Parental care and breeding strategies of the Jacky Winter and its life-history traits compared with other Australasian robins, and northern temperate and tropical songbirds

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Abstract. We studied parental care in the Jacky Winter *Microeca fascinans* at Gluepot Reserve, South Australia, for one breeding season from 16 August to 9 November 2001, supplemented by observations on breeding and social behaviour in September 2012. We monitored ten nests in 2001, nine of which were attended by pairs and one by three adults, and watched three nests for a total of c. 117 hours. Female incubation constancy was 69%, duration of incubation sessions averaged 4.58 minutes and absences from the nest 2.07 minutes. Mean number of nest visits per hour by two pairs during the incubation period was 10.6 and for a group of three adults (two males, one female) was 15.8. Female care included brooding, feeding of nestlings, and nest-hygiene. Male care included delivering food to the sitting female, feeding the nestlings, nest-hygiene, nest-defence, and territoriality. Mean female brooding constancy was 55%. Mean number of feeding trips per hour by male and female combined for the entire nestling period was 14.6. Older young, 12, 13 and 14 days of age, received 21, 20, and 29 feeds/h respectively or one feed about every 2 minutes. Mean number of visits per hour by male and female combined to a nest with two young was 16.5 for Days 1–10 and 20.4 for Days 11–18 of the nestling period. High nest-predation is discussed in relation to nest placement and concealment, high nest visitation during incubation and nestling stages, anti-predator behaviour, nest-defence and types of predators, and re-nesting capacity, and compared with other Australasian robins and northern temperate and tropical songbirds. The small nest, small clutch-size, high nest failure, and anti-predator posture and mottled plumage of nestlings suggest that nest-predation is a strong selective pressure in the Jacky Winter. However, the moderately long nestling period, brood-size reduction, high rates of feeding young and nest visits by both male and female, and short and frequent incubation and brooding bouts on and off the nest relative to other robins are not consistent with nest-predation theory, and suggest behavioural responses to food availability and an ultimate response to food limitation. Incubation behaviour on and off the nest, parental care of young, nest visitation and other life-history traits that influence reproductive effort are discussed to elucidate the breeding strategy compared with other Australasian robins.

Introduction

The Jacky Winter *Microeca fascinans* is a small (15 g), flycatcher-like, ground-pouncing and aerial insectivorous Australasian robin (Petroicidae: Subfamily Microecinae) (Recher *et al.* 2002; Loynes *et al.* 2009; Christidis *et al.* 2011) that occurs throughout Australian woodlands, open forests and mallee (Higgins & Peter 2002; Boles 2007). This paper follows the taxonomy of Beehler & Pratt (2016) for flyrobins endemic to New Guinea, but follows Christidis & Boles (2008) in usage of the common name, Lemon-bellied Flycatcher, for *Microeca flavigaster*. Taxonomy and sequence of Australian robins follow Gill & Donsker (2017). Detailed studies on the breeding biology of Australian robins have been conducted for the Grey-headed Robin *Heteromyias cinereifrons* (Frith & Frith 2000), Eastern Yellow Robin *Eopsaltria australis* (Marchant 1985a; Zanette 2000; Zanette *et al.* 2000; Berry 2001; Debus 2006a), White-breasted Robin *E. georgiana* (Russell *et al.* 2004a), Hooded Robin *Melanodryas cucullata* (Fitri & Ford 2003; Debus 2013), Flame Robin *Petroica phoenicea* (Robinson 1990), Scarlet Robin *P. boodang* (Robinson 1990; Debus 2006a), Red-capped Robin *P. goodenovii* (Dowling 2003; Powys 2004), and Southern Scrub-robin *Drymodes brunneopygia* (Brooker 2001). The breeding biology of the Jacky Winter is reasonably well known (Higgins & Peter 2002), and breeding territories and breeding success have been documented (Wood *et al.* 2008). Our study presents

the first detailed account of parental care in a microecine robin.

Our study is important for two main reasons. First, field studies of Australian robins advance our knowledge and understanding of life-history traits of 'Old Endemic' southern temperate songbirds and seek to explain variation and patterns among southern temperate passerines compared with those from tropical and northern temperate regions. We conducted an intensive study of parental care in the Jacky Winter to help elucidate the selective forces that shape the strategy of parental care in this species and identify any constraints to reproductive effort such as nest-site characteristics, incubation behaviour, care of nestlings and nest-predation. Second, the Jacky Winter is a ground-foraging, woodland bird that is declining throughout southern Australia and thus is of conservation concern (Barrett *et al.* 2003; Olsen *et al.* 2005; Watson 2011). Ground-foraging birds represent a considerable proportion of declining woodland birds (Antos & Bennett 2006; Ford 2011). Across their range in south-western and south-eastern Australia, Jacky Winters forage mainly by pouncing from a perch to the ground to capture invertebrates but also take prey aerially (hawking) and by snatching prey from a substrate. In Wandoo *Eucalyptus wandoo* woodlands in south-western Australia, the most important foraging substrates used by Jacky Winters were ground (66%) and air (26%) (Recher & Davis 1998), and in temperate woodlands of northern Victoria they were

ground-litter (49%), bare ground (20%) and air (12%) (Antos & Bennett 2006). Further understanding of social organisation, foraging and nesting habitat requirements, life-history attributes and constraints to reproductive effort can contribute to more effective conservation management for the Jacky Winter.

The main objectives of this study were to document: (1) social organisation; (2) daylight incubation constancy, the number of nest visits and the duration of on- and off-bouts during incubation; (3) brooding constancy and the number of food-delivery trips to the nest throughout the nestling period; (4) nest success, nest failure, anti-predator behaviour of adults and young, and potential nest-predators; and (5) to compare all these traits with coexisting (Red-capped and Hooded Robins and Southern Scrub-robin) and other robin species.

Study site and methods

Parental care of the Jacky Winter was studied from 16 August to 9 November 2001 at Gluepot Reserve, South Australia (33°45'S, 140°7'E), elevation 57 m above sea-level (asl). Supplementary observations of breeding and social behaviour and organisation of this species were made there in September 2012.

Gluepot Reserve (54 390 ha) is part of the 9000-km² Riverland Biosphere Reserve (formerly named Bookmark Biosphere Reserve) that protects the largest area of intact mallee in southern Australia (Mackenzie & Fitzsimons 2013). At Gluepot Reserve from 2000 to 2016, the mean annual rainfall was 285 mm (range 127.9–505.7 mm), the mean annual maximum temperature was 25.3°C, and the mean annual minimum temperature was 9.3°C. In 2001, the annual rainfall was 227.4 mm and rainfall for the months August to November was 121.6 mm (Bureau of Meteorology, <http://www.bom.gov.au>). In 2001, the rainfall at Gluepot (weather station 020028) for each season was 27.8 mm (summer), 29.2 mm (autumn), 69.7 mm (winter), and 100.7 mm (spring), compared with means over the period 2001–2016 of 78 mm, 57.4 mm, 65.8 mm and 73.4 mm, in summer, autumn, winter and spring, respectively. Thus, Gluepot had a wetter than average winter and spring in 2001, and mean seasonal rainfall from 2001 to 2016 was highest in spring and summer.

