PLUMAGE, EGGS AND NEST BUILDING BEHAVIOUR IN THE RUFOUS WHISTLER SUPERSPECIES

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INTRODUCTION

Within the whistlers *Pachycephala* (Pachycephalidae) several subdivisions have been recognised, although generally not formally maintained at subgeneric level. One consists of those forms having ventrally-streaked females, as typified by the widespread Rufous Whistler *P. rufiventris* Latham 1801 of Australia and New Caledonia. Several extra-limital populations have been considered conspecific with it, with the specific divisions varying considerably between authors.

The Black-headed Whistler *P. monacha* G. R. Gray 1858 of New Guinea and the Aru Islands was merged with *P. rufiventris* by Stresemann (1924), Mayr (1967), Mayr & Gilliard (1954) and others, but maintained at specific level by Beehler *et al.* (1986), Beehler & Finch (1985) and Rand

& Gilliard (1967). The White-bellied Whistler *P. leucogastra* Salvadori & D'Albertis 1875 (south-eastern Papua New Guinea, Rossel Island) was considered by all the before mentioned authors to comprise two non-rufous subspecies of *P. rufiventris*. White & Bruce (1986) kept it at specific level, expanding it to include populations in Wallacea. They suggested that these Wallacean forms may deserve recognition as an allospecies (*P. arctitorquis* P. L. Sclater 1883) within this superspecies. They also considered the Drab Whistler *P. griseonota* G. R. Gray 1862 (Moluccas) to warrant specific rank; it was earlier reduced to subspecific status within *P. rufiventris* by Mayr (1967).

Regardless of the taxonomic level accepted for certain members of this assemblage, it is almost universally agreed that they constitute a closely-knit group, which is usually allocated superspecific rank (for convenience of reference, all of these component taxa are recognised here at specific level). The only other member of the streaked-breasted complex is the large White-breasted Whistler *P. lanioides* Gould 1840 of northern Australia; its relationship to *P. rufiventris* has long been recognised, despite its generally more robust proportions.

Although the streaked ventral surface of females has been the major diagnostic character used for this group, there are other characters that corroborate the division between this assemblage and other whistlers. The most closely-related subdivision of the genus appears to be the species-group comprising the Golden Whistler *P. pectoralis* Latham 1801 and its allies. From these species, the *P. rufiventris*-group differs, in addition to the ventral streaking in females and obvious absence of golden colour in adult males, by three other characters: one of juvenile plumage, one of the roles of the sexes during breeding, and one of egg coloration. Their distributions of the character states among these species parallel that of female ventral patterns. Unfortunately, little has been reported on these aspects of the biology of non-Australian forms.

METHODS

Plumages of most species of whistlers have been studied in collections of Australian and North American museums. In addition, photographs of juveniles and immatures of several taxa were examined for plumage details for this study. Eggs were examined in the collections of the Australian Museum.

Much of the following comparison is, by necessity, based primarily on Australian *P. rufiventris, P. lanioides* and *P. pectoralis,* with the assumption that the characters are consistent within the group. From those characters that are known for extra-limital taxa, this assumption appears valid.

RESULTS

Female ventral streaking

The presence of streaking on the ventral surface of the females of the *P. rufiventris* species-group is the primary feature by which these forms have been segregated from other sections of *Pachycephala.* Females (and immature males) of the *P. pectoralis*-group and other whistler species, whether sexually dimorphic or not, are uniformly unmarked on the breast. In contrast, the *P. rufiventris* superspecies (known for all species) and *P. lanioides* have females with darkly-streaked breasts. These differences are well illustrated in many texts (e.g., Boles 1987, Reader's Digest 1986, Simpson & Day 1986).

Male ventral coloration

The basic ventral pattern of the adult male in both species-groups consists of a pale throat, separated by a dark breast band from a pale breast and belly. Within a taxon, the throat and remaining underparts may or may not be the same colour, but are usually white, yellow or rufous. This pattern is characteristic of those species in which sexual dimorphism is pronounced. A variation, present in both groups, has the throat black, meeting and merging with the breast band (in the *P. rufiventris*-group exhibited by *P. monacha).* In a few insular populations of both groups, the male is hen-plumaged (e.g., *P. griseonota, P. pectoralis xanthoprocta),* and it is through the female plumage that the relationships are most readily apparent. Within this generalised ventral pattern and its variations, the fundamental difference between the two assemblages is the presence of yellow (golden) colour in *P. pectoralis* and its allies and its absence in the *P. rufiventris* species-group. In the latter, white or rufous are the predominant ventral colours.

