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Welcome Swallow *Hirundo neoxena* breeding ecology in the Yarra Valley, southern Victoria: nest use and the incubation stage

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Welcome Swallows *Hirundo neoxena* breeding in eleven sites less than or equal to 12 kilometres apart in southern Victoria were studied over three successive seasons. Many aspects of nest use and egg production and survival agreed with information derived from a compendium of records for other temperate Australian localities. However, significant seasonal differences occurred in: (a) the percentage of active nests in a season that were not newly-constructed (100%, 86% and 77.5%), (b) the timing of laying of first and second clutches in a particular nest or site and (c) the causes of egg failure; parental desertion due to low ambient temperatures and for other reasons was significant only in 2009, egg 'disappearance' was particularly common in 2010 and 2011 and egg loss through flooding was particularly prominent in 2010. Variation among the largest colonies was limited to: (a) the relative use of newly-constructed nests and (b) the causes of egg failure; desertion at low ambient temperatures was particularly prominent in one colony, causing 29 per cent of egg failures. Egg failure due to flash flooding and the parents' death, respectively, were significant only in one colony each. Variations in rainfall and its impact and in ambient temperature probably accounted for some seasonal and spatial variability in pre-hatching breeding ecology.

INTRODUCTION

Studies of a bird species' breeding ecology provide insights into its reproductive adaptations and life history strategy. Collectively, such investigations are the source from which broad syntheses can be constructed to test the validity of important 'global' theories about aspects of avian life history evolution (e.g. clutch size, Lack 1968 and Case 1978; nestling growth rates, Ricklefs 1983 and Remes and Martin 2002). Despite the publication of some valuable syntheses of breeding adaptations and life history trends in Australian birds (Nix 1976; Yom-Tov 1987; Cockburn 1996; Russell 2000; Russell *et al*. 2004), our understanding of the evolution of their reproductive and life history adaptations is comparatively sketchy. This probably stems from the relative paucity of basic information on their breeding ecology and demography, which in turn is probably a function of the country's comparatively small number of professional and amateur ornithologists. There is therefore a real need to increase this knowledge base.

The cosmopolitan Hirundinidae comprises 83 species (del Hoyo *et al.* 2004), five of which occur in Australia. In terms of life history adaptations, it is an interesting family because nestlings have relatively slow growth rates and a mass overshoot growth pattern (Turner and Rose 1989). The Welcome Swallow *Hirundo neoxena* (14g) is a partial migrant that is widely distributed through mesic eastern, southern and south-western Australia, from the tropics to temperate latitudes, and occurs mainly in open habitats such as grassland, farmland, shrubland, woodland and open forest (Higgins *et al*. 2006). Its habit of constructing its conspicuous mud nest on human-made structures has resulted in its breeding biology being relatively well documented from a compendium of records from widely dispersed locations (Higgins *et al*. 2006). Marchant and Fullagar (1983) also summarised Birdlife Australia Nest Record Scheme data on the species' breeding from 1964–1976. Additionally, there have been four informative, focused studies of its breeding biology at different locations in temperate Australia (Schrader 1976; Park 1981; Brown and Brown 1991; Tarburton 1993). However, none of these studies have involved the kind of monitoring of large numbers of breeding attempts at multiple sites over more than one breeding season that is necessary to detect variability among seasons and on a local spatial scale.

While investigating body condition in Welcome Swallows nesting at several colonies in southern Victoria over three successive breeding seasons (Lill *et al*. 2013), data were systematically collected on the birds' breeding ecology. This study reports nest use patterns, the timing of egg laying, clutch size, the duration of incubation, the 'causes' of egg failure and the occurrence and timing of multiple breeding attempts by pairs within a season. The main aims were to: (1) identify aspects of breeding ecology that lacked temporal and/or spatial variation within the study and in comparison with other published records and therefore may be strongly genetically regulated, and (2) examine the possible causes of disparities in those features that exhibited such variation within the study. Breeding ecology of the nestling stage will be reported in a separate paper.

METHODS

Study area

The study was conducted over three breeding seasons (August – January) in 2009–10, 2010–11 and 2011–12 in the Yarra Valley, Victoria, near Yarra Glen (37° 39'S, 145° 22'E). Seven breeding sites were monitored in 2009 and eleven in 2010 and 2011. The sites were at Stringybark Creek (Sbk), Yeringberg Creek (Yc), Yarra Grange (Yg), Badger Creek

Rd-Maroondah Highway junction (Bcmh), Watts River (Wr), Healesville Yarra Glen Rd (Hyg), Old Healesville Rd (Ohr) and Tarrawarra Rd (Tarr). Four sites were in culverts under roads and the rest under road bridges; nine were on permanent or intermittent watercourses. Sites were 1.4–12.1 kilometres apart and the four largest colonies were 3.9–6.4 kilometres apart. Most sites adjoined agricultural land but had riparian vegetation nearby and three were also adjacent to woodland.

