for individual pairs, August 2012 to January 2018 plus August 2020 to August 2021.

Table 4

Cohen’s *d* effect sizes with confidence intervals for the difference between the time in pair bonding displays by each pair. Small effect = 0.20–0.49; medium = 0.50–0.79; ≥ 0.80 = large. Where CIs include zero, the result is left unshaded.

Month	F2M2>F1M1 [F1M1>F2M2)	F2M3>F1M1 [F1M1>F2M3]	F2M2 > F2M3 [F2M3>F2M2]
January	[0.19 (-0.01, 0.40)]	[0.19 (-0.01, 0.4)]	[0.37 (0.08, 0.65)]
February	0.61 (0.30, 0.91)	0.06 (-0.18, 0.30)	0.52 (0.20, 0.85)
March	[0.38 (0.03, 0.80)]	[0.15 (-0.08, 0.37)]	[0.57 (0.15, 1.00)]
April	0.68 (0.3, 1.06)	0.19 (-0.06, 0.44)	0.48 (0.11, 0.86)
May	1.04 (0.68, 1.39)	0.17 (-0.11, 0.46)	1.1 (0.77, 1.43)
June	1.21 (0.86, 1.56)	0.75 (0.47, 1.02)	0.73 (0.41, 1.05)
July	0.61 (0.36, 0.87)	0.99 (0.73, 1.25)	[0.13 (-0.12, 0.38)]
August	0.86 (0.60, 1.12)	0.88 (0.63, 1.12)	0.30 (0.05, 0.55)
September	0.18 (-0.06, 0.41)	0.37 (0.13, -0.60)	[0.18 (-0.08, 0.44)]
October	[0.22 (-0.07, 0.51)]	0.01 (-0.20, 0.22)	[0.16 (-0.13, 0.45)]
November	[0.57 (0.27, 0.86)]	[0.46 (0.24, 0.67)]	[0.28 (-0.02, 0.57)]
December	[0.34 (0.05, 0.63)]	[0.34 (0.13, 0.54)]	[0.08 (-0.21, 0.37)]
Year-round	0.24 (0.15, 0.32)	[0.04 (-0.03, 0.10)]	0.22 (0.14, 0.31)

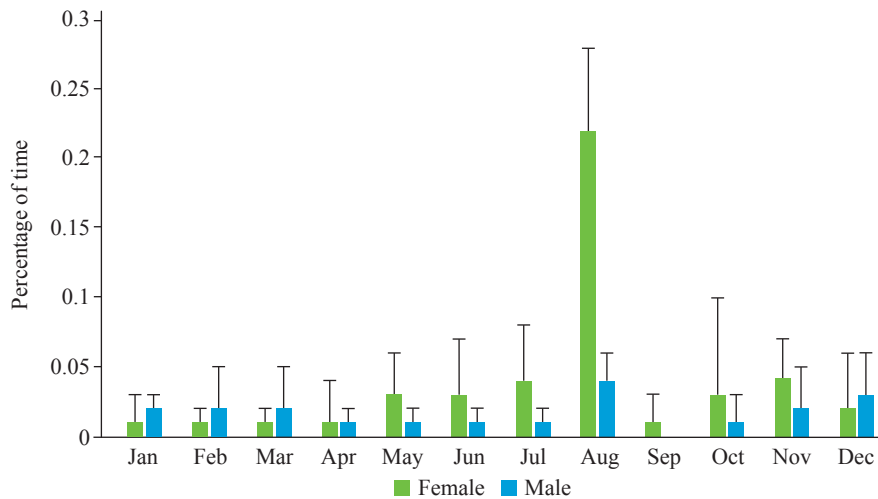


Figure 7. Percentage of time spent preparing the scrape in each month by males and females, August 2012 to January 2018 plus August 2020 to August 2021.



Figure 8. Copulation by F2 and M3 in the nestbox on 30 August 2017. Photo: screenshot from webcam.

These figures indicate that F2M2 spent more time bonding in more months than the other two pairs, and that both F2M2 and F2M3 spent more time than F1M1. The suggested order of decreasing bonding effort is F2M2>F2M3>F1M1, at least in certain months.

Scraping (scrape preparation)

The percentage of time spent scraping was reasonably consistent from December to April, after which it increased each month to a peak in August (Fig. 7). The percentage of time ranged from 0% (males) and 0.02% (± 0.03) (females), both in September, to 0.22% ± 0.06 (females) and 0.04% ± 0.02 (males) in August.

The effect sizes and confidence intervals for the year as a whole and each month for each sex and individual are shown in Table 5.

