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Post-juvenile moult in Graceful Prinia *Prinia gracilis*

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The moult pattern of the Graceful Prinia *Prinia gracilis*, a resident cisticolid warbler of the Middle East region of the Western Palaearctic, is poorly known. Characterising moult strategies in the avian life cycle is important for understanding population processes and dynamics and, therefore, we have analysed the timing, sequence, extent and duration of post-juvenile moult of Graceful Prinia in Israel. The extent of post-juvenile moult was either complete or partial (but extensive), depending on the dates of hatching and the start of moult. Compared to most European passerines, the long breeding period (February–November) in this region allows a relatively long moult period (79.3 ± 4.7 days) for this resident species, which facilitates considerable variability in the extent of post-juvenile moult.

The renewal of flight and body feathers is necessary to ensure future survival because old feathers are constantly abraded and worn due to behavioural activities, sunshine exposure and other environmental factors. Therefore, adult passerines moult all their flight feathers at least once a year (Jenni & Winkler 1994, Newton 2009). Knowledge of moult strategy, as a central component of the annual cycle of birds, is important for our understanding of population processes and dynamics (Jenni & Winkler 1994, Newton 2009) and facilitates the ageing of birds in field studies.

Most juvenile passerines of Western Palaearctic species perform a partial post-juvenile moult involving replacement of juvenile body feathers together with some wing coverts and, more rarely, some flight feathers (Svensson 1992, Jenni & Winkler 1994). In only a few species do the juveniles perform a complete post-juvenile moult as a regular strategy; in other species this is a rare strategy, commonest in southern populations (Gargallo & Clarabuch 1995) for example in the Sardinian Warbler *Sylvia melanocephala* (Shirihai *et al* 2001) and the Goldfinch *Carduelis carduelis* (Jenni & Winkler 1994). Birds that perform this moult strategy renew all plumage one to three months after fledging, in the summer or autumn, and in the breeding area or nearby (Gauci & Sultana 1979, Ginn & Melville 1983, Jenni & Winkler 1994). Furthermore, differences in hatching dates lead to differences in the time available for post-juvenile partial moult and thus can create intraspecific variability in moult patterns. Birds fledged later in the season tend to have a lower proportion of moulting feathers than birds fledged earlier (Newton 1966, Norman 1990, 1997, Meril 1998, Neto & Gosler 2006).

Graceful Prinia *Prinia gracilis* is a common resident cisticolid warbler in the eastern Mediterranean, occurring in grass or dry reeds in a great variety of habitats, including agricultural fields, and is similar to Zitting Cisticola *Cisticola juncidis*, a more widespread cisticolid species in Europe. The nest is built in low vegetation and the clutch usually consists of three to five eggs; incubation is carried out by males and females and lasts 12–13 days. The young are fed in the nest for 12–13 days by both parents and after fledging for about 10–15 days (Shirihai 1996). Unlike most European passerines, the moult pattern of the Graceful Prinia has not been studied extensively in the field. Simmons (1954) reported from Lower Egypt that two juveniles shot in November–December were in active post-juvenile moult.

Here we analyse the timing, sequence, extent and duration of post-juvenile moult in Graceful Prinia. The period available for breeding and moult in the Middle East is much longer than in northern regions, conditions which can facilitate the breeding of juveniles within their hatching season (Shirihai 1996). Thus, we might expect the post-juvenile moult of Graceful Prinia in this region to be more extensive than the post-juvenile moult of most passerines, with variability in moult extent influenced by different hatching dates within the long breeding season.

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METHODS

Site and data collection

We examined post-juvenile moult in 278 mist-netted first-year individuals of Graceful Prinia; 18 birds were examined more than once during active primary moult. The data were collected in Soreq Valley (31°46'N 34° 55'E) and Beit-Shean Valley (32°32'N 35°33'E), Israel, in 2012–14 (2012 – 98 individuals, 2013 – 88, 2014 – 92), as part of extensive effort for moult-data collection in Israel. Most individuals were caught in autumn, during the post-breeding period, but a few were caught during winter after the end of their post-juvenile moult. Ageing before the post-juvenile/breeding moult was based on the wear of flight feathers, particularly the remiges and rectrices (Svensson 1992, Jenni & Winkler 1994), together with iris colour, which was helpful only in recently fledged juveniles. Juveniles were identified by their fresher plumage than adults and a more olive-grey iris, as against orange in adults.

Moult recording

Post-juvenile moult was recorded for wing and tail feather tracts: lesser (LC), median (MC), greater (GC) and carpal (CC) coverts, alula (Al), primary coverts (PC), tertials (T), secondaries (S), primaries (P) and rectrices (R). In birds with active moult, all feathers were scored from 0 to 5, as usual for primary moult (Ginn & Melville 1983); for birds with no active moult we applied scores of 0 to non-moulted feathers (juvenile feathers) and 1 to moulted (post-juvenile) feathers.

