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Timing, nest site selection and multiple breeding in House Martins: age-related variation and the preference for self-built mud nests

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Almost all accounts of the reproductive biology of House Martins *Delichon urbicum* are based on studies of birds breeding in artificial nests that are monitored every few days. Here, I provide a study on House Martins using self-built mud nests at a single colony in Gaast, The Netherlands (225 nest attempts in 2004–2011); the stages of breeding were inferred from 'remote' observations of parental and chick behaviour. Small chicks were noticed from 30 May onwards, with a first peak of nestling appearance in 5–9 June. A second, and larger, peak in small chicks occurred in late June. Large chicks from first broods were noticed from mid June to mid August, and the first large chicks from second broods from late July onward. The last fledglings left nests in late September. Among the 205 successful nest attempts, 62% had one brood, and 38% had two broods (three in one case). The first nest sites to be occupied in mid-April were always old nests that had survived the winter. Surprisingly, the use of old nests did not result in earlier incubation and chick-rearing activities. Nevertheless, re-used near-intact old nests hosted multiple broods in 72% of cases, a much higher percentage than in newly built nests (20%). The earlier occupation of old nests and the greater incidence of second broods was further associated with a relatively high percentage of older House Martins. Whereas only 8% of 126 nests hosting one brood were occupied by at least one known >2nd calendar year bird, no fewer than 30% of the 79 nests with two broods were. Despite a steady offering of clean wood-concrete nests at the colony, such artificial alternatives were occupied in only 23 out of 307 possible cases, rather than the near-100% occupancy of old mud nests and nest remains. Also, the start date of occupation was later than that of intact or partial old mud nests. This strong preference by older birds for (the remains of) existing mud nests and the rejection of clean, strong artificial nests, implies that any costs of being exposed to greater numbers of ectoparasites such as louse flies *Crataerina hirundinis* overwintering in old nests are outweighed by the signal of quality inherent in the occupation of parasite-infested old mud nests.

Key words: age effects, artificial nests, *Delichon urbicum*, Hirundinidae, louse flies, parasites, reproductive effort, timing of reproduction

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Trade-offs are fundamental to the evolution of 'life histories in the broadest sense of the word' (e.g. Lessells 1991, Stearns 1992, Daan & Tinbergen 1997, Piersma & van Gils 2011). To bring reproductive schedules forward, and/or free-up time and energy for other reproductive activities, birds that invest heavily in the

building of nests (Hansell 2007) might gain an advantage if they could capitalise on their own previous building efforts, or on the work of others. Life-history cost-benefit functions, and these may well include nest-building decisions (Collias 1964, Soler *et al.* 1998a), vary with age for good biological reasons (Roff 1992).

The swallows and martins Hirundinidae are a speciose family of passerines showing little variation in size and shape (Turner 2004). This lack of variation in the shape of the birds themselves is made up by the large variety in the type of nests that swallows use, variation that has served as a basis for the first modern taxonomy of the Hirundinidae (Mayer & Bond 1943). Since then, the evolutionary relationships within the swallow family have been verified by molecular approaches (Winkler & Sheldon 1993, Sheldon *et al.* 2005). The clade of mud nesting swallows that includes the genera *Hirundo* (barn swallows) and *Delichon* (martins) evolved from swallows digging their own burrows for nesting. Among the mud nesters, the more elaborate nests are built by the most derived species (Winkler & Sheldon 1993), with *Delichon*, a genus characterised by their covered but otherwise unadorned mud cups, occupying a middle position.

Every year House Martins *Delichon urbicum* need to build a mud nest, or usurp an existing nest that survived the ravages of the northern winter. The requirement to provide over 1000 pellets of wet mud to construct a new nest in the course of 2–3 weeks (Lind 1960), represents a considerable reproductive investment (collecting, flying in, and applying the equivalent of 20 to 40 times a body mass of 18.3 g; Piersma & van der Velde 2009, pers. obs.). By adopting intact old nests, or by rebuilding damaged old nests, House Martins would save time and energy (Lind 1960). Nevertheless, there is a downside to reuse, in the form of abundant ectoparasites such as louse flies (Diptera: Hippoboscidae), fleas (Siphonaptera) or swallow bugs (Hemiptera: Cimicidae) awaiting their returning hosts in spring (Summers 1975, Brown & Brown 1996, Pilgrim & Galloway 2003). Summers (1975) assembled observational and experimental evidence that louse fly *Crataerina hirundinis* populations build up in groups of old nests that survive the winter. This would suggest that House Martins face a trade-off between taking the time and effort to build a new and initially clean mud nest, or accepting an intact or damaged nest from the previous summer, in the latter case accepting the overwintering ectoparasites that come with it.

In his classic studies on the life-history of House Martins in southern England (Bryant 1975) and southern Scotland (Bryant 1979), David Bryant established that older birds made earlier starts to the breeding season and also reared more young partly because older birds were more likely to breed twice, rather than once, within a summer season. Multiple breeding occurred in 87% of the pairs in England and 77% of the pairs in Scotland. In southern Germany, Hund &

Prinzinger (1985) similarly found that 1-year old birds are less likely to start a second brood (35%) than older birds (51%). That raising a second brood correlated with lowered overwinter survival in females, but not males, in Scotland (Bryant 1979), is evidence for a sex-linked life-history trade-off that could also vary with age.