The range in long-term average monthly weather statistics for the study period in the area is: mean maximum ambient temperature (T_a) 14.8°C in August to 27.7°C in January; mean minimum T_a 4.1°C in August to 11.6°C in January; mean rainfall 68.4 millimetres in September to 46 millimetres in January.

Spring 2009 was unusually warm in south-central Victoria, particularly November and December, but rainfall overall was close to the long-term average. However, rainfall was heavy in September, particularly late in the month when it was accompanied by unusually low T_a for several days (maximum daily T_a 10.1–13.5°C). In contrast, spring 2010 had strong La Niña conditions, with exceptionally heavy rainfall, particularly in November. Daytime T_a was close to long-term average levels, but nocturnal T_a were relatively elevated. The heavy rainfall caused a series of flash floods. Late winter and spring 2011 were warmer than normal, with $T_{a\,(max)}$ and $T_{a\,(min)}$ both elevated by up to 2°C. Spring was also 1.5 times wetter than average and a particularly heavy rainfall event in early November resulted in flash flooding at several colonies.

Monitoring nests

Low nests were inspected directly and higher nests with an extendable pole, mirror and flashlight and/or by ladder. Active nests were checked (a) on alternate days throughout incubation if the timing of hatching could not be predicted or (b) daily around the projected hatching time if it could be predicted. The inception of egg-laying was not accurately recorded for all clutches, so conceivably some clutch sizes were underestimated; as nest predation appeared uncommon, this was probably only a very minor source of inaccuracy. However, intra-specific egg dumping and destruction are quite common among swallows (del Hoyo *et al*. 2004) and could potentially have influenced clutch size estimation in the study species. Disney (1988) records destruction in this species, where there was an excess of males, albeit in captive birds. I assumed that during a season re-use of a particular nest or the construction and use of a new one very close-by after nest destruction was by the same pair of birds; however, most adults were not banded and in other swallow species pairs sometimes switch nests after a breeding failure (del Hoyo *et al*. 2004), so this was not always completely certain.

Data analysis

Statistical analyses were conducted with *Systat* v. 13. Data were transformed where necessary to meet the assumptions of parametric significance tests. Comparisons among years, within a season and among colonies for continuous variables were made with analysis of variance (ANOVA) and *t* tests and for frequencies in discrete categories with chi squared and extended Fisher exact tests. Spatial variation was examined by comparing variables among the four largest colonies, sample sizes for the smaller ones being too small to permit their inclusion. It is important to note that some apparent incongruities among sample sizes stem from the fact that, mainly due to inaccessibility and logistics, not all variables could be measured on all nests. Thus analyses of many variables are based on large samples, but not the absolute number, of breeding attempts; however, exclusion of breeding attempts from some aspects of analysis was not done selectively. Results are presented as a mean ± standard error (SE).

RESULTS

Breeding sites and nest use

Sites had been used in at least 1–7 breeding seasons prior to this study and many probably for more than seven seasons. The range in the number of active nests per site was 1–25, 1–32 and 1–35 in 2009, 2010 and 2011, respectively. Fairy Martins *Petrochelidon ariel* sometimes use similar breeding sites to those of Welcome Swallows, but only one site had both species breeding simultaneously in any study year, although two others had been used by both species prior to the study. Some martin nests had been constructed to incorporate a swallow nest and a few swallows (1.1, 0.9% and 0.04% of active nests in 2009, 2010 and 2011, respectively) bred in unfinished or partly-destroyed Fairy Martin nests from previous seasons (Fig. 1). House Sparrows *Passer domesticus*, European Blackbirds *Turdus merula* and Grey Shrike-thrushes *Collurincincla harmonica* nested in some of the swallow breeding sites in small numbers.

