

specimens in the collection of the British Museum (Natural History) and in literature, are here described.

The main criterion for the separation of the three is size. Measurements (mm) are as follows:

pectoralis (9 specimens), wing 90–98, bill 29–32, tarsus 28–30

brachipus (2 specimens), wing 101–102, bill 35–37, tarsus 31–32

clelandi (3 specimens), wing 109–114, bill 39–45, tarsus 35–37

A little more data on *brachipus* are available. Littler (1910) gave these measurements (mm) for Tasmanian birds: wing 104, bill 36, tarsus 32. Skemp (1955) gave the length of bill as one and a half inches (= c. 38 mm). These measurements would appear to confirm those already given. Mathews (1910) gives measurements (mm) for *clelandi*: wing 114, bill 42, tarsus 36, but his data for *pectoralis* represent an average of the other two subspecies.

From the material available there appear to be differences of colour between the three. *Clelandi* is generally darker than *pectoralis*, particularly as regards the chestnut of the head and the olive-brown of the back. It is a clearer grey on breast and neck and whiter on the throat. *Pectoralis* has olive tips to the grey feathers on head, throat and sides of the breast, giving less well-defined areas of colour.

Brachipus is similar to *pectoralis* but the colour of head and breast is still more obscured by olive tips to the feathers, and the belly, which is white in the other subspecies, has a distinct buffish tint, described by Littler as 'isabelline'.

The distribution of the subspecies, with *pectoralis* occurring on the eastern side of Australia from Queensland to Victoria, and *clelandi* in the south-west, suggests subspeciation based on early separation in 'refuges' during an arid period, such as is apparent for many other Australian birds (Gentilli 1949; Keast 1961). *Brachipus* probably represents a later isolation of a part of the population of *pectoralis*.

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DEVICES FOR REDUCING AGGRESSION IN THE WHITE-PLUMED HONEYEATER AND THE WILLIE WAGTAIL

INTRODUCTION

Dow (1973) in part discussed the significance of the oral flange in adult Australian honeyeaters and the unreliability of ageing specimens on the basis of colour and type of flange. He suggested that this characteristic might be useful in promoting certain types of social organization by reducing aggression towards individuals exhibiting a pale flange. He demonstrated in the White-plumed Honeyeater a statistically significant trend between type and colour of flange: pale with fleshy flange; intermediate colour equally associated with fleshy and non-fleshy flanges; dark with non-fleshy. Graphically he showed smooth monthly changes of colour of flange in his sample. He stated that no irregularity of type or colour of flange had been described in this species and implied that a pale flange was associated with immaturity.

My observations of the White-plumed Honeyeater *Meliphaga penicillata* in aviculture, however, show

the situation to be more complex. Six individuals of this species housed in one of my planted aviaries, measuring 3 × 7 × 2 m, exhibit a clear gradation in intensity of colour of plumage as well as colour and type of flange. These birds were taken on 8 October 1971 near the Murchison River at Twin Peaks Station, Western Australia (27°21'37" S, 115°53'42" E). Each had adult plumage with similar intensity of colour. Although characteristics of their flanges were not noted at the time of capture, all had black bills. All birds were individually identified with coloured bands (see Table I). Two birds, already mated, were given green bands; the bird with an orange band on the left leg subsequently lost its left eye, possibly as a result of fighting. In keeping with many Meliphagidae, *M. penicillata* proved very quarrelsome, but by May 1972 erratic scrapping had given way to systematic bullying. The dominant bird proved to be an unmated male.

TABLE I

Social rank and related characteristics at March 1973.

| Social Rank | Colour of Band | Leg | Type of Flange | Colour of Flange | Colour of Beak | Colour Intensity of Plumage | Call |
|-------------|-----------------|---------------|-----------------|------------------|--------------------|-----------------------------|--|
| 1 | Orange Black | Left Left | non-fleshy | Black | Black | Normal | Normal |
| 2 | Orange | Right | non-fleshy | Yellow | Black | Normal | Normal |
| 3 | Green | Left | non-fleshy | Black | Black | Pale | Normal |
| 4 | Green | Right | non-fleshy | intermediate | Black | Pale | Normal |
| 5 | Orange | Left | fleshy | Yellow | Black pale base | Pale | Fledgeling scolding call |
| 6 | Orange Black | Left Right | large fleshy | Yellow | Pale dark tip | Very Pale | Fledgeling 'location' and scolding calls |

DEVICES FOR REDUCING AGGRESSION

Table I shows the order of dominance of the birds with the most dominant male occupying the first position. It is at once evident that intensity of colour of plumage, type and colour of flange, and voice all show some relation to the individual's rank. In conjunction with a number of submissive displays these devices for reducing aggression occurred in combinations that varied from one individual to another. Observations indicate that behaviour may influence the combination of characteristics present in each individual.