For easy access to eggs and young, Bryant (1975, 1979) and Hund & Prinzinger (1979, 1985) studied House Martins breeding in nestboxes, rather than the usual repaired or entirely new, self-built mud nests. Sometimes martins were even moved from natural mud nests to artificial nests. The use of nestboxes means that these authors were unable to examine the role of nest site selection with respect to the use of old nests, the rebuilding from the remains of old nests, or the building of new nests (for the discussion of the problems and opportunities of nestbox studies, see Møller 1989, Lambrechts *et al.* 2010). Also, disturbance caused by near-daily nest checks might encourage House Martins to make a move between successive broods (and perhaps even influencing the likelihood of 2nd broods) (Bryant 1975). The present study aimed to establish whether the links between timing, multiple breeding and age are general and also occur under 'natural' conditions by collecting 'non-invasive' observations of House Martins using non-manipulated nests in a colony in The Netherlands. To contribute to the general problem of nest site selection, I included an experimental angle to the study by (1) removing all nests and nest remains in one sub-colony in one year to examine post-breeding nest mass and content, and (2) providing House Martins returning in spring with clean and ready-to-use alternatives in the form of a large array of artificial wood-concrete nests.

METHODS

Observations on breeding House Martins were carried out in the spring and summer of the years 2004–2011 at two sub-colonies on a single large red-brick house in Gaast (53°01'N, 05°24'E), a small village in the province of Friesland, The Netherlands (see Piersma 2008, Piersma & van der Velde 2009, 2012, for more information on the study system). Gaast is situated between a region with modern industrial dairy farming (Groen *et al.* 2012 for a landscape description) and the shoreline of Lake IJsselmeer, with extensive reed bed areas within 500 m of the colony. Nests were built at heights of 3 to 7 m under an eastward facing gable and under a northward facing gable (respectively the East



Figure 1. View of the House Martin study site in Gaast (with the East sub-colony visible). Martins construct their nests under the gable, or choose among the 42 artificial nests. Photograph T. Piersma, end of May 2007.

and North sub-colonies). At a height of 4 m under the East colony a linear array of 42 artificial wood-concrete nests (15 cm wide, 9 cm high, and 12 cm deep, 2 cm thick walls, and with a 6.5 cm wide and 2.3 cm high nest entrance, all mounted under a 35 cm wide overhang) was present during all study years (Figure 1). One of the nests had a model martin peeping from the nest entrance and was thus unavailable. In the last three years, 2009–2011, seven of the artificial nests were reduced to their base, a 5.5 cm deep ring of wood-concrete outlining the shape of the nest and providing a base on which the House Martins could build. The artificial nests were removed and cleaned in October or November, and then kept dry and indoors until they were put back in early April the next year.

In early April I scored the extent that nests from previous years survived the winter (in percentages of the remaining fabric). From late April to mid September the presence and activity of adult birds, the

development of all the nests of the colony, and the presence of chicks of various sizes were recorded in ca. 1-hour observation sessions carried out at weekly intervals. Every year the nests were numbered and identified on the basis of drawings and/or photos of the sub-colonies (also with reference to the history of the same nest, or nest location, in previous years). In the following analyses I assumed that every nesting attempt was statistically independent. Although some individuals in the colony were individually marked with colour-rings (Piersma 2008, see below), observations were too sparse to enable advanced statistics on nest fates that account for ties such as precise location on the gable and the identities of birds occupying the nests. This seems reasonable as the ‘fluency’ of colony life (House Martins do move extensively between parts of the extended village colony between years, and even between successive breeding attempts) limits the potential effects of such pseudoreplication.

To establish the start and finish dates of individual nests, from mid May to early June notes on the completion and use of nests were made more frequently. On the basis of regular scores of the percentage of the outer surface that individual nests were completed, I estimated dates that nests were 10, 25, 50, 75, 90 and 100% complete. As even old nests usually received some addition of wet clay pellets, especially around the entrance, the approximate dates of completion of such nests could be established too. Nest cup completion is followed by several days where grass stems and then feathers are brought into the nest, followed by a period where there is a high likelihood that fights will occur at the nest entrance. This probably indicates the days that pre-laying females are fertile; during such times it is obvious that males are very alert (often hanging half out of nests and watching the movements of potential extra-pair mating partners/competitors and their social mates; see Hammers *et al.* 2009).

The period of egg-laying is indicated by the two partners making very frequent exchanges on the nest, with shifts lasting only a few minutes (Lind 1960). Hereafter, shifts take up to 45 min (Lind 1960); the occurrence of regular shifts at the nest entrance (one adult going in is immediately followed by another coming out) and the absence of fights at the entrance thus indicated incubation. After nest completion, the first really good observational fix of the stage of breeding is when adults come out of the nest with faecal sacs (indicating freshly hatched chicks), or when the bold heads and pale orange-coloured beaks of ca. 1-week-old young are visible in the entrance hole for the first time (usually a few days later). Half-grown chicks are recognizable by their 'feather plumes' at both sides of

the heads. Fully feathered 'large' chicks comprised the third chick stage that I distinguished. The large chick stage lasted the longest (over 2 weeks), and at some point included a session during which I recorded that large chicks (usually still begging and fed by their parents), would fly out of, and into, the nest (or a neighbouring empty nest). This was the fledgling stage. For second broods, especially late in the day, there could be some confusion on stages, as fledglings from the first brood would come to sleep in the nests (or pass by during daytime, and sometimes even help to provision second brood chicks).