Nests immune to destructive flash-flooding often survived intact and were re-used for several years, so that only 11 per cent of nests used during the study were newly constructed in the season of use. The percentage of nests that were new varied among years for all sites combined (2009, 0%, n = 89 nests used; 2010, 14.1%, n = 128; 2011, 22.5%, n = 138; $\chi^2_{(2)} = 22.959$, $P < 0.001$), but only varied among the four largest (n > 10 nests per season) colonies in one of three seasons (2009, all colonies 0%; 2010, 8.7%, 6.3%, 4.3% and 0%, n = 95, P = 0.764; 2011, 38.7%, 25%, 3.2% and 0%, n = 108, $P < 0.001$). One colony (Hyg) lacked new nests throughout the study. As 66 per cent and 6.5 per cent of new nests in 2010 and 2011, respectively, were second nests built (presumably usually by the same pair) very close to a nest used earlier in the season which had been destroyed, the propensity to use pre-existing nests in first breeding attempts of the season was very pronounced. Constructing a new nest for their first 2011 breeding attempt was necessary for all pairs at two colonies because of nest destruction by flash-flooding late in the previous breeding season, but the reason for the relatively high percentage of new nests used in initial breeding attempts in 2011 at Yc colony, which did not experience destructive flooding, was unclear. In all seasons, some old nests were patched up with fresh mud (Fig. 1), although this was rare in certain colonies (e.g. Hyg).

Timing of laying first clutches

Completion of the first clutch of the season in the entire study area occurred in late August (23–29 August) in 2009 and 2011, but in early to mid-August (4–17 August) in 2010. The last clutch of the season in the whole study area was completed in early December in 2009 and 2011, but not until late December in 2010.

Figure 1. *Use of each other's nests by Welcome Swallows and Fairy Martins. Left photograph shows the incorporation of a swallow nest into a martin nest, with a 'normal' swallow nest to the right. Right photograph shows a half-built martin nest without a 'spout' that was used by swallows.*

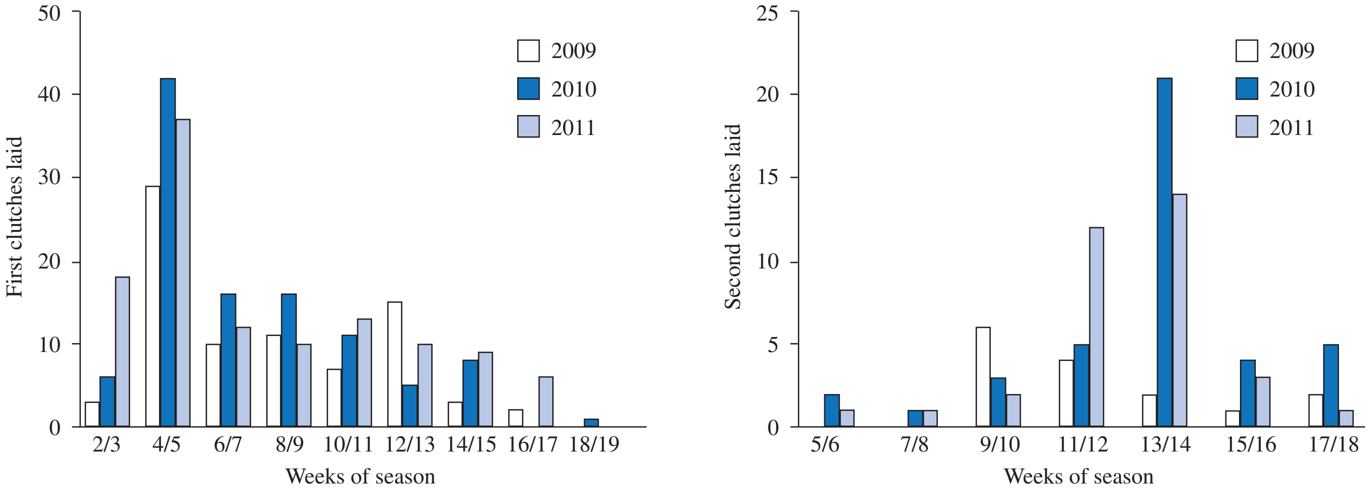

Figure 2. *Timing of laying in Welcome Swallows' first and second breeding attempts of the season in three breeding seasons. Breeding season is divided into two-week time periods; weeks 2-3 were from 21 August to 3 September and weeks 20-21 from 25 December to 7 January.*

During a season, first clutches were defined as the first to be laid in a particular nest or individual nest-site for the season. There was significant variation among years in the timing of first clutch completion ($\chi^2_{(14)} = 31.041$, $P = 0.005$) (Fig. 2).

In 2009, 79 accurately monitored first clutches were laid over 16 weeks from late August (week 2 of breeding season, W2) to early December (W17), 91 per cent being laid between early September and late October/early November (Fig 2).

In 2010, 105 first clutches were laid over 17 weeks from late August (W2) to mid-December (W18), 98 per cent being produced from late August/early September to late November. The two peak laying periods, 4–17 September (W4 and 5) and 25 September–8 October (W7 and 8), when collectively 60 per cent of first clutches were laid, were closer together than those in 2009.