The predominant vegetation association inhabited by Jacky Winters was Acorn Mallee or Oily Mallee *Eucalyptus oleosa* over shrubs in swales and to a lesser extent Beaked Red Mallee *E. socialis* over Porcupine Grass *Triodia scariosa*, and Black Oak *Casuarina pauper* open forest edge with mallee eucalypts (Hyde 2001). Both *E. oleosa* and also *E. socialis* are called Red Mallee (Chippendale 1988; Brooker & Kleinig 2001). *E. socialis* is also called Summer Red Mallee or Pointed Mallee (New South Wales Flora Online, <http://www.plantnet.rbg Syd.nsw.gov.au>). We searched for Jacky Winters around campgrounds, off roads and tracks, and found ten active nests (Nests 1–10). Nests were watched from hides and adults were observed through a 25× telescope. To determine the time that Jacky Winters spent incubating, we conducted three 12-hr watches at three nests during the late incubation period for 2150 minutes (35.83 h). In this study, nest-attentiveness is the total number of minutes spent incubating by a female Jacky Winter during

a defined period of daylight. Incubation constancy is the percentage of hours of daylight spent in incubation. The duration of all bouts on and off the nest were timed to the nearest second with a lap/split stop-watch. An incubation session or 'on-bout' is the duration of time in minutes and seconds spent at the nest in incubation. An absence or 'off-bout' is the duration of time in minutes and seconds that an incubating female spends away from the nest. Male incubation feeding (feeding of a female by her mate on and off the nest during the incubation period) was recorded during mornings and afternoons at two nests (Nest 2 of a pair and Nest 9 attended by three adults). The time that females spent brooding was determined by watching three nests (Nests 2, 5 and 9), each with a brood-size of two, from 0600 h to 1800 h throughout the nestling period for a total of 4862 minutes (81.03 h). Brooding constancy is the percentage of daylight hours that a female spends at the nest brooding young. Nest 2 was watched for 350 minutes (5.8 h) on only 1 day as the nest was depredated. Nest 9 was observed for 900 minutes (15 h) on Days 1, 4, and 6 of the nestling period, but 2 days later it failed. The third nest (Nest 5) was watched for 3612 minutes (60.2 h) from Day 1 (the day that the first egg hatched) to fledging of the two young, on Days 19–20, to determine the time spent brooding, the number of feeding trips per hour, and the role of the male and female in the removal of faecal sacs. Up to Day 13 of the nestling period, the female was identified by her brooding and food-solicitation behaviour. During afternoon watches from Days 8–13, when the bird carrying food to the nest did not brood it was not possible to determine the sex of the individual bird. After Day 13 the sex of all adults was unknown. To calculate mean feeding rates for each half of the nestling period, we first averaged feeding rates for all nest-watches for a particular day of the nestling period, and then averaged all those means. Anti-predator behaviour, such as nest-defence and predator avoidance, and cryptic behaviour by nestlings, were recorded. Nest success is the proportion of nests in which eggs are laid and young fledge. Heights of all nests above the ground were measured and nest-site characteristics were recorded after the end of nesting.

Results

Observations of breeding system and social behaviour

Jacky Winters are socially monogamous, territorial pair-breeders (Higgins & Peter 2002; Wood *et al.* 2008). We observed cooperative breeding in Jacky Winters once in 2001 at Gluepot Reserve when two adults (presumably both males) fed the incubating female, and also fed the brooding female, which then fed the young (R. Donaghey in Higgins & Peter 2002; RHD & CAD pers. obs.).

From 1 to 7 September 2012 at Gluepot Reserve, RHD recorded the social, foraging, and breeding behaviour in nine Jacky Winter territories, six of which were occupied by a pair of Jacky Winters. In one territory at 0715 h on 4 September, RHD watched a synchronised sexual display flight of two Jacky Winters fluttering their wings and with tails fanned while hovering ~50 m above the ground. Both birds were ~40 cm apart, and when the lead bird moved a few centimetres, the other shifted position so that both

birds remained close. When the lead bird flew further on, the other followed close behind until both were out of sight.

A group of three Jacky Winters was seen together in three of the nine territories. In Territory 9 on 7 September, RHD observed a metal-banded Jacky Winter (presumably the female) building a nest on a dead horizontal fork of a mallee eucalypt. It gathered nest material from the ground and made ten trips to the nest while its mate (presumably engaged in mate-guarding) perched 5 m from the nest and sang. The third Jacky Winter perched 10 m away, and once all three birds perched 5–10 cm apart on the same dead branch 6 m from the nest. In Territory 3 at 0800 h on 2 September, RHD watched three Jacky Winters engaged in foraging and social behaviour. Two birds perched together and mutually preened while the third perched on a dead twig <5 m away. One of the two closely perched individuals flew off, and the other two followed in an aerial pursuit with no overt antagonism between them. In Territory 7 at 1545–1600 h on 5 September, RHD watched a group of three Jacky Winters foraging together. Initially two of them foraged and perched close to each other while the third was 20 m away. Several times, all three birds perched together on the same branch after perch-pounce foraging. It was not known if these last two groups of three Jacky Winters stayed together and bred.

Nest initiation

In 2001, the first Jacky Winter nest was found on 19 August when RHD observed a bird wiping spider web on a nest foundation. Of the ten nests found, two were initiated in August (Nests 1 and 2), five were being built in September (Nests 3–7), and three nests with eggs were found in October. The last nestling fledged on 8 November.

Nest-site characteristics and nest outcome in relation to height of nest above the ground

All ten Jacky Winter nests in 2001 were built on an exposed horizontal fork of a dead branch, nine in Acorn Mallee and one in Black Oak fringing the mallee eucalypts. Mean nest height above the ground was 2.5 m (range 1.55–4.25 m). Of five nests that failed (one during construction and four with eggs), three (Nests 1, 3 and 6) were <2 m and two (Nests 4 and 8) were >2 m above the ground. Of three nests with nestlings that were depredated, two (Nests 9 and 10) were <2 m and one (Nest 2) was >2 m above the ground. Eggs hatched in half the nests, two of which were <2 m and three >2 m above the ground. The two nests where young fledged (Nests 5 and 7) were >2 m above the ground.

Male incubation feeding and female foraging off the nest

Male incubation feeding (typical breeding behaviour of Australasian robins) was observed when an incubating Jacky Winter solicited food by quivering and elevating her wings and emitting high cheeps and squeaks; in response, the male either flew to the nest and fed her or fed her off the nest. The rates of male incubation feeding per hour for one 6-h morning watch and one 6-h afternoon watch, at a nest of a pair and at a nest attended by two males, are presented in Table 1. At the nest of the pair (Nest 2), the male fed the female on the nest 15 times during the

Table 1. Incubation feeding of Jacky Winters, Gluepot Reserve, South Australia, 2001: number of times that an incubating female was fed at the nest by a male or by two males during a morning and an afternoon nest-watch.