Data analysis

The duration and start date of moult were estimated using the model of Underhill & Zucchini (1988) for type 2 data (moult scores for birds in active primary-feather moult, and birds not started and finished moult), using the R package 'moult' (Erni *et al* 2013) and R version 3.1.1. Statistical comparisons between groups with respect to data for moult progression were carried out using linear models and SPSS 19.0 (IBM inc, Armonk, New York).

RESULTS

In total, 35 juveniles were recaptured after the end of their post-juvenile moult. These birds were caught for the first time before moult or before the end of moult. In this group, 15 individuals (43%) had performed a complete moult and 20 (57%) an extensive partial moult (Fig 1). In addition, 27 individuals caught during the late autumn and winter after the end of moulting season had also performed an extensive partial moult. After the end of post-juvenile/breeding moult, first-year birds which have carried out a complete post-juvenile moult cannot be separated from adults, which undergo a complete post-breeding moult in the same period.

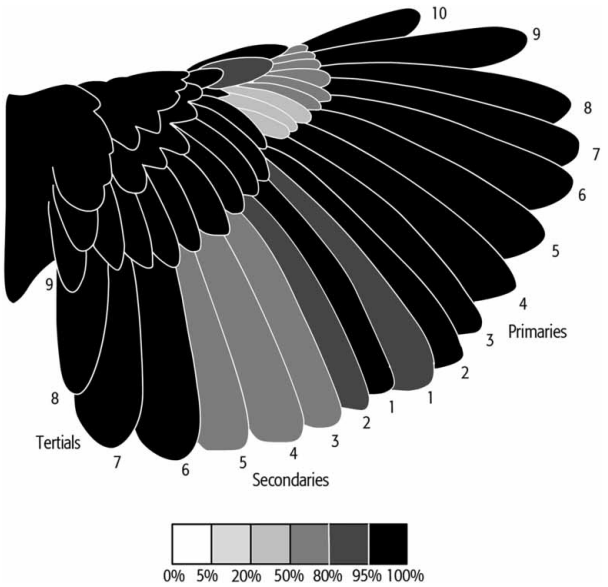

Figure 1. Extent of post-juvenile moult on the wing in 1y/2y Graceful Prinia: data for all birds recaptured after complete or partial post-juvenile moult (n = 35).

In those individuals which did not complete their post-juvenile moult (n = 47), the most common unmoulted (retained juvenile) feathers were PC (96% of individuals

Figure 2. Second-year Graceful Prinia after extensive partial post-juvenile moult, 25 January. The primary coverts and fourth secondary are still juvenile plumage, while the rest of the wing is post-juvenile.

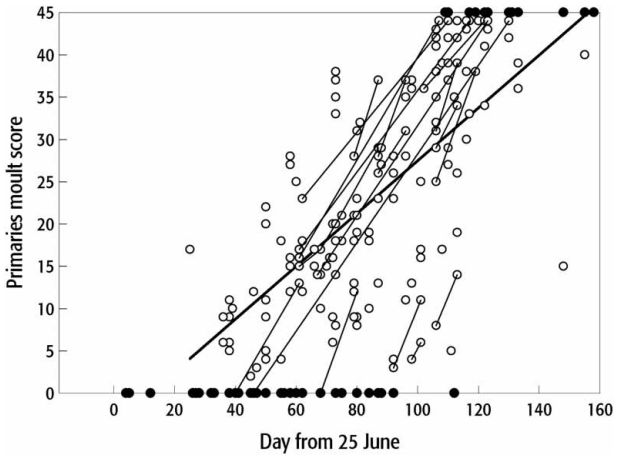

Figure 3. The relation between primary moult scores and date of capture for Graceful Prinias, for all juveniles (n = 233), as shown by the linear regression line $y = 0.32x - 3.92$ ($R^2 = 0.42$, $P < 0.0001$), and for each individual that was examined more than once during active primary moult (n = 18). Active moult, open symbols; no active moult, filled symbols.

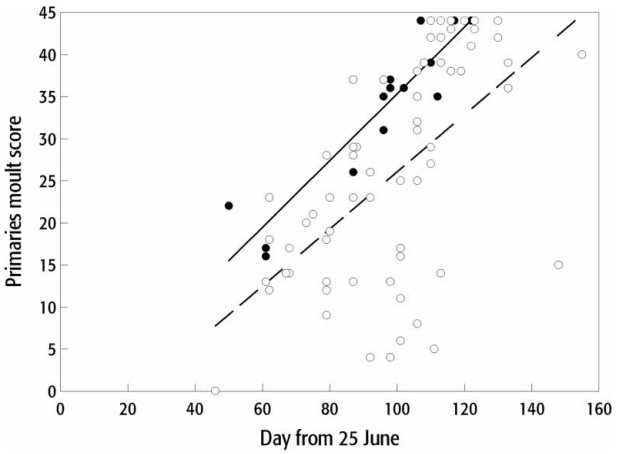

Figure 4. Primary score in relation to date of capture for birds in complete moult (filled symbols, solid line; n = 14; regression line $y = 0.40x - 4.31$, $R^2 = 0.86$, $P < 0.0001$) and partial moult (open symbols, broken line; n = 68; regression line $y = 0.34x - 7.57$, $R^2 = 0.32$, $P < 0.0001$).