In 2011, first clutches (n = 107) were laid over 15 weeks from late August/early September (W3) to early December (W17), similar timing to that in 2009. Ninety-four per cent of these clutches were laid between W3 and early November (W13). Fifty-nine per cent of first clutches in 2011 were laid during two peak laying periods, 28 August–17 September and 25 September–1 October.

Timing of laying second and third clutches

Second clutches were defined as the next clutch laid in a nest already used once earlier in the season or in a new nest built very close-by at the same individual site. The variation among years in the timing of laying of second clutches was substantial. The peak laying period was 2 October–12 November in 2009, but 30 October–26 November in the other years.

In 2009, 32 accurately monitored second clutches were laid over 10 weeks from mid-October (W9) to mid-December (W18) (Fig. 2).

In 2010, 41 second clutches were laid over 13 weeks, starting earlier (18–24 September, W6) but finishing at a similar time (11–17 December, W18) as in 2009, 34 per cent of them being produced in mid-November.

In 2011, second clutches were laid over 12 weeks from mid-September (W6) to early December (W17), most being laid in early November.

There were too few second clutches to examine spatial variation in the timing of their production. Five third clutches (i.e. clutches laid in a nest or site already used twice that season) were laid from 4–17 December in 2010 and one between 13–19 November in 2011. How the production of second and third clutches related to overall reproductive success will be considered elsewhere (A. Lill, in prep.).

Laying interval and duration

Oscine passerines usually have one-day laying intervals (LI) (Astheimer 1985). In the three seasons combined, 24.1 per cent of 116 accurately monitored sequences of the laying of up to 4 eggs definitely contained at least one LI of one day, whilst 93.1 per cent were consistent with having one or more such intervals. The time taken to lay a clutch (laying duration, LD) ranged from at least two to at least 15 days (n= 60). For the most common clutch size (4 eggs), two per cent of clutches took minimally two days to lay, 14.3 per cent three days, 71.4 per cent four days, 8.2 per cent five days and 4.1 per cent minimally six days. Thus most LIs between successive eggs in a 4-egg clutch appeared to last one day.

The three instances of extremely long LIs occurred at different points in the laying sequence. In one instance, only one of four eggs subsequently hatched, but in the other two cases 80 per cent and 100 per cent of eggs hatched in five-egg clutches, so the protracted LD was not particularly deleterious for hatching success. Protracted LIs have been attributed to bad weather in other swallow species (del Hoyo *et al.* 2004).

Clutch size and incubation period

Mean and modal sizes of all clutches for the three years combined were 3.9 ± 0.04 and four, respectively ($n = 412$) (Table 1). Some very small clutches of one or two eggs were probably incomplete. The size of first clutches was similar among years ($F_{(2, 244)} = 0.302$, P = 0.739) (Table 1), but varied during the course of the laying season ($F_{(8, 244)} = 2.006$, P = 0.046) (Table 2), being slightly larger in October and November than earlier or later in the season. Mean size of first clutches was very similar among the four largest colonies in all years (Table 2 and legend); there were too few data to compare within-season variability in clutch size in these colonies.

Second clutches did not vary in size either among years ($F_{(2, 61)} = 1.542$, P = 0.222) or during the peak laying period for such clutches ($F_{(4, 61)} = 0.546$, P = 0.236). First and second clutches laid in the same nest or individual nest-site during a season (presumably by the same female) did not differ in size in any year (mean difference: 2009, + 0.3, paired $t_{(16)} = 2.073$, P = 0.055; 2010, + 0.2, paired $t_{(22)} = 1.096$, P = 0.285; 2011, - 0.2, paired $t_{(27)} = 0.386$, P = 0.702).

Incubation periods lasted 11/12 to 20 days, with 80.8 per cent of them lasting 15/16 to 18/19 days (Table 3).

Causes of egg failure

Failure to hatch despite being incubated for the appropriate duration was the principal 'cause' of egg failure overall (41.2% of failures) and in each season (Table 4). Egg disappearance for unknown reasons, parental desertion and flooding were the other common 'causes' of egg failure, but the relative importance of the causes varied among years (Fisher exact P <0.001). There were five 'causes' of failure in both 2009 and 2010, but seven in 2011. The main differences among years were that: (a) parental desertion (due to cold weather and other unknown reasons) was prominent only in 2009 (causing 42.1% of egg failures), (b) egg disappearance for unknown reasons was particularly common in 2010 and 2011 and (c) loss through flooding was particularly prominent in 2010 (Table 4).