Time	Nest of pair (Nest 2)	Nest attended by 2 males (Nest 9)
Morning		
0600–0700 h	1	6
0700–0800 h	1	9
0800–0900 h	4	1
0900–1000 h	4	14
1000–1100 h	3	3
1100–1200 h	2	9
Total	15	42
Afternoon		
1200–1300 h		4
1300–1400 h	2	10
1400–1500 h		9
1500–1600 h		7
1600–1700 h		2
1700–1800 h		6
Total	2	38
12-h total	17	80

morning (2.5 times/h) and twice during the afternoon (0.3 time/h). At the nest attended by three adults (Nest 9), the two males fed the sitting female 42 times during the morning (7 times/h) and 38 times during the afternoon (6.3 times/h). Over a 12-h day, two males fed an incubating female at the nest 6.7 times/h or nearly five times the rate by a single male (1.4 times/h).

At Nest 2 during a 6-h morning watch, the female sallied off the nest six times between 0700 h and 0800 h and caught flying insects, and between 0800 h and 0900 h she flew off the nest five times to catch insects in the air and on the ground. Between 0900 h and 1000 h, she flew off the nest once to hawk insects and once pounced to the ground.

Incubation rhythm

Three Jacky Winter nests (each containing a clutch of two eggs) were watched during the second week of incubation for a combined total of 2150 minutes (Nest 2 for 710 minutes, and Nests 5 and 9 for 720 minutes each). Nest-attentiveness, incubation constancy, and the number and duration of incubation sessions (on-bouts) and absences (off-bouts) by the female at these nests are shown in Appendix 1. Mean incubation constancy for the three females was 69.2%. For the three nests combined, mean incubation session length was 4.58 minutes (range 0.05–56.08 min., $n = 325$). The mean number of complete incubation sessions was 9 per hour. Mean length of absences from the nest for the three females combined was 2.07 minutes (range 0.02–19.25 min., $n = 298$). Frequency of nest visits by both male and female for two nests of pairs (Nests 2 and 5) was 8.6/h and 12.6/h respectively,

Figure 1. Relationship between daytime brooding by female Jacky Winters and nestling age. Each data point represents the mean minutes brooding per hour for each of 32 nest-watches [mean duration 180.12 min. (range 150–240 min., $n = 25$) for first 14 days and 51.3 min. (range 10–98 min., $n = 7$) for next 5 days]. Day 1 of the nestling period represents the day that the first nestling hatched. The linear regression equation is $Y = 55.4 - 2.9X$; $r^2 = 0.7$, $P < 0.0001$, significance level = 95%.

Figure 2. Relationship between Jacky Winter feeding trips and nestling age for a brood of two at one nest (Nest 5). Each of the data points represents the mean number of feeding trips per hour for each of 27 nest-watches [mean duration 162.65 min. (range 60–188 min., $n = 20$) for first 14 days and 51.3 min. (range 10–98 min., $n = 7$) for next 5 days]. Day 1 of the nestling period is the day that the first nestling hatched. The linear regression equation is $Y = 1.7 + 1.2X$; $r^2 = 0.5$, $P < 0.0001$, significance level = 95%.

whereas the cooperative group (Nest 9) made an average of 15.8 nest visits/h. For four quartiles from 0600 h to 1800 h, the mean number of visits by the female to and from the nest per hour was 18.0 (range 14.0–19.3) from 0600 h to 0900 h, 20.9 (range 17.7–26.0) from 0900 h to 1200 h, 23.2 (range 16.3–36.0) from 1200 h to 1500 h, and 13.8 (range 4.7–20.0) from 1500 h to 1800 h. The total number of nest visits by both male and female per 12-h day was 102 and 151 for the two nests of pairs, and 189 for the cooperative group.

Hatching, nestling period and growth of nestlings

In three nests in which hatching synchrony was observed (Nests 2, 9 and 10), the two young hatched within 24 hours of each other. At the nest where two young fledged (Nest 5), one egg hatched 25–36 hours after the other. The nestling period at one nest (Nest 5) was 19 days. At two accessible nests that were depredated, the young were weighed. At Nest 9, the two young each weighed 1.55 g on the day of hatching (Day 1), 3.6 g and 3.8 g on Day 3, and 5.5 g and 4.7 g on Day 5; 2 days later, one weighed 8.4 g and the other was dead, presumably from starvation. At Nest 10, two young were 1–2 days old when first observed, and 1 day later weighed 3.7 g and 2.9 g.

Parental care of nestlings

Three nests (Nests 2, 5 and 9) were watched for a combined total of 2902 minutes (59.7% of watches) in the morning and 1960 minutes (40.3% of watches) in the afternoon.

Only the female brooded the young, but the male brought food to the nest and passed it to the brooding female, which either consumed the food or fed the young directly. Time spent brooding varied with ambient temperature, time of day and nestling age. No brooding was observed after Day 15 of the nestling period (Appendix 2). Figure 1 shows a significant inverse linear relationship between time spent brooding and nestling age. Time spent brooding was mostly greater in the cooler mornings and lower in afternoons (12 of 15 data points above the line of best fit were morning watches and eight of 11 below this line were afternoon watches). Brooding declined from 54.2 min./h on the day of hatching (Day 1) to 1.5 min./h on Day 15 (Appendix 2). The time spent brooding on Days 1–10 and Days 11–18 is shown in Table 2. For the whole nestling period, mean brooding duration was 33.03 min./h, and mean brooding constancy was 55%.

Up to Day 13 of the nestling period at the nest where two young fledged (Nest 5), the female was identified by her brooding and food-solicitation behaviour. The male contributed to parental brood care by catching and delivering food to the female, which either consumed the food or passed it to the young. He also fed the young directly, as did the female when she visited the nest carrying food. This complexity in parental care roles is quantified in Appendix 2. The number of feeding trips to the nest varied with time of day and nestling age. Figure 2 shows a significant linear relationship between number of feeding trips to the nest and nestling age. The number of feeding trips per hour per nest-watch increased from 2.7

Table 2. Brooding by female Jacky Winters at three nests (Nests 2, 5 & 9), Gluepot Reserve, South Australia, 2001: total brooding time, time per hour and constancy (C).

Days of nestling period	Observation time (min.)	Brooding		
		Total time (min.)	Min./h	C (%)
1–10	3030	2089.1	41.37	69
11–18	1832	587.5	19.21	32
1–18	4862	2676.6	33.03	55

Table 3. Mean numbers of feeding trips and nest visits per hour (ranges in parentheses) at one Jacky Winter nest with two young (Nest 5), Gluepot Reserve, South Australia, 2001.