The females spent more time scraping than the males in all months from April to November and year-round, but the effect sizes were small except in certain months when they were near moderate (in May and July), moderate (in June) and large (in August).

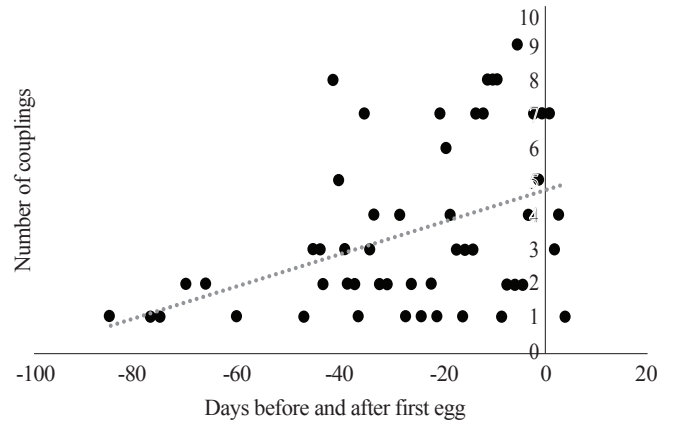


Figure 9. Frequency of coupling against the number of days before the first egg was laid, 2023.

F2 scraped more than F1 in all months except September to November, with a reversal in October and December. Based on year-round figures, there was little difference between the males. In July, during the pre-breeding season, there was a strong indication that M3 was a more diligent scraper than the others during the pre-breeding season, but the differences were less evident than between the females.

Mating

In 2022, mating was observed on the tower roof from 2 June (81 days before the laying of the first egg) to 29 August (the day after the laying of the second egg, when incubation began in earnest). Mating in 2023 also commenced on 2 June, 85 days before the laying of the first egg, and terminated on 31 August, the day after the second egg was laid. Although all data were collected visually from the outside cam, mating calls could be clearly heard via the nest and box cams and were invariably loud rapid ‘chitters’. No pre-mating rituals were observed.

In both years, mating was sporadic until August, when it increased to 14 times a day and up to three times an hour (both events occurring on 18 August 2022). Mating was also observed in the box, but only on two occasions. One of these

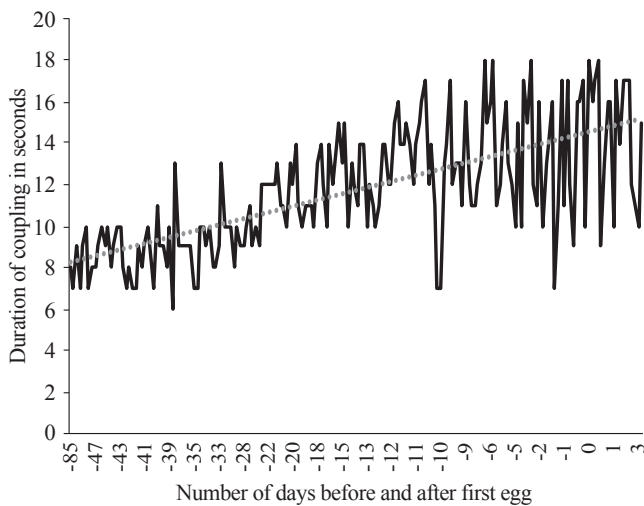


Figure 10. The duration of coupling relative to the number of days before and after the first egg was laid, 2023.

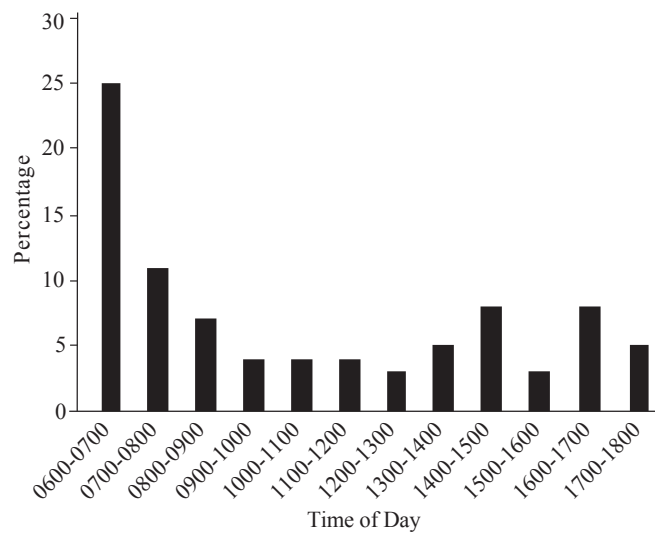


Figure 11. Percentage of couplings related to time of day, 2023.