The 'causes' of egg failure varied among the four largest colonies for the three years combined (with some necessary category pooling, $\chi^2_{(9)} = 50.479$, P< 0.001) (Table 4). Failure to hatch despite being incubated long enough was two to four-fold more common than the next most common cause of egg failure at each of these colonies. However, whilst egg disappearance was the second most frequent 'cause' of egg failure at three of the colonies, desertion at low T_a ranked second at one colony (Hyg). Desertion accounted for 9–34 per cent of egg failures at three of the colonies, but was not observed at one (Tarr).

Re-nesting and inter-breeding intervals

Second and third breeding attempts in a nest already used earlier in the season or in a new one built close to the original nest after its destruction were probably mostly conducted by the same pair of adults. The percentage of active nests/sites that accommodated a second breeding attempt was similar in the three years (2009, 25%; 2010, 28.6% and 2011, 34.6%; $\chi^2_{(2)} = 2.161$, P = 0.339, N = 320) and the same was true for the small number of third breeding attempts (2009, 0%; 2010 and 2011, 0.02%). Second and third breeding attempts also comprised a similar percentage of all breeding events in each season (2009, 19%; 2010, 22.4 % and 2011, 30%; $\chi^2_{(2)} = 2.013$, P = 0.366, N = 428).

The percentage of active nests/sites that accommodated multiple breeding attempts was similar among the four largest colonies in 2009 (29.4%, 26.6%, 20% and 23.5%, Fisher exact P = 0.967, N = 74) and 2010 (36.8%, 18.8%, 16.7% and 10%, P = 0.622, N = 63). However, in 2011 Yc and Tarr colonies had 2.5 to 3.2-fold higher percentages of nests/sites accommodating multiple breeding attempts than Sbk and Hyg colonies ($\chi^2_{(3)} = 14.215$, P = 0.003, N = 92). Mean intervals (days) between the 1st and 2nd, and, 2nd and 3rd breeding attempts made in a nest/nest site were similar, although there were only a few of the latter (25 ± 2.84, $n = 31$ and 27.3 ± 7.9, $n = 4$, respectively; $t_{(4)} = 0.270$, P = 0.801). Two thirds of second and third attempts occurred after some degree of fledging success in the preceding brood in that nest/individual site in that season. However, the mean interval between successive attempts was similar after fledging failure (23.7 ± 6.2 days, $n = 10$) or fledging success (25.9 ± 2.8 days, $n = 25$) of the preceding attempt ($t_{(13)} = 0.317$, P = 0.756). The latter interval was much shorter than that reported for the species by Higgins *et al.* (2006).

Table 1

Variation in Welcome Swallow clutch size *(n)* over three seasons in the Yarra Valley.

	Percentage of clutches of 1-6 eggs in each year and overall			
All clutches:				
Clutch size	2009	2010	2011	All years
1	0	0	1.3	0.5
2	2	5	1.9	4.1
3	11	16.9	11.8	14
4	62	60.1	78	65.5
5	24	18	7	15.7
6	1	0	0	0.2
Mean ± SE	4.2 ± 0.1	3.9 ± 0.01	3.9 ± 0.05	3.9 ± 0.04
Mode	4	4	4	4
	(100)	(153)	(161)	(414)
First clutches all colonies:				
Mean ± SE size	4.1 ± 0.08	3.9 ± 0.07	3.8 ± 0.06	3.9 ± 0.04
	(83)	(108)	(124)	(315)
First clutches large colonies:				
Colony				
Yc	4 ± 0.2	3.9 ± 0.1	3.9 ± 0.1	3.9 ± 0.1
	(17)	(20)	(28)	(65)
Tarr	3.9 ± 0.2	3.9 ± 0.2	4 ± 0.2	3.9 ± 0.1
	(15)	(22)	(19)	(56)
Sbk	4.2 ± 0.2	3.9 ± 0.2	3.8 ± 0.1	3.9 ± 0.1
	(19)	(22)	(27)	(68)
Hyg	4.1 ± 0.2	3.9 ± 0.2	3.7 ± 0.1	3.9 ± 0.1
	(15)	(14)	(19)	(48)
Second clutches all colonies:				
Mean ± SE size	4.2 ± 0.16	4.05 ± 0.11	4 ± 0.0	4 ± 0.08
	(17)	(40)	(36)	(93)

ANOVA for first clutch size at four largest colonies over three years
Colony $F_{(3, 225)} = 0.024, P = 0.995$
Year $F_{(2, 225)} = 1.427, P = 0.242$
Colony × Year $F_{(6, 225)} = 0.667, P = 0.676$

Table 2

Variation in mean ± SE *(n)* clutch size during the breeding season. Data in two-week time blocks for the three study seasons combined.