In late October 2008 I removed all mud nests of the East sub-colony, cutting the mud walls so that a contour a few mm thick was left on the walls. I took this opportunity to: (1) count the number of pupal cases (puparia) of louse flies (Hippoboscidae; see Summers 1975), (2) score the incidence of fleas, (3) weigh (to the nearest g) the dry nest content (feathers and dry grasses) and (4) weigh the amount of dry mud comprising the nest.

During the breeding season the nests were never disturbed during daytime, e.g. by trying to examine nest content (the routine of most students of House Martin breeding biology so far). However, on a few occasions each summer (usually in June and July), birds were captured using mist nets right in front of the two sub-colonies (and indeed at sub-colonies elsewhere in the village; see Piersma & van der Velde 2009, 2012). This caused some disturbance, including birds being taken away for ringing for up to 45 min and the alarm-calling of individuals that escaped the net or that were set free again. On 17 June and on 5, 14 and 16 July 2007, after having blocked their nest entrances

Table 1. Number of failed, single and multiple breeding attempts in 225 'natural' House Martin nests in Gaast in 2004–2011 (the two nests that were aborted upon completion were excluded here). Failed = given up in the course of incubation or brood rearing, 1 = raised one brood, 2 = raised two broods.

Year	Sub-colony								Totals						
	East				North				Failed		1		2		Sum
	Failed	1	2	Sum	Failed	1	2	sum	n	%	n	%	n	%	n
2004	1	2	3	6	0	1	4	5	1	9.1%	3	27.3%	7	63.6%	11
2005	1	11	0	12	0	2	2	4	1	6.3%	13	81.3%	2	12.5%	16
2006	0	9	9	18	0	2	3	5	0	0.0%	11	47.8%	12	52.2%	23
2007	3	14	13	30	0	2	5	7	3	8.1%	16	43.2%	18	48.6%	37
2008	4	16	9	29	0	3	4	7	4	11.1%	19	52.8%	13	48.6%	36
2009	4	18	2	24	0	2	8	10	4	11.8%	20	58.2%	10	29.4%	34
2010	4	19	1	24	0	7	7	14	4	10.5%	26	68.4%	8	21.1%	38
2011	1	13	3	17	2	5	6	13	3	10.0%	18	60.0%	9	30.0%	30
Totals	18	102	40	160	2	24	39	65	20	8.9%	126	56.0%	79	35.1%	225

with soft paper props the evening before, I captured birds leaving their nests at day break. In addition, in 2007–2009 over 130 birds received individual combinations of two colour-rings on one tarsus, in addition to the metal ring on the opposite leg (Piersma 2008). Ringing ensured that for some individual birds their relative age (2nd calendar year or older) was known. In a minority of cases, but more so for the colour-ringed birds, birds could be assigned to the use of individual nests (e.g. Piersma 2008).

All statistical analyses were carried out in program SYSTAT 13.

RESULTS

Nest success

The number of ‘natural’ nesting attempts (i.e. in structures other than artificial nests) on the house varied between 11 in 2004 and 38 in 2010 (Table 1). In addition to these 225 attempts to breed in natural mud nests, there were two occasions where House Martins worked on a nest in which they did not start breeding. In most years the sub-colony at North was smaller than the sub-colony at East, but by 2011 North had built up to a similar level (respectively 17 and 13 nests in East and North). A small number (20) of the 225 completed nests failed during incubation or the early chick stage, the remaining 91% of nests yielding one or two broods (Table 1). Among the 205 successful nests, 61.5% had one brood in a season, and 38.5% hosted two (or in one case three) broods.

Among the successful nests, in the East sub-colony 28.2% of the nests had two broods (and in one case a third, further included in the 2-brood category); at 61.9%, the percentage of multiple breeding was more than twice as high at the North sub-colony (Pearson $\chi^2 = 20.1$, $df = 1$, $P < 0.0001$). The higher incidence of multiple breeding at North correlated with a lower percentage of nests being entirely newly built at North than at East (23.8% and 63.4% among the successful nests, respectively, with the percentage nearly intact (71–100% intact) reused old nests being 50.9% and 8.5%; Pearson $\chi^2 = 49.9$, $df = 2$, $P < 0.0001$).

Timing of breeding

Nesting activities started in late April, with a first peak in start dates from 5–10 May (Figure 2A). The early nesting attempts were usually in intact or damaged old nests. Later on, with old nests becoming unavailable, the tendency to begin completely new nests increased (Figure 2A). The suggestion of a two-peaked pattern

