INTRODUCTION

There is much interest in the seasonality of tropical birds: how activities with high metabolic demand—breeding and moult, plus migration in species where that applies—are seasonally distributed in an annual cycle that is subject to a less fluctuating food supply than is normal for birds in temperate areas. Studies have nevertheless established that breeding in tropical environments remains strongly seasonal and, as in temperate zones, is correlated with food supply (Skutch 1950, Fogden 1972, Leighton & Leighton 1983, Poulin et al. 1992, Steward & Pierce 2011, Steward et al. 2013). In general, most wholly or partly insectivorous birds breed during the late dry season and the early wet season, when arthropods are more abundant. However, patterns of nesting throughout the tropics are very variable and the preceding statement oversimplifies what is, in reality, a complex picture.

Moult provides a measurable window on avian breeding and seasonality as it can be easily recorded among samples of birds caught for ringing (Newton 2009). It is therefore important to understand moult patterns among a range of birds, both forest and non-forest species. Moult and breeding are typically mutually exclusive activities, a complete moult usually taking place after the conclusion of breeding. Most South-East Asian insectivorous landbirds usually breed during the first half of the year, between January and July. Moult follows thereafter, mainly taking place from April or May to October or November (Ward 1969, Fogden 1972, Round 1982, Round et al. 2006, Wells 2007, Pierce 2009). Some individuals within a population can be expected to be still breeding when others have commenced their moult. There is also evidence of limited temporal overlap in breeding and moult within individuals among both temperate and tropical bird species (Foster 1975, Franklin et al. 1999, Hembeg 1999).

Although some of the earliest and most significant studies of seasonality in South-East Asian birds (Ward 1969, Wells 1969) examined non-forest species, most subsequent studies have focused on forest birds. How does seasonality vary between birds in forest habitats and non-forest or human-modified habitats? On the one hand, tropical non-forest habitats may be subject to greater seasonal extremes (e.g. periodic droughts, lower and higher temperatures) than forest habitats. On the other, human influence in non-forest habitats (particularly the extensive use of irrigation for agriculture) through artifically reducing the extremes of wet/dry seasonality could, at least in theory, enable open country birds to extend their breeding seasons compared to those inhabiting forest. Additionally, over a longer period, human-induced climatic change may be expected further to influence patterns of avian seasonality.

METHODS

Study area
The study was conducted at H.M. The King’s Royally Initiated Laem Phak Bia Environmental Research and Development Project, Phetchaburi province, Thailand (13.050°N 100.083°E). The site is about 1 km from the sea, between a roughly 500 m wide belt of dense, secondary, Avicennia-dominated mangroves, and salt-flats and aquaculture ponds further inland. It receives nutrient-rich municipal waste-water which is treated by filtering through muddy, brackish water, lagoons planted with widely spaced small mangrove trees, and by grass filter-beds in which various species of Gramineae and Typha angustifolia are planted (Round et al. 2009).

Data collection and analysis
Asian Pied Starlings were caught in mist-nets as they emerged after dawn from a communal mangrove roost shared with White-vented Mynas Acridotheres grandis and smaller numbers of other starlings. Occasionally birds fed in the project area and were caught around the margins of grass filter-beds, used for water purification, especially when the beds were being replanted and bare earth was exposed.

Birds were caught during routine ringing activities at weekends, year-round, from September 2000 to November 2012. Mist-nets were usually opened at 05h30 and netting continued until late...
morning or midday, depending on conditions. All birds were measured, weighed, aged, examined for moult and marked with numbered metal rings supplied by the Department of National Parks, Wildlife and Plants Conservation, Bangkok, Thailand.

The stage of primary moult was recorded on the right wing using the well-established method in which a moult score of 0 is assigned to an old, unmoulted feather, 5 to a new, full-grown feather, with moult scores 1 (missing/fully in pin), and 2–4 representing feathers in intermediate stages (Ginn & Melville 1983). Since starlings and mynas have a tiny, vestigial outermost primary (p10), only pp 1–9 were scored for moult, so that a bird with nine fully grown long primaries (moult score 45) was considered to have completed primary moult. The stage of moult in actively moulting birds was recorded on British Trust for Ornithology-format moult cards.

Duration and timing of moult were estimated using the models developed by Underhill & Zucchini (1988) and Underhill et al. (1990), hereafter ‘UZ models’: a likelihood based on the observed moult index or ‘proportion feather mass grown’ (PFMG) is constructed, and maximised with respect to the parameters mean and standard deviation of start of moult and duration of moult. The PFMG index is subjected to a power transformation because the index used must increase linearly with time. The likelihood or probability of observing a certain moult index value is based on the assumption that start date is normally distributed, but the programme is not a regression model which would necessitate other assumptions. Further details are given in Erni et al. (2013).