Days of nestling period	Observation time (min.)	Feeding trips/h	Nest visits/h
1–10	1780	8.8 (4.0–13.2)	16.5 (9.0–25.0)
11–18	1822	18.2 (10.8–28.9)	20.4 (11.5–34.0)
1–18	3602	14.6 (4.0–28.9)	19.0 (9.0–34.0)

(Day 1) to highs of 34 (Day 15) and 36 (Day 20) (Appendix 2, Figure 2). Higher feeding rates per hour were recorded in the afternoons on Day 1 (6.7), Day 4 (9.5), Day 6 (14.2), Day 10 (17.5) and Day 13 (28), whereas higher morning feeding rates per hour were observed for Day 8 (27), Day 12 (12.3) and Day 14 (25), possibly reflecting prey availability (Appendix 2). Most data points above the line of best fit are for afternoon watches (Figure 2). Mean number of feeding trips per hour was 8.8 for Days 1–10 and 18.2 for Days 11–18 of the nestling period, and 14.6 for the entire nestling period (Table 3). Older young, 12, 13 and 14 days of age, received 21, 20 and 29 feeds per hour, respectively, or one feed about every 2 minutes. On the morning just before the second young fledged, it was fed ten times in 6 minutes or one feed every 1.7 minutes. Mean total number of visits to the nest per hour by both male and female for Days 1–10 of the nestling period was 16.5, and 20.4 for Days 11–18, excluding a 10-minute watch on Day 20 just before the second young fledged, and 19.0 for the whole nestling period (Table 3).

In addition to feeding of the nestlings, both the male and female assisted in nest-hygiene by removing faecal sacs. The male also alerted the female and young to potential predators and both male and female defended the area around their nest.

Anti-predator behaviour of adults and nestlings

Anti-predator behaviour includes nest-defence and predator avoidance. In this study, nesting Jacky Winters responded to the presence of nearby large, uncommon potential avian predators such as Collared Sparrowhawk *Accipiter cirrocephalus* and Grey Currawong *Strepera versicolor* by darting off the nest and not returning for up to an hour until the predator left. Jacky Winters attack and pursue small to medium-sized birds that intrude into their nest area. During the late incubation period, RHD observed a male Jacky Winter make an attack flight at a male Crested Bellbird *Oreica gutturalis* foraging on the ground 5 m from the nest-tree, and in response the Bellbird flew away. On another occasion, a brooding female Jacky Winter swooped off the nest, and attacked and expelled a male Crested Bellbird foraging on the ground 2 m away. Twice, a male Jacky Winter flew at and expelled a Yellow-plumed Honeyeater *Ptilotula ornata* near the Jacky Winter nest. Other potential avian predators observed in Jacky Winter territories at Gluepot Reserve include the Grey Shrike-thrush *Colluricincla harmonica* and Australian Raven *Corvus coronoides*. During the last half of the nestling period, particularly from Day 13 to fledging, after the two young were fed and ceased comfort behaviour they adopted a cryptic anti-predator posture. During periods when the adult Jacky Winters were absent, the two young sat motionless with their bills pointing upward.

Nest success, nest failure, brood-reduction and productivity

Of the ten nests, one (Nest 3) was partially destroyed and abandoned during construction, four nests with eggs failed (Nests 1, 4, 6 and 8), two young hatched in each of five nests (Nests 2, 5, 7, 9 and 10), and young fledged in two nests (Nests 5 and 7). Egg success was 55.6% (10 of 18 eggs laid in nine nests hatched). Nest success was 22.2%. Two young fledged in one nest (Nest 5), and brood-size was reduced to one in another nest when one young disappeared during the first week (Nest 7). Two of nine territories produced a total of three fledglings, a productivity of 0.33 fledgling per pair.

Discussion

Some Jacky Winter breeding traits that influence reproductive effort are compared below with coexisting and other Australasian robins to try to elucidate the parental care strategy of the Jacky Winter.

Length of breeding season

An extended breeding season should enable birds to increase reproductive output through more replacement clutches and multiple broods. In the present study in 2001, fieldwork was conducted for 86 days (2.8 months), not long enough to determine the duration of the breeding season. In two studies that documented multiple breeding in the Jacky Winter, in the warm temperate Sydney region of New South Wales (NSW) and in subtropical south-eastern Queensland, the breeding season was c. 4 and 5 months respectively (Keast 1994; Wood *et al.* 2008). In north-western Victoria in a wetter region than Gluepot Reserve, multibrooded Red-capped Robins bred during 5 months in each of two seasons, and initiated new nests from August to December (Dowling 2003). In the Northern Tablelands of NSW, the Eastern Yellow Robin laid eggs from mid August to early January (a nesting season of c. 5 months), and the Scarlet Robin laid eggs from mid August to early December (a nesting season of c. 4 months) (Debus 2006b). In the same region, McLean *et al.* (2005) found that for a woodland bird community the timing and length of breeding activity varied amongst species in response to rainfall and predator presence. In the mallee region of south-eastern Australia, most birds breed in spring in response to increasing day length (Emison & Bren 1989; RHD & CAD pers. obs. at Gluepot). Recher & Davis (2014) documented declines in abundance and reduced breeding of birds in response to less rain after above-average summer rainfall in the semi-arid Great Western Woodlands, Western Australia. Stevens & Watson (2013) evaluated the influence of reduced rainfall on declining woodland birds

over a 21-year period on the north-western slopes of NSW, and attributed decreasing summer–autumn rainfall as the most likely factor driving declines in small insectivorous birds. Reduced summer rainfall reduces soil moisture and thus has the greatest effect on soil- and litter-dwelling invertebrates, the food of ground-foraging birds (Taylor 2008; Watson 2011).

Breeding seasons of passerines in a semi-arid environment such as Gluepot probably vary between 3 and 4 months depending on seasonal rainfall before, and during, breeding, and food availability. Thus, above-average summer rainfall can extend the breeding season of robins through replacement nests after nest failure and nest success and, conversely, reduced rainfall and droughts can shorten the breeding season. Around monsoonal tropical Darwin, Northern Territory, the Lemon-bellied Flycatcher has a biannual breeding season of c. 5 months, two in the late wet and three in the late dry season (Noske & Franklin 1999; Noske 2011). In tropical New Guinea, the breeding season extends for 7 months in the lowland Olive Flyrobin *Kempiella flavovirescens* and montane Papuan Flyrobin *Devioeca papuana* (Bell 1982; Coates 1990; Donaghey 2017). These few observations of Australasian robins lend support to the notion that passerines in the tropics generally have longer breeding seasons than in temperate latitudes (Ricklefs 1966; Wyndham 1986; Noske & Franklin 1999; Russell *et al.* 2004a).

Clutch-size

Food limitation and nest-predation are significant interacting selection pressures in the evolution of avian clutch-size (Martin 1995). In the present study, the clutch-size of Jacky Winters was two. In Australian robins, clutch-size is one to four (usually two or three but mostly two), and usually three in four *Petroica* species and the Dusky Robin *Melanodryas vittata* (Higgins & Peter 2002). In New Guinean robins, clutch-size is one in montane species, and one or two in lowland species (Donaghey 2015). The mean clutch-size of landbirds is just over two in the tropics and most southern latitudes in Australasia, the Afrotropics and Oceania compared with 4.5 in northern latitudes (Jetz *et al.* 2008).

Incubation and nestling periods

In this study, the Jacky Winter's incubation period of c. 17 days falls within the range of 16–19 days (Higgins & Peter 2002). This is longer than the mean of 14 days in the

Red-capped Robin (Dowling 2003) but similar to the Grey-headed Robin (17–19 days: Frith & Frith 2000), Lemon-bellied Flycatcher (c. 18 days: Noske 2011), and five New Zealand robins (17–22 days: Higgins & Peter 2002).