Two-week period	Mean clutch size	
	First clutch	Second clutch
14 – 27 August	3.1 ± 0.40	
	(7)	
28 August – 10 September	3.9 ± 0.06	
	(90)	
11 – 24 September	3.9 ± 0.09	
	(65)	
25 September – 8 October	3.9 ± 0.13	
	(33)	
9 – 22 October	4.1 ± 0.18	4.5 ± 0.2
	(20)	(10)
23 October – 5 November	4.3 ± 0.13	4.3 ± 0.1
	(27)	(21)
6 – 19 November	4.1 ± 0.16	3.9 ± 0.1
	(11)	(30)
20 November – 3 December	3.8 ± 0.22	4.0 ± 0.2
	(9)	(8)
4 – 17 December	3.8 ± 0.17	4.3 ± 0.2
	(6)	(7)

Retained eggs

Eggs remaining in a nest when a breeding attempt failed during incubation were usually removed by adults before a further attempt commenced. However, occasionally they were still present embedded in the nest-lining or lying amongst the eggs of the new clutch until well into incubation or even half-way through nestling development in the subsequent attempt. Such egg retention occurred in three of 20 (15%) second breeding attempts in 2009, two of 35 (5.7%) second or third attempts in 2010 and in two of 38 (5.3%) accurately monitored second or third attempts in 2011.

Table 3

Frequency distribution of incubation period duration of Welcome Swallows in three breeding seasons. Frequency is the number of times that a particular duration was recorded with sufficient (1-2 days) accuracy.

Incubation period (days)	Frequency
11-12	1
14	1
14-15	4
15	1
15-16	7
16	9
16-17	14
17	7
17-18	14
18	4
18-19	8
19-20	7
20	1
Total	78

DISCUSSION

Comparative perspective

Many aspects of the Welcome Swallow's nest use, laying and incubation behaviour in the Yarra Valley conformed to reports for the species in other south-east Australian locations and for other mud-cup nest-builders in the genus *Hirundo* and allied genera. This is consistent with the family Hirundinidae being evolutionarily conservative (del Hoyo *et al*. 2004). In particular, the timing of laying (August–December), the frequent re-use of nests within seasons and among years, clutch size (usually 3–5 eggs, with a mean and mode of 4) and the estimated usual duration of LI (1day) and the incubation period (15–19 days) all broadly agreed with published values for the species for coastal south-eastern Australia (Marchant and Fullagar 1983; Tarburton 1993; Higgins *et al*. 2006). These aspects of the species' breeding ecology are therefore probably under strong genetic regulation and common to populations in temperate eastern Australia. The causes of egg failure listed by Higgins *et al*. (2006) were similar to those recorded in this study, except that predation appeared to be rarer in the Yarra Valley, probably accounting for less than five per cent of failures. To some extent, this conclusion is based on the assumption that egg disappearance was not attributable to predation (see below), but geographic variation in predation intensity is not unexpected.

Temporal variation within the study

Some of the temporal disparities in nest use and other features of the incubation stage appeared to be at least partly related to differing weather conditions (Australian Bureau of Meteorology 2012). In 2009, the swallows exclusively used nests remaining from previous seasons, whereas in 2010 and 2011approximately 14 per cent and 23 per cent, respectively,

Table 4

Percentage of egg failures attributable to various 'causes' in three breeding seasons and in the four largest colonies. T_a = ambient temperature. *(n)* = number.

'Cause' of egg failure	Season			
	2009	2010	2011	All years
Hatching failure	42.1	49.1	66.1	41.2
Disappearance and breakage	13.7	30.3	14.7	26.5
Flooding	0	11.4	5.7	8.7
Discarded/depredated	0	6.3	3.4	4.9
Parents' death	0	2.9	2.8	2.9
Parental desertion (cause unknown)	15.8	0	4	6.3
Parental desertion due to low T_a	26.3	0	0	7.2
Nest collapse	2.1	0	3.4	2.3
n	*(95)*	*(175)*	*(177)*	*(347)*
	Colony			
	Yc	Tarr	Sbk	Hyg
Hatching failure	64.5	70.6	49.4	56.5
Disappearance/breakage	16.3	22	32.6	9.7
Discarded/depredated	4.6	7.4	9	0
Desertion at low Ta	5.5	0	9	29
Desertion –unknown reason	7.3	0	0	4.8
Nest collapse	1.8	0	0	0
n	*(110)*	*(68)*	*(89)*	*(62)*

of breeding attempts were conducted in newly-built nests. Twenty per cent of the 49 new nests built in the latter years were constructed by pairs after destruction of their original nest in a flash flood during the season or at the end of the preceding one. There were four such floods in the exceptionally wet 2010 season, but only one each in 2009 and 2011. The significantly higher rates of re-nesting in 2011 and particularly 2010 were thus attributable partly to this flooding, but they may also have been facilitated by greater food abundance for parents resulting indirectly from the higher than average rainfall in these two seasons (Holmgren *et al*. 2001). Flash flooding was responsible for 8.7 per cent of egg failures overall, but the losses were restricted to 2010 and 2011. The late September 'cold snap' in 2009 resulted in many adults deserting their eggs, a phenomenon that did not recur during the study but which is common in swallows generally (del Hoyo *et al*. 2004). Thus directly or indirectly, variation in weather contributed to the annual variation in the occurrence of re-nesting and the 'causes' of egg failure.