Feather masses of individual primaries were obtained from a fresh roadside carcass of a full-grown juvenile Asian Pied Starling, weighed in the laboratory to the nearest 0.001 g. Primary moult scores were converted to PFMG using the conversion formula given by Underhill & Zucchini (1988) and Underhill & Summers (1993) to give a range of values 0.00–1.00, where 0 indicates moult not yet started and 1 indicates moult completed. The combined mean body mass (adults and juveniles) of the Asian Pied Starling was 68.5 g ± SD 6.52 g, (n = 457, authors’ own data).

We were interested to estimate the duration and timing of moult in adult starlings and compare the progress of moult between adults and juveniles. Younger juveniles could be easily aged by their browner, but unweathered, upperparts, dusky brown cheeks and all-blackish crown (Plate 1). Additionally, the youngest juveniles had a pale grey-brown iris (compared with whitish in adults) although the transition to an adult-coloured iris was very rapid, and was almost always attained long before the moult into adult plumage was completed.

Adults were recognisable by their white cheeks, usually brighter orange orbital ring and base to the bill, and more worn flight feathers. Additionally, a characteristic of adult floweri—an extensively white fore-crown—is formed by the pointed white tips (‘hackles’) to the feathers of the crown. These break off due to wear so that the crown becomes more extensively black towards the end of the breeding season, making adults and juveniles superficially harder to distinguish (Plates 2 & 3).

Since juveniles undergo a complete post-juvenile moult (and adults a complete post-nuptial moult) we could not easily distinguish between age classes among birds that were in the final stages of moult or which had already completed moult. We therefore selected the UZ Type 5 model, which incorporates data from birds that have not yet commenced moult and those that are undergoing active moult, but which excludes those in which moult has been completed (Underhill & Zucchini 1988, Underhill et al. 1990). Additionally the UZ Type 2 model, which considers all birds (those not yet started, those in active moult and those that have completed moult), was used to illustrate the progress of moult in the population as a whole, including birds in which the age was undetermined (Figure 1).

Analysis was restricted to those birds caught from 1 April to 30 November, extending from approximately one month before any birds were first recorded in active moult to one month after the

**Plate 1.** Young juvenile Asian Pied Starling *Sturnus contra floweri*, Phetchaburi province, Thailand, 9 July 2005.

**Plate 2.** Freshly moulted adult Asian Pied Starling showing white-tipped hackles on forecrown, Phetchaburi province, Thailand, 20 September 2009.

**Plate 3.** Worn adult Asian Pied Starling with white-tipped hackles on crown having broken off, Phetchaburi province, Thailand, 12 August 2007.
last bird was recorded in moult. Data from a small number of
moultng individuals that were retraps of birds ringed earlier were
reated in the dataset as if from new individuals, following the
practice of Rothery & Newton (2002) and Newton & Rothery
(2005). Additionally, data from nine individuals caught elsewhere
during the study period in central Thailand, three at Khao Sam
Roi Yot National Park, Kuiburi district, Prachuap Khiri Khan
province (12.133°N 99.983°E) and six from Huai Krajao, Krajao
district, Kanchanaburi (14.333°N 99.650°E), were also
incorporated. The analysis was performed in R (R Development
Core Team 2008) using the package moult (Erni et al. 2013).

RESULTS
Of a total of 457 handlings of Asian Pied Starlings, 306 were
examined for moult and moult score was recorded. The total
comprised 99 adults, 149 juveniles and 58 classified as ‘age
undetermined’ (Figure 1).

Moult in adults
The average duration of primary moult in adult Asian Pied Starlings
was estimated from the UZ Type 5 model as 110.2 days, with a
mean start date of 8 June ± SD 13.6 days, corresponding to a
completion date of 26 September (Table 1). The earliest adult in
active primary moult was caught on 31 May, and all adults caught
between early July and mid-September were moultng. The earliest
adult known to have completed moult (a retrapped individual) was
cought on 20 September (day 173 in Figure 1) and the latest
identifiable still-moultng adult was caught on 9 October (day 192
in Figure 1).

If the start-of-moult date for individuals of known moult score
is estimated using the mean duration of moult obtained from the
UZ model, then the earliest moultng adults started moult during
11–20 May, with most adults commencing moult during the period
21 May–20 June. The distribution of start-of-moult dates was
normal and unimodal (Figure 2).

Table 1. Estimates of moult onset and duration for adult and juvenile
Asian Pied Starlings using Underhill-Zucchini models for Type 5 data
and Type 2 data (* all age classes combined).