Table 5

Cohen’s *d* effect sizes with confidence intervals for the difference between the time spent in scrape preparation by individual females and males. **Small effect = 0.20–0.49**; **moderate = 0.50–0.79**; and **large ≥ 0.80**. Where CIs include zero, the result is left unshaded.

Month	F>M [M>F]	F2>F1 [F1>F2]	M2>M1 [M1>M2]	M3>M1 [M1>M3]	M3>M2 [M2>M3]
January	[0.01 (-0.17, 0.20)]	0.74 (0.46, 1.02)	[0.18 (-0.23, 0.59)]	0.13 (-0.16, 0.42)	0.39 (-0.02, 0.80)
February	[0.24 (0.02, 0.45)]	0.60 (0.29, 0.91)	0.40 (-0.02, 0.83)	[0.35 (0.01, 0.69)]	[0.78 (0.32, 1.25)]
March	[0.34 (-0.12, 0.55)]	0.83 (0.51, 1.14)	[0.34 (-0.24, 0.92)]	[0.26 (-0.07, 0.58)]	0.25 (-0.35, 0.85)
April	0.17 (-0.06, 0.40)	0.60 (0.27, 0.93)	[0.32 (-0.17, 0.80)]	0.26 (-0.09, 0.62)	0.50 (0.01, 0.98)
May	0.42 (0.17, 0.66)	0.58 (0.19, 0.96)	[0.24 (-0.23, 0.72)]	0.29 (-0.12, 0.69)	0.40 (-0.04, 0.84)
June	0.56 (0.32, 0.80)	0.78 (0.42, 1.14)	[0.33 (-0.13, 0.79)]	0.16 (-0.22, 0.54)	0.45 (0.00, 0.89)
July	0.44 (0.23, 0.64)	0.70 (0.38, 1.01)	0.35 (0.00, 0.71)	0.91 (0.53, 1.27)	0.77 (0.40, 1.13)
August	0.87 (0.66, 1.08)	0.32 (0.03, 0.61)	0.54 (0.18, 0.90)	0.58 (0.24, 0.91)	0.21 (-0.14, 0.57)
September	0.14 (-0.06, 0.33)	[0.25 (-0.03, 0.52)]	0.12 (-0.21, 0.45)	[0.14 (-0.19, 0.47)]	[0.18 (-0.18, 0.54)]
October	0.21 (0.01, 0.40)	[0.54 (0.27, 0.82)]	[0.30 (0.11, 0.71)]	[0.31 (0.02, 0.61)]	0.12 (-0.29, 0.53)
November	0.12 (-0.07, 0.32)	[0.10 (-0.18, 0.38)]	[0.46 (0.04, 0.88)]	[0.18 (-0.12, 0.47)]	0.30 (-0.12, 0.71)
December	[0.16 (-0.03, 0.35)]	0.70 (0.42, 0.98)	[0.31 (0.10, 0.71)]	0.37 (0.07, 0.66)	0.58 (0.16, 0.99)
Year- round	0.24 (0.18, 30)	0.25 (0.17, 0.34)	[0.10 (-0.01, 0.22)]	0.12 (0.03, 0.21)	0.21 (0.10, 0.33)

was an unsuccessful attempt while the female was incubating in 2012 and the other was on 30 August 2017 (see Fig. 8). Whether they mated in other locations is unknown, but it was never observed.

In 2023, 184 copulations were observed, of which 167 were on the top of the tower roof, and 17 were on tower structures. The frequency of each coupling in relation to the laying of the first egg is shown in Figure 9.

The average coupling duration was 11.71 (\pm 3.00) seconds with a range of 6 to 18 seconds. The duration increased as the date of the first egg-laying approached, although with considerable variability (Fig. 10).

The time of day was also important. Copulations were highest 0600–0700 h (29%), followed by 0700–0800 h (13%). The quietest times of day for mating were 1200–1300 h and 1500–1600 h (both 3%) (Fig. 11). The tower was not observed at night during 2022 or 2023, but observations from a new cam in 2024 showed that the birds are active and even hunting at night, so mating at night cannot be ruled out.

There was little or no relationship between the number of minutes before or after copulation with respect to bonding and prey delivery. The percentage of cases where the number of minutes was over two hours between events was as follows: after copulation and before bonding (90%); after copulation and before prey delivery (84%); after prey delivery and before copulation (93%); and after bonding and before copulation (59%). In the last case, only 15% of the remaining periods between events were under half an hour.