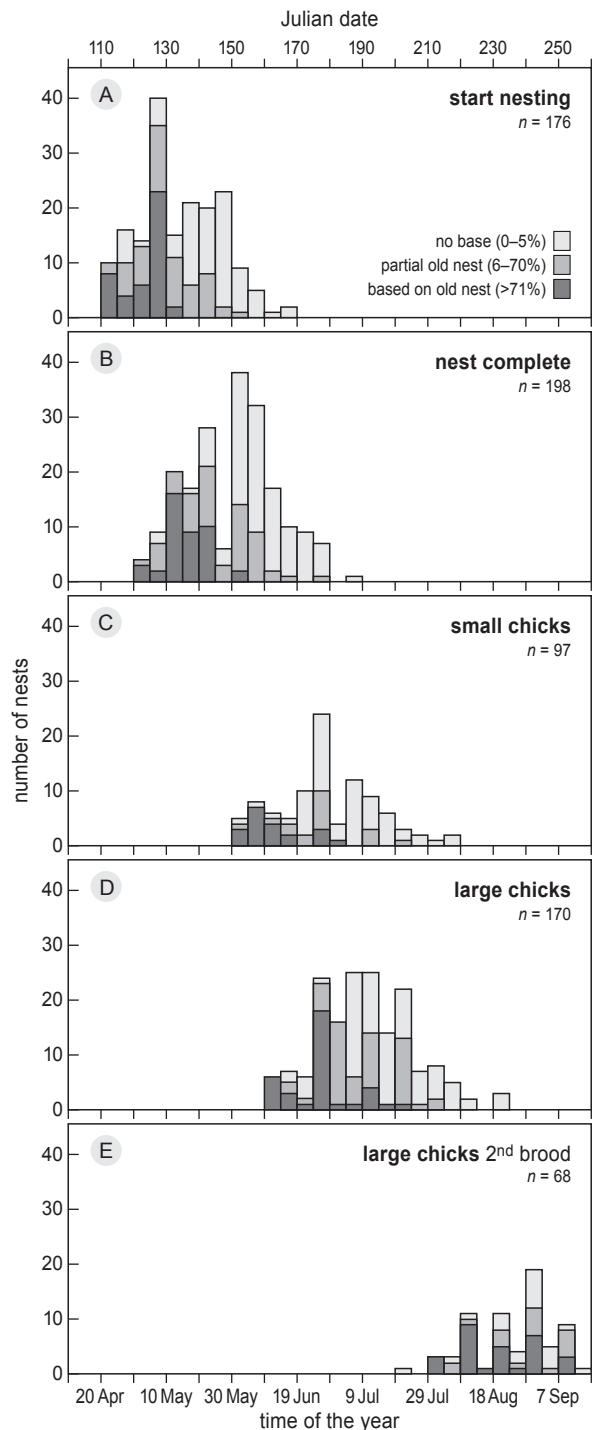


Figure 2. Timing of the different stages of breeding as a function of the base of the mud nest in House Martins at a colony in Gaast. This incorporates observations on 227 nests in 2004–2011 (two of which were immediately deserted upon completion). Not all nests were characterised during all stages which caused variation in sample sizes. See Methods for the definitions of the various stages.

was still present in the timing of nest completion (Figure 2B), and in the timing of the small chick phase as well (Figure 2C).

The first small chicks were observed in late May, and the first peak in their presence was from 5–9 June. The second, and much larger, peak in the first observations of small chicks was from 25–29 June. The first large chicks of the first brood were observed from 9–14 June, and the last large chicks from 18–23 August (Figure 2D). The first large chicks of the second brood showed up from 24–29 July onward, with a peak in late August and the last being seen in mid September (Figure 2E). The maximum number of chicks observed begging in first broods was slightly larger than in second broods, with averages of 2.1 and 1.8 chicks respectively (two-sample *t*-test, $t = 3.4$, $df = 167.4$, $P = 0.001$).

Surprisingly, with an average time of 15 days, near-intact old nests were not much faster to complete than partial old (which took 0.2 days more) or newly built (which took 2 days more) nests (ANOVA, $F_{2,174} = 3.6$, $P = 0.03$). However, whereas the rebuilding of nearly intact old nests in the period 20 April–12 May was strongly negatively correlated with starting date (Figure 3, one day spent less on ‘nest-building’ for every day started later), the time to completion of partial old nests and new nests hardly changed in the course of the summer (for 170 successful nests with known starting and completion dates, a General Linear Model showed significant effects of starting date, $F_{1,164} = 24.5$, $P < 0.0001$, nest category, $F_{2,164} = 13.7$, $P < 0.0001$, and the interaction between the two, $F_{2,164} = 14.3$, $P < 0.0001$). Thus, whereas the first occupied old nests in mid April were ‘played with’ for almost four weeks, the last ones only took a few days of occupation before breeding started (Figure 3).

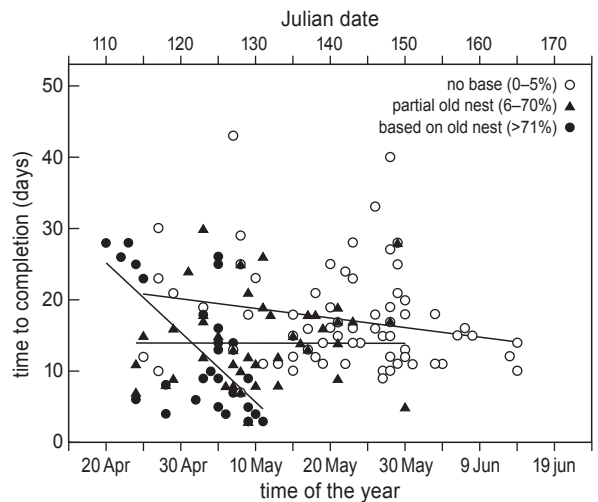


Figure 3. Time spent on building the nest as a function of the base of the mud nest in House Martins at a colony in Gaast. This is based on observations of 227 nests in 2004–2011, two of which were deserted upon completion. See Methods for the definitions of the various stages.

