

Paedomorphosis in *Sporophila* seedeaters

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SUMMARY.—Paedomorphosis can be defined as the ‘retention of ancestral juvenile characters by later ontogenetic stages of descendants’. Female and immature *Sporophila* resemble each other, and are similar among several species. Here I present some cases of presumably sexually mature *Sporophila* males with immature-like plumage, and discuss the possible role of paedomorphosis in Dark-throated Seedeater *S. ruficollis*, Marsh Seedeater *S. palustris*, Capped Seedeater *S. bouvreuil*, Drab Seedeater *S. simplex* and Temminck’s Seedeater *S. falcistrostris*. Paedomorphosis in *Sporophila* might be the outcome of protracted plumage maturation. Additionally, the unrelated but also seed-eating Dull-coloured Grassquit *Tiaris obscurus* apparently originated through paedomorphosis. Although paedomorphosis seems a most likely explanation for the observed patterns, alternative explanations, like feminisation and retention of winter plumages (‘eclipse’), should be further tested with the aid of detailed phylogenies and a thorough knowledge of moults and plumage features.

The remarkable similarity between the drab females and immatures in most *Sporophila* seedeaters make them among the most difficult birds in the Neotropics to identify both in the field and in the hand. Unidentified specimens held in several museums testify to this difficulty. In nature, females and immatures of the c.30 species of the genus can be generally separated with confidence only if accompanied by the usually diagnostically patterned males (Sabel 1990, Ouellet 1992, Remsen *et al.* 2007). The remarkable plumage variation in the genus *Sporophila* has been attributed to many different causes, among them: pigment abnormalities (Olson 1966), gynandromorphosis (Sick 1967), winter plumages (Sick 1967, 1997), hybridisation (Sick 1968, Narosky 1977, Olson 1981a, Stiles 1996), geographic variation (Olson 1981b, Stiles 1996), clinal / geographic variation (Kirwan 2007), ageing (Stiles 2004, Restall 2006) and the existence of plumage morphs (Stiles 2004, Restall 2006, Areta 2008). Another ubiquitous cause of variation is that of mature males with non-definitive or fundamentally immature-like plumage (Skutch 1954, Olson 1968, 1981a). Olson (1968) reported finding an immature-plumaged Ruddy-breasted Seedeater *S. minuta* with enlarged testes, as well as immature male Thick-billed Seed Finches *S. funerea* (= *Oryzoborus funereus*) with enlarged testes, and a transitional-plumaged Variable Seedeater *S. aurita* (*sensu* Olson 1968) also suspected to be breeding based on its swollen gonads. Skutch (1954) found White-collared Seedeaters *S. torqueola* breeding in transitional plumage. Amongst the ‘capuchino’ seedeaters of the *S. ruficollis* group (*cf.* Lijtmaer *et al.* 2004 and Areta 2008 for clade delimitation), full singing and territorial (potentially breeding) males of all species exhibit a plethora of different, partially mature, plumages (*pers. obs.*). At least some adult Marsh Seedeaters *S. palustris* occasionally moult into a, dull immature-like, non-breeding winter plumage (‘eclipse’) after the nesting season. This appears to be the rule in Dark-throated Seedeater *S. ruficollis*, Capped Seedeater *S. bouvreuil pileata* and Black-bellied Seedeater *S. melanogaster*, which then regain their adult or near-adult plumage prior to the next breeding period (Sick 1967, 1997; *pers. obs.*).

Changes in timing of development can play a pervasive role in the evolution of several vertebrate groups (Gould 1977, McNamara 1995, Carroll 1998). Delayed plumage

maturation is a relatively widespread phenomenon in males, in which sexually mature individuals retain an essentially immature-like plumage for a period prior to attaining adult male plumage (Rohwer *et al.* 1980, 1986, Thompson 1995). Paedomorphosis is one possible outcome of changes in developmental timing and refers to the 'retention of ancestral juvenile characters by later ontogenetic stages of descendants' (Gould 1977: 484). In this context, the difference between delayed plumage maturation and strict paedomorphosis is that, in the latter, the birds would never acquire typical adult plumage.

My aims here are, firstly, to expose a series of previously unreported observations of anomalous wild and captive birds that can be properly understood as cases of paedomorphosis and delayed plumage maturation in the capuchinos, and, secondly, to explore the presence of paedomorphosis in the genera *Sporophila* and *Tiaris*.