DISCUSSION

Prey delivery and holding

It is known that prey is transferred by males to females (and occasionally vice versa) during July and August as courtship gifts and to provide evidence of their hunting prowess (Olsen 1995), so the results from this study are consistent with this behaviour. It was also anticipated that prey delivery would drop in September during incubation. In this period, the male brought the prey and took over nest duties, and the female usually left immediately with the prey. This explains why the prey-holding time was so much shorter relative to the number of prey brought at this time.

In October and early to late November there was at least one nestling present in all years apart from 2013, when all the eggs broke. During this period, both adults held prey for short durations only. The male usually dropped (once threw) a whole bird (occasionally still alive) into the nest for the young to deal with. The female almost never did this. As the nestlings got older, they became quite feisty, and the female appeared more tolerant of juvenile aggression than her smaller mate. After fledging in November, adults both held prey for a while in anticipation of the fledglings' arrival to take it, explaining why prey-holding then is so much longer relative to the number of prey.

The bringing and holding of prey from December to June, albeit in small numbers and percentage of time, was unexpected. It is true that the nest is a safe place to bring and eat prey, but this does not explain why the birds would hold the prey for such long periods. Adults could still be provisioning juveniles, but this is unlikely in March through to June when the latter, if still around, were catching their own prey. In his study of Peregrines in south-east England, Baker (1967) frequently observed birds waiting several minutes before eating, so whether they birds were simply resting or providing early courtship gifts is hard to determine unless the actual transfer is witnessed. A study by Carlier and Gallo (1995) showed that female-to-male food transfers were common during the courtship period although

they were less frequent outside that period. Only male-to-female transfers were observed in the current study. Females often cached prey later taken by males, however.

The differences between males were smaller than between females. F2 brought over three times the prey than F1 in October and over double in November. This anomaly can partly be explained by the difference in nestling numbers (F1 hatched a mean of 1.3 and fledged 1.1; and F2 hatched 2.1 and fledged 1.7). It may also be because F2 was lame in her last year and had to leave much of the hunting to her mate.

Male individual behaviour may have been affected by female prey preference or hunger. If the female did not arrive or rejected his offering, the male eventually flew off with it, ate it himself or cached it in the box. When the prey was rejected, the male held the prey longer or left and returned to the nest several times with the same prey, and this affected the duration of time recorded for the relevant male.

Pair bonding

While most pair bonding sessions were short, from half a minute to two minutes, some were much longer, with one August session lasting just over two hours. In Wrege and Cade's (1977) study, the female usually left first, and that is supported by this study in which the females frequently appeared to lose interest first, sometimes turning their back on the male, who continued to bow (as was the case in the two-hour session described above). More recently, however, it was observed that it was often M3 who broke the stance, providing another example of variability in individual behaviour.

There is scant but conflicting advice with respect to bonding displays in the non-breeding season. There have been observations of aerial interactions, which may or may not have been pair bonding, e.g. by Meier *et al.* (1989) in Puerto Rico in autumn. A pair of Peregrines using a nest-box in California displayed pair bonding behaviour 'all year around' in about 2021, but Armstrong's (2022) report lacks detail. According to Wrege and Cade (1977), Peregrine mates (in captivity) avoid each other in the non-breeding season, which is clearly not the case in this study. The behaviour of birds in captivity, however, is likely to be very different as there is no extrapair competition. Sale and Watson (2022) stated that pair formation or renewal in the northern hemisphere starts in January or February (which approximates to July and August in this part of Australia) but noted that it can be earlier.

Scraping

As with pair bonding, both sexes prepared one or more scrapes in the nest-box throughout the year, with an increase in winter. F2 scraped more than F1 in all months except October, when the situation was reversed. F1 had an empty nest in 2013 after the eggs broke, so she could resume scraping earlier than usual.

Both sexes put considerable effort into scrape preparation, pushing deep into the gravel, but there were differences: males usually scraped continuously for shorter periods while females often took breaks. Furthermore, males often started new scrapes, sometimes near the ledge, which the females generally ignored.

Although considered part of courtship (Wrege and Cade 1977), the solitary nature of this activity throws doubt on this suggestion, although they can, of course, see the results of each other's efforts. It has been hypothesised that the male starts a new scrape, hoping that the female, who makes the final determination, will choose his effort (Nethersole-Thompson and Nethersole-Thompson 1943 cited in Sale and Watson 2022). That is an interesting hypothesis, but it is not clear how either of these ideas regarding male aspiration and female choice could be tested.