had at least one unmoulted PC) and secondaries (50% had one or more unmoulted secondaries; eg Fig 2). Other feathers retained from the juvenile plumage were the innermost primary (20%), alula (13%), rectrices (9%), tertials (4%) and GC (2%).

Most juveniles performed their post-juvenile moult from July to November. Early moulters started in June; those starting to moult later completed their post-juvenile moult in December (Fig 3). The mean (± SD) start date of moult was August 14 (± 23.7 days) with a mean duration of 79.3 ± 4.7 days, estimated using the Underhill & Zucchini (1988) method (Fig 3). No differences were found between moult rate and timing in both study locations (Soreq Valley and Beit-Shean Valley) as indicated by comparing the slopes and intercepts of linear regression lines for moult score and date at the two locations (t = 0.015, 96 df, $P = 0.99$).

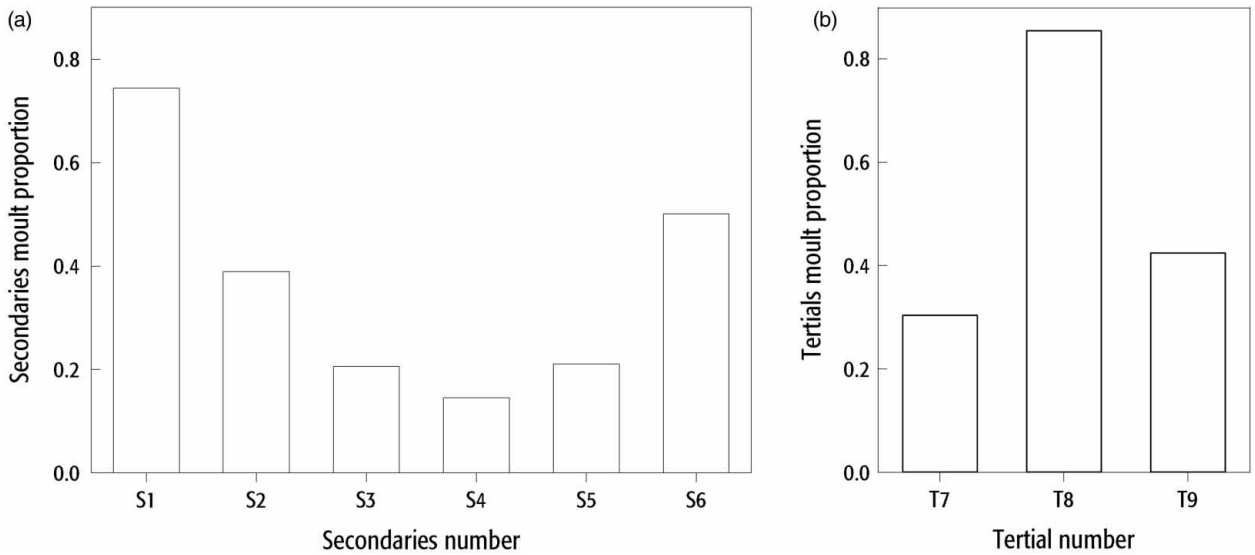

Figure 5. The most common moult sequences of (a) secondaries and (b) tertials, as shown by the proportions of active moult of secondaries (n = 71 individuals) and tertials (n = 85) for individuals actively moulting those plumage tracts.

Many birds in primary moult can be assigned to a partial moult group on the basis of retained PC. For birds that could be assigned to a complete moult group (recaptured once moult was complete) or a partial moult group (birds recaptured once partial moult had finished, and birds in primary moult but with retained PC), there was a significant difference between groups in the timing of post-juvenile moult (linear model to compare the intercept of regression lines, t = 3.12, 79 df, P = 0.003; Fig 4). This analysis suggests that birds that performed a complete moult started to moult earlier than those which performed an extensive partial moult; there was no apparent difference in the rate of moult (slope) between the two groups (t = 045, 78 df, P = 0.66).