The bird handicapped by the loss of one eye became shy, avoiding contact with its fellows whenever possible and giving a display of abject submission on those occasions when it was confronted by those of higher rank. This behaviour could explain the retention of some social standing and intensity of colour of plumage by this bird. The submissive display used by this individual involved hanging upside-down below the aggressor while emitting high-pitched juvenile scolding calls. Its beak was opened wide as the calls were given. Because the birds were face to face for the duration of the display the pale base of the beak and the pale fleshy flange of this bird (5 in Table I) would be emphasized. An immediate return to normal behaviour usually followed this display.

An entirely different response to aggression was given by birds 3 and 4. They crouched close together low on the perch and gave a low twittering call while turning the head from side to side along the long axis of the beak. Quivering or fluttering of the wings sometimes occurred during the display. The dominant bird sometimes returned a number

of times in quick succession to stand over the two. (This resembles the sequence of display that may follow when fledgelings, their appetites having already been satisfied, are confronted by an adult carrying food.) Should either bird then retreat or be confronted on its own, a ruthless chase followed. Intensity of colour of plumage was in keeping with status in the group but corresponding regression of the flange had not taken place. This may be because of the type of display employed or the strength of union or both. These devices for reducing aggression were carried to their ultimate in the bird occupying the lowest rank.

This bird superficially resembled a normal full-grown fledgeling, with very pale plumage, the beak pale with a dark tip and a pale fleshy flange. The image was reinforced by the use of fledgeling calls. Both the higher-pitched scolding call and the location call of fledgelings were emitted by this bird. After being examined on 18 April 1973, this individual was released into an aviary, 5 × 10 × 2 m high. No other specimens of *M. penicillata* were in this aviary. On 20 May 1973, at which time this bird had been outside the group for four weeks, I found that the bill was noticeably darker. Characteristics of flange and intensity of colour of plumage were unaltered. I again examined it on 10 June 1973 and found that the bill was now entirely black and that the flange was non-fleshy and of intermediate colour. Intensity of colour of the plumage had not altered. When I examined it again on 23 June 1973 some ten weeks after separation from the group, the flange was black and non-fleshy. Intensity of colour of the plumage was still unaltered, suggesting that variations of intensity may be reversed only by moulting.

DISCUSSION

Dow (1973) stated that the smooth decline in the numbers of pale-flanged males, from a high in March–April to a low in September–October, would be ‘... expected of a population containing individuals losing juvenile characteristics as they grow older or through depletion of their numbers by heavier juvenile mortality. . . .’ However, because characteristics of flange (and even colour of beak) are also responses to social pressures, more probably the seasonal variation referred to is also associated with breeding activity and a consequent shift in emphasis away from strict maintenance of an order of dominance in the social organization of the species.

Suppression of adult aggressive characteristics is not uncommon and investigation may well prove that this phenomenon is more widespread than is suspected. A very interesting example of the use of a device for reducing aggression within a pair is to be found in the Willie Wagtail *Rhipidura leucophrys*.

This species, in which there is no difference in colour between the sexes, can control the display of an aggressive signal—the white eyebrow of the adult. The same signal has been described as being used in courtship (Hough 1969). The behaviour of a trapped pair of *R. leucophrys* that was already mated confirmed my previous observations of this aggressive signal in wild birds. Under normal conditions this species assumes a similar appearance to that of a juvenile by concealing most of its white eyebrow. Displays of various degrees of aggressiveness are achieved by increasing the exposed part of the eyebrow by the appropriate amount. The female of a bonded pair maintains her subordinate position by displaying less of the eyebrow than does her mate. Similarly, the changing attitude of the male toward the female can be read in the varying degrees

of concealment or exposure of *his* eyebrow. The birds respond to any invasion of their territory with the same highly aggressive display.

Through continual aggressive displays (both birds showing the entire eyebrow) the captive pair succeeded in driving off a single Wagtail that had foraged near the aviary before their arrival. Once the birds were reconciled to captivity they were released in the walk-through aviary at the South Perth Zoological Gardens. Normal displays continued until a pair of wild *R. leucophrys* settled in the grounds and included the walk-through aviary in their new territory. Protracted display by the confronting pairs ensued, with the wild birds displaying from the roof of the aviary. The advantage of height thus gained helped these birds eventually to dominate the captive pair. This domination is now so complete that the birds in the aviary display *any* of the white eyebrow only rarely (T. Spence pers. comm.).

Erectile crests, plumes or tufts of feathers and concealable patterns in wing and tail are other examples of aggressive signals under voluntary control. Devices for reducing aggression are probably no less important as a means of maintaining pair-bonds by avoiding tension than they are in the more easily recognized area of social domination.

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