<table>
<thead>
<tr>
<th>Age class</th>
<th>Starting date (mean ±SD, days)</th>
<th>Completion date</th>
<th>Duration (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults (n = 99)</td>
<td>08 June ±13.6</td>
<td>26 September</td>
<td>110.2</td>
</tr>
<tr>
<td>Juveniles (n = 149)</td>
<td>28 May ± 45.1</td>
<td>17 November</td>
<td>173.7</td>
</tr>
<tr>
<td>Juvenile cohort J1 (n = 58)</td>
<td>16 May ±21.8</td>
<td>11 October</td>
<td>147.4</td>
</tr>
<tr>
<td>All combined (n = 306) *</td>
<td>04 June ±30.57</td>
<td>11 October</td>
<td>129.4</td>
</tr>
</tbody>
</table>
Moult in juveniles

The earliest recorded moulting juvenile was 10 May, and thereafter until 10 October most juveniles caught were in active primary moult (Figure 1). The earliest completion date for juveniles could not be judged from captures since no undoubted, identifiable juveniles that had completed moult were retracted during the same season. Five presumably late-fledging juveniles caught between 7 August and 1 September had yet to commence moult.

Application of the UZ Type 5 model, repeated for the entire sample of juveniles, yielded an unrealistically long estimate of the duration of moult of 174 days, with a mean start date of 28 May ± 45 days (Table 1). The much greater standard deviation reflects a wider scatter of moult commencement dates in juveniles, which violates the assumption of normality for the starting date, and invalidates the estimate of duration. It can immediately be seen (Figure 1) that moult in juveniles was much less synchronised than that of adults. One cohort of juveniles (J1) trapped around days 50–60 had moult scores of up to 0.40 at that time, while other much later moulting juveniles in the sample had similar moult scores at around days 120–160. This wide scatter of moult scores is presumed to correspond to juveniles from first broods (early-moult birds, J1) and those that originated from later nesting attempts, either as second or replacement broods.

Therefore, in order to refine the estimate of moult duration for juveniles, we treated the early moulters (cohort J1), i.e. those up to and including day 65 (4 June) separately. These could be easily identified from Figure 1. We then ran the UZ Type 5 model for this group. This yielded an estimated duration of 147 days, with a mean start date of 16 May ± SD 21.8 (Table 1). This is not ideal because it is estimating duration from many fewer individuals (n = 58) from only the first part of the moult cycle, but there is no obvious alternative. If we assume that the rate of moult is similar in both early and later moulting juveniles we may then use the value of duration obtained from cohort J1 to estimate the start-of-moult dates for all juveniles (Figure 2). This indicates that start-of-moult peaked among birds from first broods from the last ten days of April to the last ten days of May. There was then a long tail of birds starting moult up to the last days of August, with a slight suggestion of a second peak in mid-August (Figure 2). Fully 35% of juveniles handled (44 birds out of a total of 119 for which start-of-moult date was estimated) started moult after 1 June. This would suggest that later fledging among Asian Pied Starlings through either re-nesting or double-brooding, and therefore later onset of post-juvenile moult, is a frequent occurrence.

Progress of moult

The incremental increase in proportional feather mass from known actively moulting birds (caught after moult had already started, then later retracted while still in moult) ranged from 0.84% to 1.39% per day in three adults, and 0.68% and 1.37% per day in two juveniles (Table 2). Data from three further juveniles and another adult (Table 2) are omitted from consideration here. Since the birds had not yet started to moult at the time of first capture, and moult starting date was not known, any assessment of daily rate of increase would necessarily be an underestimate in those cases.

Moult of the vestigial p10 was usually completed before that of p9. Moult of secondaries typically commenced when primary moult was approaching one-third completion (moult score 15) and the last secondary (p6) was often still growing when moult of primaries was already complete. Tail moult started after the secondaries, typically when the primary moult score was 20–30, though a few birds apparently started renewing tail feathers before primary moult started. As in most birds, tail-moult started with the central pair of rectrices and proceeded outwards, more or less symmetrically.

DISCUSSION

This study presents the first description of the seasonality and duration of moult in the Asian Pied Starling—both post-nuptial moult in adults and the complete post-juvenile moult. Moult followed breeding, but within the population there was overlap between these activities. Occupied nests of Asian Pied Starlings in and around the study area were encountered as early as February, with the earliest recorded full-grown fledged juveniles appearing at least as early as 10 April. However, the fact that moult in a few juveniles apparently started in the first 10 days of that month indicates that some juveniles had fledged even earlier than this. Some starlings were still nest-building in mid-May (Round & Gardner 2008), so that the later-nesting birds would have still been incubating at a time when other adults were already beginning to moult.