Juvenile plumage

Most whistlers, including all the Golden Whistler complex and both the larger and smaller

monomorphic species (e.g., Olive Whistler *P. olivacea,* Grey Whistler *P. simplex)* have unpatterned, rufous juveniles (see, for example, photographs of juvenile *P. pectoralis* in Boles 1987: 211). In *P. rufiventris* and *P. lanioides,* however, the ventral surface is streaked. The dorsal surface may be rufous but frequently exhibits varying amounts of other colours. A series of photographs of *P. rufiventris* in Boles (1987: 222, 228–229) demonstrates this plumage.

Erickson (1951: 163) wrote of *P. rufiventris,* "fledglings plumage, similar for both sexes, i.e. pale grey abdomen with very broad dark streaks from beak to tail." The dorsal surface is, as described by Mathews (1920: 238, who incorrectly called the plumage the immature), "cinnamon with lead-grey bases to the feathers of the mantle, back and lesser wing-coverts." F. L. Whitlock (quoted by Campbell 1908) and Galbraith (*in* Hall 1974: 254) discussed the juveniles of *P. lanioides,* Galbraith's description reading, "white below with club-shaped fuscous shaft-streaks, and the feathers of the back are pale grey to whitish basally and pale rufous terminally with similar streaks". A specimen of *P. architorquis* in the American Museum of Natural History appears to be in entirely juvenile plumage. It is rufous on the upperparts and scapulars; the face is light rufous. The underparts are light rufous on the chin and throat, and white on the remainder, with dark rufous streaks from the chin through the undertail coverts. The rectrices, remiges and wing coverts are rufous.

I have examined specimens of *P. griseonota* and *P. leucogastra* in post-juvenile moult. They have retained rufous secondaries and secondary coverts and some rufous feathers on the side of the face, but otherwise moult has proceeded too far to confirm the juvenile ventral pattern. I have not seen juveniles of *P. monacha.*

Role of sexes

In Australian species of whistlers, except for *P. rufiventris* and *P. lanioides,* both sexes construct the nest, incubate the eggs, and feed the young (Boles 1987). The streaked-breasted species differ in that the female alone is responsible for building the nest. This trait of *P. rufiventris* was noted by both Erickson (1951) and Jack (1949). According to Erickson (1951: 155), the female, after some deliberation, begins to construct the nest, "work in which the male takes no part". Campbell (1908: 145), quoting Whitlock on the division of roles in *P. lanioides,* stated, "as a rule the male sings at no great distance from the nest, but he takes no part in building, or even in feeding the young." The last observation is unusual if true, for in other Australian whistlers, including *P. rufiventris,* the male is an active and almost equal participant in caring for the chicks.

Egg coloration

There is a noticeable difference between the eggs of *P. rufiventris* and *P. lanioides* on one hand and of *P. pectoralis* and the remaining Australian species on the other. This is despite considerable variation within some species, which results in a slight overlap in the range of egg colours and markings. The two groups produce eggs that are almost always separable, differences that are particularly obvious when eggs of both are compared in series. Those of *P. pectoralis* and most Australian whistlers have an off-white, cream or salmon background with an overlay of brown, black or lavender spots and blotches. The basic pattern of markings of *P. rufiventris* and *P. lanioides* is similar but the ground colour has a definite olive cast of varying intensity, producing eggs that are overall diagnostically darker and greener (Beruldsen 1980, North 1906–1909, pers. obs.).

DISCUSSION

The five characters cited here by which the *P. rufiventris* assemblage differs from the similar *P. pectoralis* species-group (streaked-breasted females; absence of golden plumage; ventrally streaked juveniles; responsibility of female alone for nest construction; different egg coloration), are probably all derived character states. That the streaked-breasted taxa form a clade is further corroborated by the parallel distribution of these characters among the members. Whether it is appropriate to formally recognise this clade at the subgeneric level within *Pachycephala* may depend on individual preference, but certainly these birds constitute a quite distinct species-group.

The characters by which it resembles the *P. pectoralis* complex (adult male pattern, pattern of sexual dimorphism, etc.) are most likely primitive for these two sections of *Pachycephala.* The relationship of these two sections of the genus, while probably at the level of sister-groups, may not be as close as usually thought. From DNA-DNA hybridisation studies, Sibley &

Ahlquist (1982) obtained a delta $T_{50}H$ value of 0.6 between *P. pectoralis* and *P. rufiventris*. The criteria used by the authors at that time indicated a divergence time of less than 4.5 million years. Sibley *et al.* (1988) now believe that the delta $T_{50}H$ values may be influenced by reproductive factors. The previously suggested divergence time, therefore, should not be taken too literally.

Should subgeneric status be deemed appropriate for the *P. rufiventris* species-group, the first available name is *Alisterornis* Mathews 1912 (type *P. lanioides),* which has priority over *Lewinornis* Mathews 1913 (type *P. rufiventris).*

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