Copulation

Timing, frequency and duration of courtship behaviour and copulation with Peregrines are influenced by location, individual pair behaviour and weather and can be highly variable (Ratcliffe 1980). For example, behaviour is likely to be different in areas with short breeding windows.

Copulation at Orange commenced 81 and 85 days before the first egg was laid, early by comparison to other studies. In a study in Madagascar, the days numbered 38 to 40 (Razafimanjato *et al.* 2007), and in closely related species such as Prairie Falcon *F. mexicanus*, copulation began 51 days prior to clutch completion (Holt *et al.* 1992). Out-of-season copulation has, however, been observed in Peregrines: in autumn in Puerto Rico (Meier *et al.* 1989) and at all times of the year in urban locations (Pagel *et al.* 2018). Mating at Orange generally terminated with the penultimate egg, which is consistent with the findings of Sale and Watson (2022).

In both the current study and that of Wrege and Cade (1977), copulation occurred at any time of day but was most frequent in the early hours of first light. None of the pre-copulatory behaviours, such as the male 'hitched wing' posturing or female 'whine' and display soliciting as described by Ratcliffe (1980) and Wrege and Cade (1977), were observed at Orange.

Frequency of copulation, of up to 14 times a day and three times an hour in the weeks leading up to egg-laying, was well within normal range (Debus 2022, Sale and Watson 2022, Wrege and Cade 1977). The observation by Sale and Watson (2022) that both frequency and duration increased in the period up to egg-laying is also supported by this study. In Wrege and Cade's (1977) study of captive falcons, early-season couplings were often incomplete but followed by short, complete copulations of five to six seconds. Two to three weeks before laying, copulation took eight to ten seconds. This study had similar findings, although late season copulation duration was up to 18 seconds in Orange.

Explanations for the timing, frequency, and duration of copulation by birds, and birds of prey in particular, have been discussed in the literature. Birkhead *et al.* (1987) posited four theories, of which the only ones showing promise in these circumstances were those relating to initiating or renewing social bonds and the notion of 'insurance matings' (should there be unpaired Peregrines in the vicinity). Other later hypotheses included that superfluous copulation was necessary to assess the quality of their partner, but this seems unlikely in pairs that mate for life (Villarroel *et al.* 1998).

Perhaps the most promising theory is that of 'territorial signalling' put forward by Negro and Grande (2001) and this would be worth testing. Signalling in this manner to potential

intruders that the territory is taken seems highly plausible, especially considering the Peregrines' noisy and conspicuous copulatory behaviour.

General conclusions

Reporting observations of activities from just one nest site does not permit generalisations about Peregrine behaviour but can, of course, add to the body of knowledge about the extent of variability between the sexes and individuals as well as the year-to-year deviations. It was evident that each of the five birds and three pairs in this study behaved differently to a greater or lesser degree, although caution is needed when interpreting some of these findings as the confidence intervals were relatively large, especially in between-month analyses. It should also be acknowledged that pair bonding behaviour might have occurred outside the view of the webcam and not therefore included in the data.

Variability due to individual behaviour has been demonstrated in other studies. Herbert and Herbert (1965) found it hard to identify patterns in behaviour due to the high variability between each bird or pair. Likewise, after 25 years of observing Peregrines in Cornwall, Treleaven (1977, p. 9) concluded that 'no two pairs of Peregrines behave alike'. An earlier study of breeding behaviour from the same birds at the nest-box in Orange also provided an example of individual behaviour with the differing incubation efforts of individual males (Kinross 2023).

Using surveillance software, citizen science and a full-time webcam, the author has been able to describe Peregrine Falcon conduct at the nest year-round 24 hours a day. The findings help fill certain gaps in our knowledge and add to our understanding of differences between male, female, individual and pair behaviour. The paucity of evidence outside the breeding seasons in other areas may simply be due to the lack of continuous observation that webcams provide. Having only one nest site helps as well, as in other places one would need to follow several sites of the same pair to gather equivalent evidence (Ratcliffe 1980). In northern Spain, for example, over three eyries were counted in each territory (Zuberogoitia *et al.* 2015).

The study has also provided evidence that the actual chronology of events did not follow the orderly sequence suggested by Cade (1960), who, however, worked with migratory Peregrines, with a tight season after their arrival back at their Alaskan breeding grounds. Mating commenced considerably earlier than expected, and behaviour generally associated with courtship – pair bonding displays, prey delivery and scrape preparation – occurred right through the year.

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