The Jacky Winter nestling period of 19 days in this study is more similar to that in the Lemon-bellied Flycatcher (18–21 days) and the longer nestling periods of some New Zealand robins (17–22 days, usually 18 days: Higgins & Peter 2002) than those in the Southern Scrub-robin (9–12 days: Brooker 2001) and Eastern Yellow Robin (11–13 days: Marchant 1985a; Berry 2001; Debus 2006a). The nest-predation hypothesis (Skutch 1949; Slagsvold 1982) predicts that tropical and southern temperate birds with small clutches should have shorter incubation and nestling (fledging) periods than those in northern latitudes. Geffen & Yom-Tov (2000) found little or no difference in either incubation or nestling periods between temperate and tropical regions (although southern temperate species were not included in their analysis). However, for North American passerines, nestling periods were shorter with increased nest-predation rate, and species with higher nest-predation rates produced more broods and had smaller clutch-sizes (Martin 1995).

Parental care during the incubation and nestling periods

In our study, the mean diurnal incubation constancy for three female Jacky Winters was 69% ($n = 2150$ minutes of observation). At Moruya, NSW, the incubation constancy of a female Jacky Winter at one nest averaged 58% (range 21–86%, $n = 513$ observation min.) depending on ambient temperature (Marchant 1985b). For seven southern temperate robin species, female diurnal incubation constancy ranged from 58% to 84% depending on temperature (latitude and elevation) and habitat (Table 4). For three tropical robin species, female incubation constancy was 66% in the Grey-headed Robin in tropical upland rainforest (Frith & Frith 2000), 54% in the Papuan Flyrobin in montane tropical New Guinea (Donaghey 2017) and only ~30% in the Lemon-bellied Flycatcher in tropical northern Australia (Noske 2011). The latitude and elevation of the tropical robin study sites ranged from 19°S, 875 m asl (Grey-headed Robin: Frith & Frith 2000) and 12°S, <100 m asl (Lemon-bellied Flycatcher: Noske 2011) to 5°S, 2800 m asl (Papuan Flyrobin: Donaghey 2017).

In passerine birds, such as Australian robins, in which only the female incubates, there is a trade-off between

Table 4. Incubation constancy (IC) of southern temperate robins in relation to latitude, elevation and habitat.

Species	IC (%)	Study site	Latitude (°S)	Elevation (m asl)	Habitat	Reference
Eastern Yellow Robin	81	Moruya NSW	35	<100	Eucalypt forest & woodland	Marchant (1985a)
Hooded Robin	65	Armidale NSW	30	900–1100	Eucalypt forest	Fitri & Ford (2003)
Dusky Robin	84	Myalla TAS	41	150	Wet eucalypt forest	Higgins & Peter (2002)
Jacky Winter	58	Moruya NSW	35	<100	Acacia woodland	Marchant (1985b)
Jacky Winter	69	Gluepot SA	33	57	Mallee	This study
Flame Robin	78	Nimmitabel NSW	36	800–900	Open eucalypt forest	Robinson (1990)
Scarlet Robin	79	Nimmitabel NSW	36	800–900	Open eucalypt forest	Robinson (1990)
Red-capped Robin	78	Gluepot SA	33	57	Mallee	Higgins & Peter (2002)

sessions spent on the nest warming the eggs and absences off the nest to gather food. The daily number of bouts on and off the nest and the duration of bouts by the female are determined by temperature, her energy needs, food availability, and the risk of nest-predation (Conway & Martin 2000). Compared with other Australian robins, the most striking feature of Jacky Winter incubation behaviour was the more frequent and shorter bouts on and off the nest. The mean duration of incubation on-bouts of the Jacky Winter at Moruya was 3.0 minutes (range 0.5–14.5 min., $n = 87$; Marchant 1985b), and 4.58 minutes at Gluepot (this study) compared with a mean of 13.8 minutes in the Red-capped Robin at Gluepot (Donaghey in Higgins & Peter 2002), 21.5 minutes in the Hooded Robin around Armidale, NSW (Fitri & Ford 2003) and 14.7 minutes in the Eastern Yellow Robin at Moruya (Marchant 1985a). In contrast, Conway & Martin (2000) found that northern temperate passerines, in which only the female incubates, had high mean nest-attentiveness (75%), long on-bouts (mean 38 min.), short off-bouts (mean 10 min.), fewer nest visits (mean 3.6 trips/h) and moderate nest-predation (mean 41%). They suggested that the incubation behaviour of these North American passerines might have evolved more in response to nest-predation than to food availability. The high nest-predation in the Jacky Winter (Wood *et al.* 2008; this study) raises the question of why this species has evolved frequent nest visits, and short on- and off-bouts, all of which increase activity at the nest, and so also the risk of predation of eggs and young by avian predators. Mean duration of absences from the nest was 2.07 minutes for three incubating Jacky Winter females (this study) compared with 3.8 minutes for an incubating female Red-capped Robin at Gluepot (Donaghey in Higgins & Peter 2002). The mean number of visits to the nest by incubating females over 12-h days was 108 for the Jacky Winter (this study), and 40 for one female Red-capped Robin (RHD unpubl. data). The female Jacky Winter's frequent short bouts off the nest to forage and solicit food from her mate to meet her energy needs is presumably a proximate response to temporal and spatial availability of invertebrate food, and possibly an ultimate response to food limitation. Chalfoun & Martin (2007) provided experimental evidence that supplementary feeding of incubating Karoo Prinias *Prinia maculosa* increased nest-attentiveness from 49% to 57% which they interpreted as a proximate response to food availability.

The mean time that female Jacky Winters spent brooding over the entire nestling period was 55% in our study, compared with 54% in the Eastern Yellow Robin (Marchant 1985a) and 33% in the Grey-headed Robin (Frith & Frith 2000), but apparently lower than for the Scarlet Robin (56% for Days 1–3 and 5% for Days 9–16) and Flame Robin (76% for Days 1–3 and 10% for Days 9–16) (Robinson 1990). In our study at Gluepot, a pair of Jacky Winters provisioned their two young at a mean rate of 14.6 feeding trips per hour over the entire nestling period compared with 17.6 feeds per hour on Day 12 of the nestling period in the Red-capped Robin (RHD unpubl. data). For other robins, the mean number of feeding trips to the nest per hour was 7 (Marchant 1985a) and 6.6 (Zanette *et al.* 2000) in the Eastern Yellow Robin, 10 in the Hooded Robin (Fitri & Ford 2003) and 9.7 in the Grey-headed Robin (Frith & Frith 2000). The feeding rates of 9.3 trips/h in the Scarlet Robin and 12.1 trips/h in the Flame Robin (Robinson 1990) are lower than those for the Jacky

Winter and Red-capped Robin. Adult Flame and Scarlet Robins delivered food to nestlings at a maximum rate of 25 times per hour (8.3 feeds/h/nestling; Robinson 1990) compared with a maximum of 34 feeding trips per hour (17 feeds/h/nestling) on Day 15 of the Jacky Winter nestling period. Compared with other Australian robins, feeding rates throughout the nestling period were higher in the Jacky Winter than in all other robins except perhaps the Red-capped Robin (although sample sizes were small).