Laying of first clutches commenced slightly earlier and ended later in 2010 than in the other two years. In 2009, the laying of second clutches started about four weeks later, but peaked one month earlier than in 2010 and 2011. However, there was no compelling association between these differences and the timing and variation in weather. Clutch size did not vary among years. The mean size of first clutches was slightly larger in the middle than early and late in the laying period, but did not show the progressive decline during the season often recorded in other swallows (del Hoyo *et al*. 2004).

Spatial variation within the study

Overall there was remarkably little variation in nest use and other aspects of the incubation period among the four largest colonies. However, some limited variability was evident in the use of newly-constructed nests and in the 'causes' of egg failure. Use of new nests was 2–3 times more common in two of the four colonies in one year (2011), but this disparity was largely due to construction of new nests to accommodate first clutches of the season rather than replacement of nests destroyed earlier in the season. One colony had no new nests during the entire three year study. Parental desertion at low T_a was a much more significant cause of egg failure at one of the four largest colonies than at the others, but the reason for this was not obvious, as T_a were probably similar in the foraging areas adjacent to all these colonies.

However, broadening the comparison to include some of the smaller colonies highlighted some further disparities. Nests in the four largest colonies were above the high water line during flash flooding, but 91 per cent of egg failures in the small Ohr colony were attributable to this cause. This breeding site had limited clearance between normal water level and the underside of the bridge on which the swallows nested, so that eight nests containing clutches were swept away in four flood events. This also meant that comparatively there was a lot of new nest construction at this site (61.5% new nests). Bcmh was the only colony in which parental death was known to contribute to egg failure (31.3% of identified failures), but some instances of apparent desertion could possibly have been attributable to this cause. Parental death causes some egg failure in other swallow species (del Hoyo *et al*. 2004).

Causes of egg failure

Failure to hatch, the major reason for egg failure, was recorded when eggs were clearly being incubated, were warm on inspection, remained in the nest to the projected hatching time (or well beyond), but failed to hatch. Inefficient incubation could have contributed to this phenomenon, but it might usually be expected to affect all the eggs in a clutch and only 35 per cent of hatching failures involved the entire clutch. Therefore infertility and embryonic growth defects seemed more likely reasons for failure to hatch.

Ricklefs (1969) and Martin (1995) showed that predation is a major determinant of fledging success in altricial birds. It accounted for up to five per cent of egg failures in the present study, but egg disappearance was associated with 26 per cent of failures and could theoretically also have been caused by predation. However, the evidence is equivocal. Very few instances of disappearance were accompanied by any nest damage. When nests are hard to access, a predator might be expected to consume the entire clutch (perhaps over several visits) and this occurred in only 38 per cent of 42 documented instances of egg disappearance. Predation of Welcome Swallow eggs has been recorded elsewhere (Higgins *et al*. 2006), but nest contents in most breeding sites in this study would have been immune to predation except by fairly small, light and agile birds, by virtue of the nests' placement well above ground level and often over water, and their adhesion to smooth, vertical surfaces. The most likely candidate predator was the Grey Shrike-thrush, which preys on small passerines' eggs (Major *et al*. 1999; Berry 2002); a pair nested in each of two swallow colonies in 2010 and the species was present in and near several other colonies in all breeding seasons. No visual evidence was noted of brood parasitism by cuckoos and they were rarely heard or seen near swallow nesting sites.

A possible alternative explanation is that eggs that were not developing normally were discarded by the parents away from the nest, but that would often have required them to distinguish non-developing from developing embryos; if they could do that, why were so many eggs and entire clutches that were not going to hatch retained and incubated to, and past, hatching time? A third possible explanation for egg disappearance is that it was effected by neighbouring adults, a well-documented phenomenon in swallows and martins (Tarburton 1993; del Hoyo *et al*. 2004).