That reused (intact or partial) old nests yielded earlier breeding phenologies (Figure 4A, in all three phases ANOVAs showed significant heterogeneity among nest categories, $P < 0.0001$), appears to be correlated with the occurrence of second broods (Figure 4B). Successful nests hosting second broods showed significantly earlier timing than nests with a single brood with respect to starting date ($F_{1,175} = 33.6$, $P < 0.0001$), nest completion date ($F_{1,196} = 41.7$, $P < 0.0001$), and large chick (first brood) date ($F_{1,163} = 39.7$, $P < 0.0001$). Thus, the use of old nests is strongly associated with the number of broods (Table 2): nearly intact old nests hosted multiple broods in 71.7% of cases, whereas newly built nests did so in only 20.0% of

Table 2. Incidence of failed, single and multiple breeding at 225 House Martin nests in Gaast in 2004–2011 as a function of the base of the nest (top, with row percentages), and the likelihood that a known ≥ 2 nd calendar year old individual was involved in the breeding attempt(s) (bottom, percentages referring to number of cases per brood category).

base of starting nest	failed		number of broods			
	<i>n</i>	(%)	1		2	
	<i>n</i>	(%)	<i>n</i>	(%)	<i>n</i>	(%)
no base (0–5%)	15	(12.5%)	81	(67.5%)	24	(20.0%)
partial old nest (6–70%)	3	(5.1%)	34	(57.6%)	22	(37.3%)
old nest (>71%)	2	(4.4%)	11	(23.9%)	33	(71.7%)
	%	(<i>n</i>)	%	(<i>n</i>)	%	(<i>n</i>)
likelihood of use by known ≥ 2 nd cy individual	5.0%	(20)	7.9%	(126)	30.4%	(79)

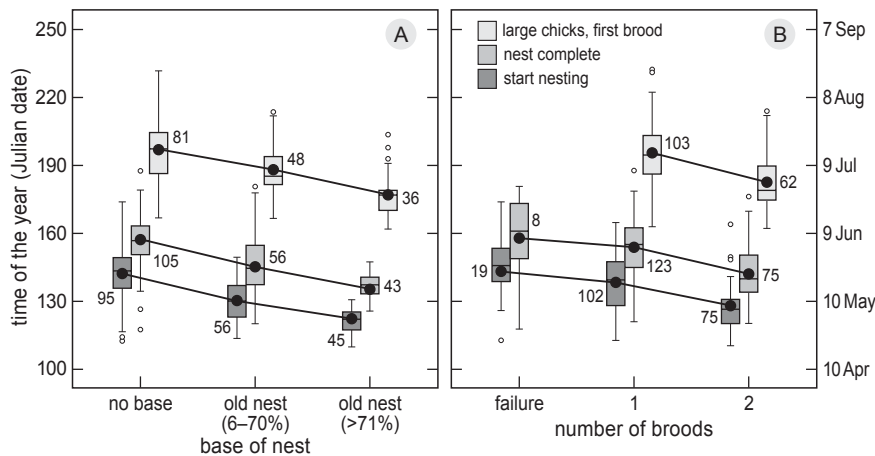


Figure 4. Timing of the different stages of breeding of House Martins as a function of the base of the mud nest (A) and in relation to the number of broods raised within a season (B). Box-plots show the variation in timing (with median and box incorporating 50% of values and the vertical bars giving the range, plus outliers) and the dots indicate the average values. *n*-values for each of the categories are given next to the boxes.

cases. Using the percentage known (on the basis of previous ringing) old (>2nd calendar year) birds associated with the various categories of nests, 5.0% of the 20 failed nests, 7.9% of the 126 nests hosting one brood, and 30.4% of the 79 nests with two broods were occupied by a known old bird (Table 2). Older birds were clearly the most successful.

Nest site selection

The 25 mud nests removed and examined in October 2006 incorporated on average 352 g (SD = 95 g, range = 210–650 g) dry mud and 28.8 g dry nest material consisting of grass stems and feathers (SD = 14.5 g, range = 5–60 g). Twenty-three of the 25 nests contained at least one intact louse fly puparium, with an average of 19.3 intact puparia (maximum 75). Only about six of the 25 nests contained fleas, but in all these cases fleas were numerous, counting in the 100s. Four nests contained a few larvae or pupae of large unidentified flies.

Despite a steady offering of clean artificial nests at the East sub-colony, House Martins only used them sparsely (Table 3). From 2004–2011 artificial nests were occupied in 23 of 307 possible cases (7.5%), and in only one case an artificial nest hosted two broods. In only 3 of these 23 cases (13.0%) a known old (>2nd cy) bird was involved. Consistently, the start of occupation including ‘nest building’ (usually some clay pellets were applied to the entrance of these wood-concrete nests) was distinctly later than that of the ‘comparable’ near-intact old mud nests (Figure 5; the difference between the starting dates of the two categories was significant, ANOVA, $F_{1,105} = 26.2$, $P < 0.0001$).