Nest success, re-nesting and multiple broods

Annual and lifetime reproductive output is determined by clutch-size, nest-predation, brood-reduction, number of broods, and longevity of adults and juveniles. Nest success of Jacky Winters at Gluepot was 22.2% (young fledged from two of nine nests). In south-eastern Queensland, 16 young hatched in eight nests and seven of these fledged from five nests (25% nest success); in three nests, brood-size was reduced to one (Wood *et al.* 2008). Jacky Winters usually build a replacement nest after failure and sometimes after success. At Greensborough, Victoria, the first three nests of a pair of Jacky Winters failed, and two young fledged from the fourth nest in December (Sharland 1929). The study by Wood *et al.* (2008) over one breeding season further demonstrates re-nesting: of the five pairs of Jacky Winters with young that fledged, one pair fledged two young on their first attempt then two repeat nests failed, another pair fledged one young from one nest, one pair fledged two young on their third attempt, another pair fledged one young from its second nest, and the fifth pair fledged one young on its fourth attempt. Of the three pairs that produced no young, two had three unsuccessful attempts and the third had four (deduced from Figures 1–2 in Wood *et al.* 2008). Keast (1994) recorded that one pair of Jacky Winters raised two broods in a season: two young fledged from the first nest on 11 October, a second brood fledged on 5 December, and the re-nesting interval was at least 15 days. The fledglings from the first brood were dependent on the adults for 10–15 days, and the second brood stayed with the adults for at least 3 weeks (Keast 1994).

Nest-predation and anti-predator behaviour of adults and young

Nest-predation is the primary cause of reproductive failure in songbirds in Australia and globally (Ricklefs 1969; Robinson *et al.* 2000; Ford *et al.* 2001; McLean *et al.* 2005; Debus 2006c; Thompson 2007; Remeš *et al.* 2012). High nestling mortality should select for shorter nestling periods, nest concealment, accelerated growth and development of young, anti-predator behaviour of young and adults, less nest visitation, and re-nesting and multiple broods. Although the mean total number of nest visits of 19/h by pairs of Jacky Winters was almost double that during the incubation period (10.6 nest visits/h), four nests failed during the egg stage and five failed during the nestling stage in the present study. However, in south-eastern Queensland, 12 of 20 nests with eggs failed and three with young failed (deduced from Figure 2 in Wood *et al.* 2008) even though nest visits are more frequent during the nestling period.

Roper & Goldstein (1997) tested the Skutch hypothesis, that activity at the nest increases the risk of predation,

in tropical birds. They found that predation at nests of the Black-crowned Antshrike (formerly Western Slaty Antshrike) *Thamnophilus atrinucha* (Thamnophilidae) did not increase during the nestling stage even though nest visitation was far higher than during the incubation phase. Martin *et al.* (2000) tested the effect of nest-site quality on nest-predation particularly during the incubation stage, and discovered that, although actual nest-predation was no greater during the nestling stage, there was a greater daily risk of nest-predation during the incubation stage because of nests in poor sites. When they removed these poor-quality nest-sites from their analysis, they found that more nests were depredated during the nestling stage when parental activity was greatest. Thus nest-site quality coupled with high nest visitation may help explain the high failure of Jacky Winter nests during incubation.

Our study identified the Collared Sparrowhawk and Grey Currawong as potential nest-predators based on predator-avoidance behaviour by Jacky Winters. Other potential predators of Jacky Winter eggs and young at Gluepot include the Australian Raven (a known predator of Southern Scrub-robin eggs: Donaghey in Higgins & Peter 2002), Grey Shrike-thrush and Grey Butcherbird *Cracticus torquatus* (Major *et al.* 1999). In the present study, we observed nesting Jacky Winters defending the nest area by attacking and expelling Yellow-plumed Honeyeaters and ground-foraging Crested Bellbirds. In the Hooded Robin, Fitri & Ford (1998) also reported aggression toward ground-foraging birds (Jacky Winter and Willie Wagtail *Rhipidura leucophrys*), and also nectar-foraging *Ptilotula* honeyeaters, such as Fuscous *P. fusca* and White-plumed Honeyeaters *P. penicillata*. Interspecific aggression by nesting, ground-foraging robins might be directed at other ground-foraging birds, which occupy a similar niche and might compete for similar food (Fitri & Ford 1998). Ley *et al.* (1997) recorded that Fuscous and White-plumed Honeyeaters steal nest material from active nests of other honeyeaters and the Eastern Yellow Robin. In south-western Australia, Fulton (2006) confirmed with cameras that the Yellow-plumed Honeyeater engages in egg-predation and steals nest materials from open-cup nests. At Dryandra Woodland, Western Australia, we observed Yellow-plumed Honeyeaters stealing nest material from an active nest of a Western Yellow Robin *Eopsaltria griseogularis* with two young (RHD unpubl. data). These observations suggest that Jacky Winters defend their nests from honeyeaters that steal nest material and disrupt nesting activities.

Our observations of the cryptic posture of Jacky Winter nestlings, sitting upright with bills pointing upward, together with their cryptic mottled juvenile plumage, suggest that these traits have evolved as camouflage against diurnal avian predators. Similar behaviour and plumage have been reported in Lemon-bellied Flycatcher nestlings by Harvey & Harvey (1919) and Noske (2011).

Nest type, placement and concealment

Nest type and size, degree of camouflage, and nest placement all contribute to nest concealment from predators. The two *Microeca* species that occur in more open habitats (Jacky Winter and Lemon-bellied Flycatcher) are similar in body size and in their use of nest materials, and both place their nests on exposed dead branches

(Higgins & Peter 2002). In the present study, the two Jacky Winter nests where young fledged were 4.09 m and 2.74 m above the ground, had live branches and foliage >60 cm above the nest, and the nest-trees were situated at the edge of a more open area with low shrubs east and north of the nest. Thus sitting females at the successful nests had a more elevated, expansive view of their surroundings (cf. Götmark *et al.* 1995). The Leadend Flycatcher *Myiagra rubecula* (length 15 cm, mass 12 g) is a small, arboreal, insectivorous monarch flycatcher (Monarchidae) with similar foraging and breeding life-history traits to the Jacky Winter. It inhabits woodlands of eastern Australia, forages by sally-snatching from foliage and by flush-pursuit, builds an open-cup nest on an exposed horizontal dead branch below a live branch, has low (23%) nest success despite repelling larger intruders from its nest area and has repeated nesting attempts after failure (Trémont & Ford 2000; Higgins *et al.* 2006). The literature is ambivalent about the influence of nest-site selection and concealment from predators in relation to avian breeding success. Some studies of Northern Hemisphere open-cup-nesting passerines (Martin & Roper 1988; Kelly 1993; Weidinger 2002) lend support to the nest-concealment hypothesis that less exposure reduces predation, whereas other studies (Wilson & Cooper 1998; Braden 1999) consider that nest-predation is random and operates at larger scales than the nest-site. Martin (1993) used real and artificial nests to simulate the coexistence of four species that used the same or different nest-sites to test the hypothesis that predation favours differences in nest-sites. Nest-density and predation increased when coexisting species used similar nest-sites, suggesting that predators develop a search image for specific nest-sites rather than search randomly (Martin 1993). Comparisons between coexisting robin species can yield significant differences in the effect of micro- and macrohabitat on breeding success (Debus 2006d). Breeding Eastern Yellow Robins selected a macrohabitat of mainly moist gullies and lower slopes, whereas breeding Scarlet Robins mainly occupied ridges and upper slopes. Eastern Yellow Robin breeding territories had denser lower storey and more eucalypt saplings and shrubs than did Scarlet Robin territories (Debus 2006d). The greater breeding success of Eastern Yellow Robins was positively related to greater shrub foliage cover and density around the nest, compared with the more open macrohabitat and more exposed nest-site of the Scarlet Robin. Furthermore, the two Eastern Yellow Robin territories with the highest habitat complexity and cover scores also produced more fledglings and recruits (Table 6 in Debus 2006d).