In addition to the estimate of moult duration in adult Asian Pied Starlings and a less reliable, apparently longer, estimate of moult duration in early-hatching juveniles, it was notable that the earliest onset of post-juvenile moult was roughly one month earlier than the earliest onset of post-nuptial moult in adults. The difference in mean starting dates between the two groups was 23 days (Table 1). In Asian Pied Starling, as in some other species of resident (both open country and forest-living) birds in which juveniles have a complete moult, the first juveniles begin moult of flight feathers well before any adults have commenced moult (pers. obs.). A later onset of moult in adults may be an adaptation to increase productivity, enabling adults to undertake a longer period of post-fledging parental care and also grant an opportunity for multiple brooding, or re-laying if the first brood is lost. Double-brooding is referred to by Feare & Craig (1998) for Asian Pied Starling. Multiple brooding may be relatively frequent among tropical birds, e.g. in the non-forest Pied Fantail *Rhipidura javanica* (Herbert 1923, Wells 2007, Round & Gardner 2008) and in forest or forest-edge birds such as Abbott’s Babblers *Malaconotus abbotti* (Pierce et al. 2004), Puff-throated Bulbul *Alpoxesus pallidus* and White-rumped Shama *Copsychus malabaricus* (A. J. Pierce pers. comm.). Additionally, since many starlings are polygynous (Feare & Craig 1998), there is also a possibility that successive polygyny might contribute to the prolongation of nesting of the Asian Pied Starling.

Uneven sampling during the study period, in which relatively few juveniles were caught in the key mid-June to mid-August period, prevented a more detailed examination of age-related differences in moult patterns between adults and juveniles.

Among birds generally a partial post-juvenile moult involving (mainly) contour feathers is more usual in temperate zone species, although the Common Starling *Sturnus vulgaris* is well known for having a complete post-juvenile moult (Bährmann 1964). Among starlings and mynas generally both partial and complete post-juvenile mouls occur, depending on species (Feare & Craig 1998),

**Table 2.** Daily proportion feather mass grown based on recaptures of four moulting adults and five juveniles (*moult score 0 on first capture, so precise onset of moult unknown).*

<table>
<thead>
<tr>
<th>Interval between captures (days)</th>
<th>PFMG accrued/day (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>1.395</td>
</tr>
<tr>
<td>12</td>
<td>0.918</td>
</tr>
<tr>
<td>14</td>
<td>0.845*</td>
</tr>
<tr>
<td>113</td>
<td>0.494</td>
</tr>
<tr>
<td>Juveniles</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>1.431*</td>
</tr>
<tr>
<td>8</td>
<td>0.681</td>
</tr>
<tr>
<td>14</td>
<td>1.362</td>
</tr>
<tr>
<td>18</td>
<td>0.613*</td>
</tr>
<tr>
<td></td>
<td>0.291*</td>
</tr>
</tbody>
</table>
In South-East Asia, where seasonality is less pronounced, a complete post-juvenile moult appears to be the most frequent pattern among resident birds (Wells 2007, Round & Gardner 2008, Pierce 2009). Among birds having a partial post-juvenile moult, it is well known that the timing and extent of moult are influenced by hatching date. Great Tits Parus major from first broods started their post-juvenile moult earlier, and replaced a greater proportion of their feathers, than those from later broods (Rymkevich & Bojarinova 1996). So far as we could discern, all later-mouling Asian Pied Starlings went on to complete post-juvenile moult, with none arresting moult and retaining unmoulted juvenile feathers. This suggests that food availability is not a major constraint on the completion of moult in the relatively benign, well-watered environment of central Thailand.

Dawson (1994) showed that the rate of moult in actively moulting Common Starlings could be experimentally manipulated, and that the rate of feather growth increased in response to a decrease in day length. This suggests that later-hatching juvenile Asian Pied Starlings might possibly adjust their moult duration and rate in response to environmental cues, so that our assumption of a similar rate of moult among earlier- and later-moult ing juveniles might not necessarily apply. A better understanding of post-juvenile moult patterns could be achieved through tracking the progress of moult of frequently recaptured, individually marked juveniles. Studying the progress of moult in captive individuals might be more practicable, however, and would allow for further study of the flexibility of moult patterns through experimental manipulation. Nevertheless, there is still much to learn about avian seasonality, and bird ringers can continue to make major contributions by opportunistically collecting moult data for a much wider range of open-country, wetland and forest species.

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REFERENCES


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