The basic lack of knowledge about plumage sequences in the capuchinos greatly impedes the use of appropriate detailed terminology to describe them. Although the Humphrey-Parkes system (Humphrey & Parkes 1959, 1963) is extremely usefully employed in studying plumage evolution, here I will use the more general traditional 'Dwightian' terms (see Humphrey & Parkes 1959, 1963, and Howell *et al.* 2003, 2004). Future workers should bear in mind the limited usefulness of these terms to study evolutionary questions, and they are used here solely because of their ability to describe plumages in general terms when detailed sequences are unknown (Thompson & Leu 1994).

Several observations suggest the existence of arrested plumage development in members of the capuchinos clade.

Dark-throated Seedeater *Sporophila ruficollis*.—Two individuals from the same nest were trapped post-fledging in Saladillo, Buenos Aires province, Argentina (35°39'S, 59°57'W), in 1990. Over the next five years both individuals vocalised typical of *S. ruficollis* and went through several moult cycles. One acquired the species' normal adult male plumage, whilst the other repeatedly moulted into a female / immature-like plumage until its death five years later. Its identity was confirmed, through dissection, as male (M. Roda & P. Ferro pers. comm.). Another singing male in female / immature plumage was found at the same locality, feeding nestlings together with a female (M. Roda pers. comm.). A full singing but immature-looking bird was trapped at Gualaguaychú, Entre Ríos province (33°00'S, 58°30'W). After four years, the bird continued to sing its *S. ruficollis* song and moult each year into female / immature-like plumage (P. Tato pers. comm.). A third anomalous bird was trapped at Gualaguaychú and is held at the CICyTTP-CONICET for ongoing studies. When this female-like male was placed close to a captive adult male of a yet undescribed dark-collared seedeater, the adult male tried to copulate with it for several consecutive days. This observation provides preliminary and tentative evidence that male seedeaters are unable to discriminate between this male plumage and female plumages using solely visual cues. The bird is now at least three years old, sings like *S. ruficollis* and after several moults still had the appearance of a female / immature. During the spring / summer of its presumed fourth year of life it started acquiring male plumage following the standard sequence of plumage acquisition in the capuchinos (pers. obs.).

Marsh Seedeater *Sporophila palustris*.—A territorial bird singing like *S. palustris* was observed in a marsh at Estancia La Marita, Entre Ríos province, Argentina (33°20'S, 58°35'W), on 12 December 2003. In plumage, it was indistinguishable in the field from the putative female accompanying it. However, each bird showed typical sex-based behaviour: the singing male was territorial and the female kept low in the vegetation, endeavouring to remain hidden, as they usually do when nesting. A second apparent male was tape-recorded giving the typical species-specific adult song at Colonia Carlos Pellegrini, Corrientes province, Argentina (28°35'S, 57°10'W), on 7 January 2005. The bird looked like

a female / immature of the species. Female capuchinos are not known to sing (Areta 2008); despite my many years of experience with capuchinos in the field and discussions with several bird-keepers, I have failed to find any evidence of females singing. Thus, birds singing structured male-like songs can be confidently considered as males (a temporally restricted and unstructured female song, very different from that of males, is known in Black-and-white Seedeater *S. luctuosa*: J. C. Eitnien *in litt.* 2007).

Without prolonged studies of marked birds, distinguishing between capuchinos displaying delayed plumage maturation, eclipse / winter plumage or paedomorphosis is problematic in the field. Although acquisition of full adult male plumage apparently takes 3–5 years in the capuchinos (Narosky 1977; pers. obs.), males usually show traces of adult plumage within one year and apparently do not start singing 'properly' until the end of their first year (R. Tato & P. Ferro pers. comm.). *Sporophila* species might be long-lived in relation to their small body sizes. For example, the oldest White-collared Seedeater *S. torqueola* reported was 11 years and eight months (Klimkiewicz & Fitcher 1987 *fide* Eitnien 1997) and captive individuals of Double-collared Seedeaters *S. caerulescens* were reported to live up to 18 years (Sick 1997). Although the natural lifespan of most capuchinos is unknown, judging from the time necessary to reach adult-patterned plumage, and from colour intensities and colour patterns of birds observed in nature, it is likely to be above seven years (and probably >10 years) (pers. obs.).

Few data are available on the sequences of plumage development in the capuchinos, however delayed plumage maturation, although occasionally noted in *S. ruficollis*, is apparently not common in the group. The *S. ruficollis* and *S. palustris* reported herein behaved territorially, vocalised like adult-plumaged males and careful observation failed to detect any sign of incipient maturity in their plumages. This suggests not only protracted retention of the immature plumage, but also raises the possibility that it is retained throughout the life of the birds concerned, as in the two confirmed cases reported here for *S. ruficollis*.