DISCUSSION

The overall percentage of successful nests that hosted two (and in a single case three) broods (38.5%) was lower than expected for a northwest European study site (60–90% in the review by Møller 1984). In central Germany the percentage of second broods was correlated with good weather conditions in July (Rheinwald 1979). Otherwise, my observational and non-invasive study on House Martins breeding in self-made mud nests has confirmed several published notions based on nestbox studies. As shown by Bryant (1975), nests with

Table 3. Availability and use of artificial wood-concrete nests by House Martins at the East sub-colony in Gaast in 2004–2011. Nests were considered ‘attended’ if they were visited several times in a season, with birds going in and out (these often contained straw or even feathers found when cleaning out in October after the breeding season), but where no chicks were seen later on. From 2009, 7 artificial nests were cut in half and could only serve as a base to an otherwise self-built mud nest (see methods).

Year	Available nests	Attended only	1 brood	2 broods
2004	41	0	0	0
2005	41	5	2	0
2006	41	8	3	0
2007	41	9	3	0
2008	41	6	0	1
2009	34	5	6	0
2010	34	2	4	0
2011	34	4	4	0

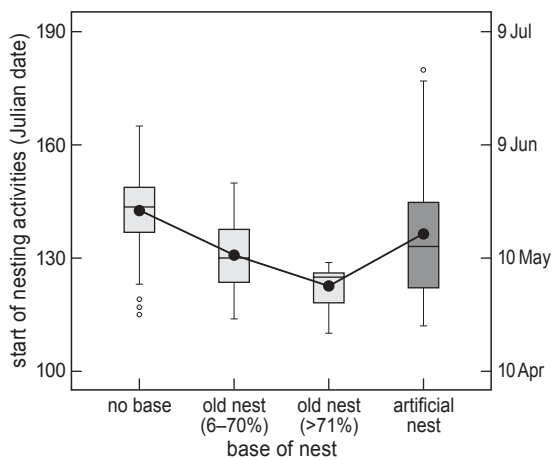


Figure 5. Timing of the start of nesting activities by House Martins using artificial wood-concrete nests (right box, $n = 62$) compared with birds building new or using old mud nests (left 3 boxes, $n = 216$, selected for 2005–2011, as no birds used artificial nests in 2004). See Figure 4 for explanation of box-plots.

two broods in a season are started much earlier than nests with single broods, and Bryant (1979) and Hund & Prinzinger (1985) also showed that the birds occupying nests with two broods or more were more likely to be over one year old. The incidence of louse flies in my sample of nests (i.e. an average of 19 puparia) compares well with Summer's (1975) estimate of 17 puparia.

That the first birds at re-occupied old nests took so long before starting egg-laying and incubation (Figure 3), suggests a benefit of such pre-emptive behaviour as well as a nutritional constraint. Bryant (1975) for southern England, and Waugh (1978) for southern Scotland, showed that the amount of aerial insects reaches a summer plateau from early or mid May onwards. This suggests that early in the season flying insect availability may be a limiting factor to egg-laying, or even the amount of time House Martins can devote to nest building rather than foraging (Lind 1960).

That especially older, experienced House Martins successfully compete for the (remains of) old mud nests (probably because they return earlier from wintering grounds in tropical Africa; see Hobson *et al.* 2012), combined with the underuse and late settlement by younger birds of the clean and sturdy artificial nests, suggests that relative to other considerations, the presence of ectoparasites is of minor concern to House Martins. Although ectoparasites have been shown to have serious detrimental effects on swallows (Brown & Brown 1996), in a recent study (Walker & Rotherham

2011) louse flies *Crataerina pallida* did not have a negative effect on the growth and survival of Common Swifts *Apus apus* chicks (but see Bize *et al.* 2004). That the artificial nests hang at a height of 4 m, whereas the self-built nests were found at heights of 3–7 m, may have made them on average less attractive (although self-built nests at even lower heights were used elsewhere in the village),

Instead, a real mud nest, whether an old one usurped early in the season or a newly built one, may be a strongly sexually selected driver of nest site and mate choice in House Martins and other mud building swallows (Soler *et al.* 1998b). This trade-off might even explain why House Martins show evidence of age-assortative mating (Hund & Prinzinger 1985). A more prosaic explanation is that by the time the young birds returned to the colony, all old nests were occupied. Nevertheless, even then the young birds in our colony did not go to the available wood-concrete nests en masse, but rather built their own.

The increase in the number of nests at the North gable during the years that the number of nests declined in the East sub-colony (Table 1), can be explained by the much smaller loss of nests over winter at North combined with a strong preference of House Martins to reuse old nests. Although artificial wood-concrete nests of the type employed here tend to be well used by House Martins in parts of Germany (Böhringer 1960, Rheinwald 1975, 1979, Hund & Prinzinger 1985), for a situation such as the one in Gaast, where wet clay apparently is sufficiently available when nests are being built, House Martins may only be encouraged to use artificial nests if such nests are better mimics of natural mud nests than the light-coloured and rather smooth-faced wood-concrete nests used here. This suggestion invites further experimentation, including into the height at which the nests are mounted. Really attractive artificial mud nests would also enable experimental assessments of the degree to which nest material or nesting site availability (Leys 2002), rather than aerial insect food availability (Bryant 1979, Benton *et al.* 2002), limits local House Martin populations.