Parental desertion at low T_a and flooding were the other main causes of egg failure. The former is common in swallows because the density of aerial insects upon which they prey decreases at low T_a (Bryant 1975; O'Connor 1984; del Hoyo *et al*. 2004). Welcome Swallows need wet mud for nest construction and culverts and bridges over creeks provide smooth, vertical surfaces for attaching nests in sites relatively inaccessible to predators. A cost of this reliance on water is occasional loss of progeny to flash flooding.

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REFERENCES

Astheimer, L. (1985). Long laying intervals: A possible mechanism and its implications. *Auk* **102**: 401–409.

Berry, L. (2002). Identifying nest predator species in a southern Victorian woodland using remotely triggered cameras at artificial nest sites. *Corella* **26**: 24–26.

Brown, R. J. and Brown, M. N. (1991). Nest records of the Welcome Swallow 1974/5 to 1988/89. Middlesex Field Study Centre report. Pp. 10–43. *RAOU Report* **77**.

Bryant, D. M. (1975). Breeding biology of house martins *Delichon urbica* in relation to aerial insect abundance. *Ibis* **117**: 180–216.282.

Case, T. H. (1978). On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Quarterly Review of Biology* **53**: 243–282.

Cockburn, A. (1996). Why do so many Australian birds cooperate: social evolution in the Corvida? In 'Frontiers of population ecology' (Eds. R. B. Floyd, A. W. Sheppard and P. J. De Barro). Pp. 451–472. (CSIRO: East Melbourne, Australia.)

del Hoyo, J., Elliott, A. and Christie, D. A. (2004). 'Handbook of the Birds of the World. Vol. 9. Cotingas to Pipits and Wagtails*'*. (Lynx Edicions: Barcelona.)

Disney, H. J. de S. (1988). Notes on breeding of Welcome Swallows in captivity. *Australian Zoologist* **24**: 211–215.

Higgins, P. J., Peter, J. M. and Cowling, S. J. (2006). 'Handbook of Australian, New Zealand and Antarctic Birds Volume 7 Boatbill to Starlings'. Pp. 1517–1548. (Oxford University Press: Melbourne.)

Holmgren, M., Scheffer, M., Ezcurra, E., Gutiérrez, J. R. and Mohren, G. M. J. (2001). El Niño effects on the dynamics of terrestrial ecosystems. *Trends in Ecology and Evolution* **16**: 89–94.

Lack, D. (1968). 'Ecological Adaptations for Breeding in Birds'. (Methuen and Co: London.)

Lill, A., Rajchl, K., Yachou-Wos, L. and Johnstone, C.P. (2013). Are hematologial variables reliable condition indicators in nestlings: the welcome swallow as a case study. *Avian Biology Research* **6***:* 57-66.

Major, R. E., Christie, F. J., Gowing, G. and Ivison, T. J. (1999). Elevated rates of predation on artificial nests in linear strips of habitat. *Journal of Field Ornithology* **70**: 351–364.

Marchant, S. and Fullagar, P. J. (1983). Nest records of the Welcome Swallow. *Emu* **83**: 66–74.

Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation and food. *Ecological Monographs* **65**: 101–127.

Nix, H. A. (1976). Environmental control of breeding, post-breeding dispersal and migration of birds in the Australian region. *Proceedings 16th International Ornithological Congress, Canberra*. Pp. 272–305. (CSIRO: Canberra.)

O'Connor, R. J. (1984). 'The growth and development of birds'. (Wiley: New York.)

Park, P. (1981). Results of a nesting study of Welcome Swallows in southern Tasmania. *Corella* **5**: 85–90.

Ricklefs, R.E. (1969). An analysis of nesting mortality in birds. *Smithsonian Contributions in Zoology* **9**: 1–48.

Ricklefs, R. E. (1983). Avian postnatal development. *Avian Biology* **7**: 1–83.

Remes, V. and Martin, T. E. (2002). Environmental influences on the evolution of growth and developmental rates in passerines. *Evolution* **56**: 2505–2518.

Russell, E. M. (2000). Avian life histories: Is extended parental care the southern secret? *Emu* **100**: 377–399.

Russell, E. M., Yom-Tov, Y. and Geffen, E. (2004). Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behavioral Ecology* **15**: 831–838.

Schrader, N. W. (1976). Breeding of the Welcome Swallow at Ivanhoe in western New South Wales. *Australian Birds* **11**: 1–7.

Tarburton, M. K. (1993). A comparison of the breeding biology of the Welcome Swallow in Australia and recently colonized New Zealand. *Emu* **93**: 34–43.

Turner, A. and Rose, R. (1989). 'Swallows and Martins: An Identification Guide and Handbook'. (Houghton Mifflin: Boston.)

Yom-Tov, Y. (1987). The reproductive rates of Australian passerines. *Australian Wildlife Research* **14**: 319–330.