The individual ontogenetic potential of creating, in the long term, paedomorphic populations is present in the capuchinos, at least in *S. ruficollis* and apparently also in *S. palustris*. Indeed a whole taxon of the clade, the subspecies *crypta* of Capped Seedeater *S. bouvreuil*, restricted to Rio de Janeiro, Brazil, can be considered paedomorphic: males never acquire a plumage obviously different from females and only show a few intermingled black crown-feathers and pale chestnut body-feathers. These few feathers suggest the derivation of *crypta*, by retention of immature plumage, from the black-crowned and chestnut-bodied *S. b. bouvreuil* (Sick 1967, 1968, 1997). Thus, the intra-population phenomenon of immature plumage retention in *S. ruficollis* and apparently in *S. palustris* provides a mechanistic explanation for the evolutionary origin of paedomorphosis in *S. b. crypta*. The highly variably plumaged Temminck's Seedeater *S. falcirostris* exhibits a very protracted period of plumage maturation, and some captive individuals were reported never to reach a plumage different from that of immatures (Sick 1997), suggesting that protracted plumage maturation can lead to paedomorphosis within a species (but see Björklund 1991). Another case in which paedomorphosis might be partially invoked as a generative explanation is in the slightly dimorphic Drab Seedeater *S. simplex*, where some males show traces of a blackish-patterned throat and greyish back recalling those found in the Parrot-billed Seedeater *S. peruviana*.

In another Neotropical seed-eating genus, both sexes of Dull-coloured Grassquit *Tiaris obscurus* look like typical immatures / females of the genus *Tiaris*, unlike congeners in which males are usually either mostly black or possess yellow and olive plumages (Sick 1967, Restall *et al.* 2006). The deep phylogenetic position of *T. obscurus* within *Tiaris* (Lijtmaer *et al.* 2004) suggests that this species' male plumage might have originated

through the evolutionary retention of immature plumage from a male ancestor of a sexually dichromatic species.

These apparently independently evolved instances of paedomorphosis in Neotropical seedeaters demand further investigation, and provide a suite of cases to elucidate the evolutionary significance, developmental pathways, ecological factors and other conditions that lead to the appearance and maintenance of paedomorphosis in birds. Regardless of the mechanism behind their origin, the cases reported here represent the loss of obvious colour dimorphism in males of usually dichromatic taxa (*cf.* Price 2008 and references therein). The protracted plumage changes of *Sporophila* seedeaters through life indicates that colour intensity and plumage patterns can be considered true signals of age, with less colourful males usually being younger birds with less breeding experience. Although no male *Sporophila* seedeaters are known to incubate, many males share some nest duties and fledgling care with their females, and in some species males even mate-feed and brood nestlings (Facchinetti *et al.* 2008 and references therein). Whilst cryptic male coloration might enhance breeding success (e.g., improved brood care through reduced predation risk or fewer disputes with other males), it could also diminish male reproductive performance (e.g., if females and males are using colour to evaluate male aptitude and for species recognition). Among other possible causes (Badyaev & Hill 2003), these natural history and other features, together with detailed phylogenetic studies, might be important to explain the loss of obvious sexual dichromatism in *Sporophila*. On purely ontogenetic grounds, the cause of such a loss of pigmentation should be sought in the genetic control of pigment deposition in feather follicles (e.g. Mayr 1931), and their study should prove enlightening to establish plumage homologies. The theoretical framework and vocabulary developed for the understanding of plumage maturation (e.g., Humphrey & Parkes 1959, 1963, Rohwer *et al.* 1980, Foster 1987, Thompson & Leu 1994, 1995, Howell *et al.* 2003) provide several lines of thought that could be fruitfully applied to the problem of paedomorphosis. Although Sick (1967) frequently referred to *S. b. crypta* as a 'hen-feathered race' of feminised plumage, this assertion suggests that he might have concurred with my view that it could have evolved through the simple retention of juvenile / immature characters along pre-existing developmental pathways. Additionally, retention of winter plumage could be responsible for the observed female-like breeding males. Since females, immature and winter-plumaged males are extremely similar in *Sporophila*, all these explanations require thorough testing. Further clarification of the details of plumage ontogeny, homology and evolution in *Sporophila* depends upon carefully designed and repeated observation of plumage development in the same individuals over long periods. Such observations are needed to firmly establish the homology of retained paedomorphic plumages to those of earlier ontogenetic stages proposed in this study.

In sum, all of the cases discussed here suggest that paedomorphosis could be an important factor in the evolution of *Sporophila*. However, given our scant knowledge of the phylogeny and moults in *Sporophila* and the vexing similarity of different plumages at different ages and seasons within a species (and even between different species), plumage homologies cannot be firmly established. Paedomorphosis must remain a plausible, but to date not satisfactorily tested, explanation for some of the plumage diversity of *Sporophila* seedeaters.

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