Four resident coexisting robin species at Gluepot Reserve partitioned their habitat for territories and nest-sites. In Jacky Winters that nested in more exposed sites, the nest success of 22.2% was less than half of that in the ground-nesting Southern Scrub-robin (50% in 2001, $n = 5$; 58.8% in 2002, $n = 17$) and in the Red-capped Robin (64.7%, $n = 17$) and Hooded Robin (66.7%, $n = 3$), which mostly built nests at low to medium heights in relatively dense foliage with good concealment (RHD unpubl. data).

Post-fledging care

The duration that fledglings are dependent on parental care (post-fledging period) may help to explain life-history variation between latitudes. Our study at Gluepot ceased

soon after the Jacky Winters fledged, so we were unable to determine the length of post-fledging dependence. Wood *et al.* (2008) determined that one juvenile Jacky Winter was dependent on the adults for c. 9 weeks, and was fed mostly by the male while the female incubated eggs in a replacement nest. In the tropical Lemon-bellied Flycatcher, the post-fledging period was at least 7 weeks (Noske 2011). In the Petroicidae, the post-fledging period was <20 days in one species, 20–40 days in six species, and >40 days in another species (Russell 2000). We gathered more recent data for 16 species of Petroicidae from the literature and, with our observations, found that the post-fledging dependence period was 20–40 days in ten species, 40–60 days in four species, and >60 days in two species (Frith & Frith 2000; Higgins & Peter 2002; Dowling 2003; Fitri & Ford 2003; Powys 2004; Russell *et al.* 2004a; Debus 2006a; Wood *et al.* 2008; Noske 2011; RHD unpubl. data). For two pairs of Western Yellow Robins at Dryandra Woodland, the post-fledging period was >21 days, and one group of four Western Yellow Robins fed two fledglings on the ground for 20 days (RHD pers. obs.), thus the post-fledging period could be at least 30 days, similar to that in the Eastern Yellow Robin. Russell (2000) showed that most northern temperate bird species were independent in <20 days, whereas most southern temperate and tropical birds were independent in 20–60 days. Thus the post-fledging period of 20–60 days in most robin species corresponds with that in southern temperate and tropical birds. Russell *et al.* (2004b) assembled a large database to conduct a comprehensive comparative analysis and, after controlling for phylogeny, found that extended parental care was widespread among passerines and significantly longer in tropical and Southern Hemisphere birds than in Northern Hemisphere birds. The relevance of extended parental care of fewer young in Southern Hemisphere and tropical birds is that it is considered to be a parental investment that contributes to higher juvenile and adult survival (Russell 2000; Russell *et al.* 2004b; Tarwater & Brawn 2010).

Survival of adults

Rowley & Russell (1991) compared annual survival in northern and southern temperate bird species and found that an annual survival greater than 70% was much more prevalent in Australia than in North America and Europe. For example, based on recapture rates of four species of resident small passerines in south-western Australia, the mean annual survival was 73.5% (range 67–78%), and maximum longevity was >10 years (Brown *et al.* 1990).

Annual survival is high in the White-breasted Robin (males 86%, females 79%; Russell *et al.* 2004a) and Eastern Yellow Robin (71%; Debus 2006b). There are few survival data for tropical Australian robins, but sedentary, small-bodied White-faced Robins at Iron Range National Park, Cape York Peninsula, Queensland, have an annual adult survival rate of 75% and individuals may live up to 18 years (Coleman *et al.* 2012; Rawsthorne & Donaghey 2012). The tropical Lemon-bellied Flycatcher (12 g) also has a high longevity of at least 13.5 years (Noske 2011). There are few survival data for Jacky Winters, but the maximum longevity recorded is 5 years 3.7 months (Australian Bird and Bat Banding Scheme <http://www.environment.gov.au/topics/science-and-research/bird-and-bat-banding-data/search-abbbs-database>, retrieved 30 June 2017).

Breeding strategy

Australian robins build open-cup-shaped nests and have a suite of life-history traits such as moderately long breeding seasons, small clutch-sizes, low reproductive rates, high nest failure, multiple broods, lower nest-attentiveness, extended post-fledging care and high adult survival and longevity that are opposite to those of northern temperate songbirds and more similar to a slow pace of life exhibited by tropical passerines (Russell 2000; Russell *et al.* 2004a,b; Robinson *et al.* 2010). More recently, Martin (2015) sought to explain latitudinal variation in avian life-history traits by comparing nestling growth rates, parental effort and mortality in temperate and tropical songbirds. He discovered that tropical birds have slower peak growth but faster subsequent growth so grow wings faster than temperate birds, thus enabling tropical fledglings to escape and evade predators and reduce mortality risk. The small clutch-sizes of tropical birds allow adults to increase food-delivery rates per young and reduce mortality risk to adults and juveniles (Martin 2015). There are insufficient data on nestling growth and development, and adult and juvenile mortality, to substantiate Martin's findings for temperate and tropical Australasian robins.

The Jacky Winter has a high rate of nest-predation, builds a small nest, has a small clutch-size, and the nestlings adopt anti-predator postures, suggesting that these traits evolved in response to a high risk of nest-predation. Its parental-care strategy is also characterised by moderate nest-attentiveness and a higher number of on- and off-bouts during incubation, a moderately long nestling period, and a higher number of total nest visits and feeding trips during the nestling phase than in any other robin species. These traits are not consistent with nest-predation theory and suggest different selection pressure(s) or trade-off(s). Some traits, such as frequent short bouts on and off the nest, male incubation feeding, asynchronous hatching, brood-reduction and nestling starvation, suggest proximate behavioural responses to food availability, and an ultimate response to food limitation. The breeding strategy of frequent short bouts on and off the nest by female Jacky Winters coupled with high rates of male incubation feeding appears to have evolved to meet the energy needs of the female and her young in response to the temporal and spatial availability of invertebrate prey. We postulate that annual productivity in the Jacky Winter is constrained mostly by high nest-predation because of exposed nests and high nest visitation rates but also by food availability, and is counteracted by frequent replacement nests and an extended breeding season. Future research could include the spatial dispersal of breeding Jacky Winters in relation to habitat and social behaviour; temporal variation in food availability; growth and development of nestlings, asynchronous hatching and brood-reduction; causes of nest failure and identity of nest-predators; dispersal, survival and recruitment of juveniles; and annual and lifetime reproductive effort.