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REFERENCES

- Benton T.G., Bryant D.M., Cole L. & Crick H.Q.P. 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. *J. Appl. Ecol.* 39: 673–687.
- Bize P., Roulin A., Tella J., Bersier L.F. & Richner H. 2004. Additive effects of ectoparasites over reproductive attempts in the long-lived Alpine Swift. *J. Anim. Ecol.* 73: 1080–1088.
- Böhringer, R. 1960. Die Naheorientierung der Mehlschwalbe (*Delichon urbica* L.). *Z. Vergl. Physiol.* 42: 566–594.
- Brown C.R. & Brown M.B. 1996. Coloniality in the Cliff Swallow. The effect of group size on social behaviour. University of Chicago Press, Chicago.
- Bryant D.M. 1975. Breeding biology of House Martins *Delichon urbica* in relation to aerial insect abundance. *Ibis* 117: 180–216.
- Bryant D.M. 1979. Reproductive costs in the House Martin (*Delichon urbica*). *J. Anim. Ecol.* 48: 655–675.
- Collias N.E. 1964. The evolution of nests and nest-building in birds. *Am. Zool.* 4: 175–190.
- Daan S. & Tinbergen J.M. (1997). Adaptation in life histories. In: Krebs J.R. & Davies N.B. (eds) *Behavioural ecology: An evolutionary approach*, 4th edition. Blackwell Science, Oxford, pp. 311–333.
- Groen N.M., Kentie R., de Goeij P., Verheijen B., Hooijmeijer J.C.E.W. & Piersma T. 2012. A modern landscape ecology of Black-tailed Godwits: habitat selection in southwest Friesland, The Netherlands. *Ardea* 100: 19–28.
- Hammers M., von Engelhardt N., Langmore N.E., Komdeur J., Griffith S.C. & Magrath M.J.L. 2009. Mate-guarding intensity increases with breeding synchrony in the colonial Fairy Martin, *Petrochelidon ariel*. *Anim. Behav.* 78: 661–669.
- Hansell M. 2007. *Built by animals. The natural history of animal architecture.* Oxford University Press, Oxford.
- Hobson K.A., van Wilgenburg S.L., Piersma T. & Wassenaar L.I. 2012. Solving a migration riddle using isoscapes: European House Martins from a Dutch village winter over West Africa. *PLoS One* 7(9): e45005. doi:10.1371/journal.pone.0045005.
- Hund K. & Prinzinger R. 1979. Untersuchungen zur Biologie der Mehlschwalbe *Delichon urbica* in Oberschwaben. *Ökol. Vögel (Ecol. Birds)* 1: 133–158.
- Hund K. & Prinzinger R. 1985. Die Bedeutung des Lebensalters für brutbiologische Parameter der Mehlschwalbe (*Delichon urbica*). *J. Ornithol.* 126: 15–28.
- Lambrechts M.M. and 55 co-authors. 2010. The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. *Acta Ornithol.* 45: 1–26.
- Lessells C.M. (1991). The evolution of life histories. In: Krebs J.R. & Davies N.B. (eds) *Behavioural ecology: An evolutionary approach*, 3rd edition. Blackwell Science, Oxford, pp. 32–68.
- Leys H.N. 2002. Huiszwaluw *Delichon urbica*. In: SOVON Vogelonderzoek Nederland, Atlas van de Nederlandse broedvogels 1998–2000 – Nederlandse Fauna 5. nationaal Natuurhistorisch Museum, KNNV Uitgeverij & European Invertebrate Survey-Nederland, Leiden, pp. 318–319.
- Lind E.A. 1960. Zur Ethologie und Ökologie der Mehlschwalbe, *Delichon u. urbica* (L.). *Ann. Zool. Soc. 'Vanamo'* 21 (2): 1–123.
- Mayr E. & Bond J. 1943. Notes on the generic classification of the swallows, Hirundinidae. *Ibis* 85: 334–341.
- Møller A.P. 1984. Geographical trend in breeding parameters of Swallows *Hirundo rustica* and House Martins *Delichon urbica*. *Ornis Scand.* 15: 43–54.
- Møller A.P. 1989. Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds. *Oikos* 56: 421–423.
- Piersma T. 2008. Female House Martin *Delichon urbica* provisions chicks at nests in two separate subcolonies. *Ardea* 96: 140–144.
- Piersma T. & van der Velde M. 2009. Breeding season-specific sex diagnostics in the monomorphic House Martin *Delichon urbicum*. *Bird Study* 56: 127–131.
- Piersma T. & van der Velde M. 2012. Dutch House Martins *Delichon urbicum* gain blood parasite infections over their lifetime, but do not seem to suffer. *J. Ornithol.* 153: 907–912.
- Piersma T. & van Gils J.A. 2011. The flexible phenotype. A body-centred integration of ecology, physiology, and behaviour. Oxford University Press, Oxford.
- Pilgrim R.L.C. & Galloway T.D. 2003. Descriptions of flea larvae (Siphonaptera: Ceratophyllidae, Leptopsyllidae) found in nests of the House Martin, *Delichon urbica* (Aves: Hirundinidae), in Great Britain. *J. Nat. Hist.* 37: 473–502.
- Rheinwald G. 1975. The pattern of settling distances in a population of House Martins *Delichon urbica*. *Ardea* 63: 136–145.
- Rheinwald G. 1979. Brutbiologie der Mehlschwalbe (*Delichon urbica*) im Bereich der Voreifel. *Vogelwelt* 100: 85–107.
- Roff D.A. 1992. The evolution of life histories. Theory and analysis. Chapman & Hall, New York.
- Sheldon F.H., Whittingham L.A., Moyle R.G., Slikas B. & Winkler D.W. 2005. Phylogeny of swallows (Aves: Hirundinidae) estimated from nuclear and mitochondrial DNA sequences. *Mol. Phylog. Evol.* 35: 254–270.
- Soler J.J., Møller A.P. & Soler M. 1998a. Nest-building, sexual selection and parental investment. *Evol. Ecol.* 12: 427–441.
- Soler J.J., Cuervo J.J., Møller A.P. & de Lope F. 1998b. Nest building is a sexually selected behaviour in the barn swallow. *Anim. Behav.* 56: 1435–1442.
- Stearns S.C. 1992. The evolution of life histories. Oxford University Press, New York.
- Summers R.W. 1975. On the ecology of *Crataerina hirundinis* (Diptera: Hippoboscidae) in Scotland. *J. Zool., Lond.* 175: 557–570.
- Turner A.K. 2004. Family Hirundinidae (swallows and martins). In: del Hoyo J, Elliott A & Christie D.A. (eds) *Handbook of the birds of the world. Vol. 9. Cotingas to pipits and wagtails.* Lynx Edicions, Barcelona, pp. 602–685.
- Walker M.D. & Rotherham I.D. 2011. No effect of the ectoparasite *Crataerina pallida* on reproduction of Common Swifts *Apus apus*. *Ibis* 153: 416–420.
- Waugh D.R. 1978. Predation strategies in aerial feeding birds. PhD-thesis, University of Stirling.
- Winkler D.W. & Sheldon F.H. 1993. Evolution of nest construction in swallows (Hirundinidae): a molecular phylogenetic perspective. *Proc. Natl. Acad. Sci. USA* 90: 5705–5707.