The moulting sequence of the primaries was conventional, proceeding sequentially from P_1 to P_{10}. Occasionally P_{10} started growing before P_9. The commonest (mode) moult sequence of other plumage tracts was calculated by summing the moult scores of all individuals in an active moult of specific plumage tracts (Fig 5). The moulting of secondaries was descendant and ascendant: the commonest sequence was S_1–S_6–S_2–S_5–S_3–S_4 (Fig 5a), but sometimes S_2 was renewed before S_6, or S_3 before S_5. Only in one individual was S_4 renewed before S_3; in all others the last renewed was S_4. The moulting of secondaries started after moult of P_4 or P_5 (primary moult scores of 15–20), and ended after the moult of the primaries.

The most common sequence of tertial moult was T_8–T_7–T_9 (71%), but the sequence T_9–T_8–T_7 was not unusual (29%, n = 24; Fig 5b). In Graceful Prinia the number of tail feathers is only 10, and not 12 as in most passerines. The tail was usually moulted centrifugally (from the centre outwards), but tail moult was occasionally irregular. The greater coverts were shed simultaneously or irregularly over a few days. Each primary covert was shed shortly after the growth of its primary.

DISCUSSION

The extent of post-juvenile moult of Graceful Prinia was complete (43%) or partial (57%). The partial moult regularly included all feathers except a few or all PC and secondaries. We suggest that this moult pattern is referred to as 'extensive partial moult', after Gargallo & Clarabuch (1995). The extensive partial moult is not a typical pattern for Western Palaearctic passerine juveniles, where the juveniles typically show two patterns of post-juvenile moult: species in which all individuals regularly perform a complete post-juvenile moult and species which perform a partial post-juvenile moult. However, in species that perform partial post-juvenile moult in southern latitudes in Europe, some individuals perform a complete post-juvenile moult. A comparable pattern of extent was documented in the first pre-breeding moult of Spotted Flycatcher *Muscicapa striata* (Jenni & Winkler 1994). Some other long-distance migratory passerines, wintering in a tropical zone, also have a similar pattern in their first-year pre-breeding moult, for example, the Eastern Orphean Warbler *Sylvia crassirostris* and Common Rosefinch *Erythrina erythrina* (Jenni & Winkler 1994, Shirihai *et al* 2001). The similarity of the post-juvenile moult strategy in the Graceful Prinia to the first-year pre-breeding moult of long-distance migrants may indicate some common evolutionary processes, or a separate evolution but in similar environmental conditions.

Our results suggest that individuals which had started to moult early in the season performed a complete moult, while those that started later performed an extensive partial moult. Similar within-season differences in the extent of partial post-juvenile moult in other passerine species have been explained by the time available for their moult (Newton 1966, Norman 1990, Bojarinova *et al* 1999, Rohwer 2013). For Graceful Prinia juveniles, the main feathers that were not moulted in the partial post-juvenile moult were feathers at the start of the normal moult sequence, such as the inner primary and inner PC, or feathers in the end of the moult sequence, such as secondaries. This may have functional significance with respect to ensuring the renewal of key flight surfaces during the shorter time available for moult in later-hatching individuals.

Most of the feather tracts in Graceful Prinia juveniles were moulted in the usual sequence seen in other passerines, apart from the secondaries. The moult sequence of the secondaries, absolute descendant and ascendant (S_1–S_6–S_2–S_5–S_3–S_4), has not been reported for any Western Palaearctic passerines. A few individuals of many species may moult S_6 before S_5 (Jenni & Winkler 1994). A very similar pattern was reported by Gauci & Sultana (1981) for the Zitting Cisticola, with a sequence of S_1–S_2–S_6–S_3–S_5–S_4. Descendant and ascendant is a common sequence for the secondary moult in non-passerines, especially in species with many secondaries, such as gulls and kingfishers (Baker 1993); the adaptive role of this sequence strategy for the Graceful Prinia is not clear.

Prinia species are common in Asia and Africa, in temperate, arid or tropical zones. This variation in zones and climates also causes considerable variation in moult strategies. Some species in this group perform one yearly moult, others a biannual moult. In equatorial species with more erratic climate the moult extent, timing and

duration are also erratic (Herremans 2006). The Graceful Prinia, like other *Prinia* species breeding in a temperate zone, maintains a yearly cycle of moult and breeding. However, the long breeding period, compared with European passerines, produces a relatively long moult period with variation in the extent of moult. The breeding season runs from (January) February–November (December), usually with three breeding cycles and more rarely four or five cycles (Shirihai 1996). First-year birds hatched earlier in the season, in March–April, can breed in their hatching season. This feature increases the variation in moult timing, extent and duration. A complete post-juvenile moult in European passerines is predominantly found in tropical taxa whose tropical representatives also normally perform a complete post-juvenile moult (Jenni & Winkler 1994). The Graceful Prinia is a good example of a species in the temperate zone with a juvenile moult strategy shaped by phylogenetic origins together with the constraints imposed by the seasonality in this region.

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