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Appendix 1. Incubation by female Jacky Winters at three nests during the last half of the incubation period, Gluepot Reserve, South Australia, 2001: incubation constancy (IC), nest-attentiveness (NA, total of on-bouts), absences (off-bouts) and number of visits to nest. The date is given as day, month; obs. = observation time; min. = minutes; n = number of observations; F = female, M = male.

Date	Time	Obs. (min.)	Min. on nest	Min. off nest	IC (%)	On-bouts (sessions)		Off-bouts (absences)		No. visits to nest		
						NA total (min.)	Mean (& range) (min.)	Total (min.)	Mean (& range) (min.)	By F	By M to feed F	Total
Nest 2												
17.9	1000–1300 h	180	115.56	64.44	64.2	109.42	4.56 (0.27–15.58), n = 24	64.44	2.48 (0.22–8.15), n = 26	24	5	30
17.9	1300–1500 h	120	43.57	76.43	36.3	47.01	2.47 (0.52–7.57), n = 19	76.43	4.25 (0.48–7.78), n = 18	19	4	23
17.9	1500–1800 h	180	124.78	55.22	69.3	124.78	16.00 (1.1–56.08), n = 8	55.22	7.89 (2.67–15.42), n = 7	8	2	10
18.9	0610–1000 h	230	190.68	39.32	82.9	190.13	6.56 (0.23–28.75), n = 29	39.32	1.4 (0.02–7.17), n = 28	29	10	39
Total		710	474.59	235.41	66.84	471.34	5.89 (0.23–56.08), n = 80	235.41	2.98 (0.02–15.42), n = 79	80	21	102
Nest 5												
14.10	1500–1800 h	180	133.43	46.57	74.13	133.43	5.34 (0.05–11.78), n = 25			25	7	32
15.10	0600–0900 h	180	142.81	37.19	79.34	146.51	4.58 (0.5–22.42), n = 32	37.28	1.17 (0.18–4.52), n = 32	32	5	37
15.10	0900–1200 h	180	109.08	70.92	60.6	103.29	2.72 (0.17–10.5), n = 38	69.31	1.87 (0.17–8.23), n = 37	38		38
15.10	1200–1500 h	180	86.77	93.23	48.21	92.23	2.31 (0.25–10.02), n = 40	95.82	2.40 (0.17–19.25), n = 40	40	4	44
Total		720	472.09	247.91	65.57	475.46	3.52 (0.05–22.42), n = 135	202.41	1.86 (0.17–19.25), n = 109	135	16	151
Nest 9												
16.10	0600–1000 h	240	201.5	38.50	84.00	203.07	5.49 (0.13–20.67), n = 37	38.50	1.07 (0.07–3.52), n = 36	37	30	67
16.10	1000–1300 h	180	140.8	39.20	78.2	140.11	4.67 (0.08–15.68), n = 30	39.20	1.31 (0.05–4.42), n = 30	30	15	45
16.10	1300–1800 h	300	199.52	100.48	66.51	198.79	4.62 (1.03–17.82), n = 43	100.71	2.29 (0.1–5.45), n = 44	43	34	77
Total		720	541.82	178.18	75.25	541.97	4.93 (0.08–20.67), n = 110	178.41	1.62 (0.05–5.45), n = 110	110	79	189

Appendix 2. Biparental care of two nestlings at one Jacky Winter nest (Nest 5), Gluepot Reserve, South Australia, 2001: brooding by female, feeding of nestlings, and number of nest visits during nestling period. Day = day of nestling period; the date is given as day, month; obs. = observation time; min. = minutes; F = female, M = male, U = unknown sex, and Y = young.

Day	Date	Time	Obs. (min.)	Brooding by F										No. visits to nest					
				Total (min.)				By F		By M		By U		Total no. nest visits/h					
				Total	Min./h	No. bouts	Total	Fed Y directly	Brought food to nest	Fed F at nest	Fed F, which fed Y	Fed Y directly	Fed Y	Total	No./h				
1	19.10	0600–0900 h	180	162.5	54.2	30	30	1	19	12	7			8	2.7	16.3			
1	19.10	0900–1200 h	180	148.2	49.4	37	40	4	16	12	4			8	2.7	18.7			
1	19.10	1400–1700 h	180	125.5	41.8	37	37	9	16	5	11			20	6.7	17.7			
4	22.10	1100–1200 h	60	38	32.6	15	17	3	6	1	2	3		8	8	23			
4	22.10	1200–1400 h	120	85.1	42.5	14	16	3	20	4	8	8		19	9.5	18			
6	24.10	0600–0900 h	180	137.1	45.7	12	12	3	22	4	16	2		21	7	11.3			
6	24.10	1430–1715 h	165	52.8	19.2	12	12	4	37	2	5	30		39	14.2	17.8			
8	26.10	0605–0905 h	180	144.9	48.3	17	21	9	20	2	13	5		27	9	13.7			
8	26.10	1400–1700 h	180	44.4	14.8	9	9	1	9	3	4	2	9	16	5.3	9			
10	28.10	0600–0900 h	180	123.7	41.2	13	13	6	23	3	18	2	1	27	9	12.3			
10	28.10	1455–1750 h	175	118.2	40.5	31	33	13	23	2	18	3	17	51	17.5	25			
11	29.10	0630–0930 h	180	102.6	34.2	28	29	7	31	1	13	17		37	12.3	20			
12	30.10	0605–0900 h	175	103.9	35.6	19	25	10	30	4	13	13		36	12.3	18.9			
12	30.10	0900–1208 h	188	79.5	25.4	23	23	6	20		8	12	3	29	9.3	14.7			
12	30.10	1500–1800 h	180	86.7	28.9	14	14	6	13		9	4	14	33	11	13.7			
13	31.10	0830–1100 h	150	79.7	31.9	15	20	13	26	1	5	20		38	15.2	18.4			
13	31.10	1500–1700 h	120	17.1	8.6	14	23	19	29			29	8	56	28	30			
14	1.11	0600–0900 h	180	64.9	21.6	22	41	41	28			28	6	75	25	25			
14	1.11	1000–1200 h	120	4.8	2.4	5	19	17	23			23	10	50	25	26			
14	1.11	1400–1700 h	180	22.2	7.4	5	7	6	2			2	30	38	12.7	13			
15	2.11	0622–0800 h	98	24.6	15.1	6	10	10	2			2	30	42	25.7	25.7			
15	2.11	0800–0900 h	60	1.5	1.5	2	12	12	14			14	8	34	34	34			
16	3.11	0638–0714 h	36										8	8	13.3	13.3			
16	3.11	1030–1056 h	26										5	5	10	11.5			
17	4.11	0700–0804 h	64										22	22	20.6	20.6			
18	5.11	0655–0800 h	65										21	21	19.4	19.4			
20	7.11	0540–0550 h	10										6	6	36	36			