SAMENVATTING

Huiszwaluwen *Delichon urbicum* komen in heel Europa vrij algemeen en dicht bij mensen voor. Toch zijn studies aan hun broedbiologie verrassend schaars. In de beschikbare publicaties gaat het vrijwel altijd om Huiszwaluwen die in kunstnesten broeden. Kunstnesten hebben, net als mezen- en uilenkasten, het grote voordeel dat het maken van de nestbodem, het leggen van de eieren en de groei van de kuikens zonder risico van nestbeschadiging (een nest van gedroogde klei is kwetsbaar) door de onderzoeker gevolgd kunnen worden. Echter, ook zonder de inspectie van nestinhoud valt de broedcyclus van Huiszwaluwen goed vast te leggen door geregeld vanuit een tuinstoel visueel te registreren wat zich in en rond het vlieggat afspeelt. Hier rapporteer ik over de broedbiologie van Huiszwaluwen in door de vogels zelf gemaakte nesten van klei in twee subkolonies aan mijn huis in Gaast, een dorpje aan het IJsselmeer in het zuidwesten van Friesland. Van 2004–2011 volgde ik in totaal 225 nesten met één of meer broedpogingen. Bij deze kolonie, en ook elders in het dorp, werden 130 Huiszwaluwen met mistnetten gevangen, geringd en aan het linker of rechter loopbeen voorzien van twee kleurringetjes. Deze individuen konden soms bij hun nesten worden gelokaliseerd. Kleine, bedelende kuikens werden vanaf 30 mei in de nestopening gezien, met een eerste piek in de periode 5–9 juni. Eind juni was er een tweede en hogere piek. Grote kuikens van de eerste legsels werden van half juni tot half augustus in de nestopening waargenomen, de eerste grote kuikens van de tweede legsels vanaf eind juli. De laatste kuikens verlieten eind september het nest. Van de 205 succesvolle nesten werd in 62% gevallen één broedpoging

gedaan, in 38% van de gevallen twee of drie (laatste in één geval). De eerste nesten werden half april al door Huiszwaluwen bezet en zonder uitzondering ging het daarbij om oude nesten van klei die de winter min of meer intact hadden overleefd. Toch begonnen deze vroege zwaluwen pas begin mei met broeden. Het bezetten van oude nesten ging dus niet gepaard met extra vroeg broeden. Het bezetten van oude nesten was wel vaker geassocieerd met een tweede broedpoging (72% van de gevallen tegenover slechts 20% voor nieuw gebouwde nesten). Nesten met twee broedpogingen betroffen ook vaker (30,4%, $n = 79$) meer dan twee jaar oude gekleurde vogels dan nesten met slechts één legsel (7,9%, $n = 126$). Het heeft mij verbaasd (1) dat in vergelijking met de vrijwel complete bezetting van oude nesten van klei die de winter hadden overleefd, de 34–41 ook aan het huis beschikbare kunstnesten van houtbeton zo weinig werden gebruikt (slechts in 23 van 307 mogelijke gevallen), en (2) dat ze pas vrij laat in het seizoen werden bezet. Immers, in de (resten van) oude nesten van klei overwinteren volop bloedzuigende vlooiën en luisvliegen, terwijl de kunstnesten bij de terugkeer van de zwaluwen schoon zijn. Toch gaat de voorkeur sterk uit naar een geparasiteerd en fragiel, oud nest van klei of naar het bouwen van een nieuw nest. Dit opmerkelijke keuzegedrag van Huiszwaluwen leent zich prima voor verdere experimentele studies. Zulk onderzoek kan ook belangrijke informatie leveren om de vele pogingen om broedende Huiszwaluwen te helpen met kunstnesten en zwaluwtilen succesvoller te laten zijn.

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