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# Variable plumage and bare part colouration in the Brown Falcon, *Falco berigora*: the influence of age and sex

*Paul G. McDonald*

School of Botany and Zoology, Australian National University, Canberra, ACT 0200, Australia.
Email: p.mcdonald@anu.edu.au

*Abstract.* The Brown Falcon, *Falco berigora*, is one of Australasia's most common raptors, yet considerable confusion remains over the influence of geography, age and sex on plumage and bare part colouration in this species. To address this issue, 160 immature and adult falcons from an individually marked, closely monitored population were examined. In contrast to previous studies, all were of known sex, age-group and part of the resident population or their offspring. Adult males had significantly lighter upperpart, cap, ventral and underwing covert plumage in comparison with other birds, closely resembling what has previously been described as a 'rufous morph'. Immature females were significantly darker than other ages and sexes in upperpart and underwing covert plumage, resembling descriptions of 'dark morphs'. In contrast, plumage of immature males and adult females tended to be similar and intermediate between these extremes, resembling the 'brown morph'. The buff-tinged, not white, ventral plumage and darker underwing covert plumage of immature males separated them from adult females. Cere and orbital ring colour also differed with sex and age: immature females had the dullest facial bare parts and adult males the brightest, adult females and immature males again being intermediate between the two. The results indicate that most variation in plumage and facial bare part colouration observed in the population could be attributed to age and sex differences as opposed to racial clines or the existence of colour morphs. Moreover, the brighter colours of adult falcons may function as honest signals of quality.

## Introduction

The Brown Falcon, *Falco berigora*, exhibits one of the most varied plumages of all falcons, with birds ranging in colour from a very dark brown, almost black, plumage through to a light red 'phase' reminiscent of the Australian Kestrel, *F. cenchroides* (Marchant and Higgins 1993; Olsen 1995). Despite its ubiquitous nature (Blakers *et al.* 1984), the marked variation in plumage colouration in this species remains poorly understood: as many as seven races have been described, with many more plumage types or phases (Condon 1951). To date, uncertainties associated with individual, sexual and regional differences in plumage colouration have led some to raise doubts over the validity of many proposed subspecific splits (Baker-Gabb 1986; Marchant and Higgins 1993). The most recent review has rejected all but the nominate subspecies (*berigora*) of Australia and the subspecies *novaeguinae* of New Guinea, subject to the attainment of more information on plumage variation (Marchant and Higgins 1993).

Several authors have described geographic variation principally through examination of museum skins (Amadon 1941; Condon 1951; Marchant and Higgins 1993), while McDonald (2003) described plumage and development characteristics of nestlings. Weatherly *et al.* (1985) identified features of juvenile plumage through observations of known-age captives and examination of skins. In doing so, Weatherly and colleagues identified age-related plumage traits that had clearly been mistaken for individual variation in other studies (e.g. Amadon 1941), such as mottled markings on flank feathers and buff plumage.

While the initial plumage of juveniles is now apparently well described and applicable throughout much of the species' range (Weatherly *et al.* 1985), the procession of subsequent moults between juvenile and adult plumage remains poorly understood. Weatherly *et al.* (1985) suggest that ventral surfaces progressively whiten with age and that this, along with the presence of spotted flank feathers, enables birds to be aged 'with considerable accuracy' to adulthood. Despite this, details of intermediate plumages were not provided, making this claim difficult to assess. The number of moults required to obtain adult plumage also remains debatable, variously listed as 4 or 6 years (Weatherly *et al.* 1985; Baker-Gabb 1986). While Weatherly *et al.* (1985) described plumage maturation in an unknown number of captive birds, they were all sourced from Tasmania, a population reputed to show little plumage variation in comparison with mainland birds (Marchant and Higgins 1993). Moreover, Olsen (in Marchant and Higgins 1993), in contrast to Weatherly *et al.* (1985), reports little comparative change in three captive birds from south-eastern Australia following their initial

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moult, further clouding the sequence of transition from juvenile to adult plumage.

Sexual differences in plumage also remain poorly described. Weatherly *et al.* (1985) suggest that females of equivalent age were darker than their male counterparts, as progressive whitening of ventral surfaces proceeded faster in males. Some females also retained a yellow speckled breast band, although this too was apparently lost with age (Weatherly *et al.* 1985). These sexual differences were not quantified and the extent to which they are applicable to mainland populations is yet to be assessed.

On top of this uncertainty with plumage colouration, differences in bare part colouration also remain poorly understood. In general, bare part colours of the orbital ring, cere, feet and legs are usually described as grey or bluish-grey; however, a consistent proportion of records list specimens with varying degrees of yellow in these areas (Condon 1951; Weatherly *et al.* 1985; Marchant and Higgins 1993). Given the importance of both non-plumage (Picozzi 1981; Rosenfield and Bielefeldt 1997) and plumage characters (e.g. Village 1990) in ageing and sexing other raptors, some of the confusion arising from these varied reports may be due to age- and/or sex-related differences. Thus the aim of this study was to examine plumage and bare part characteristics of a closely monitored, colour-marked population of Brown Falcons during the course of a long-term investigation of their breeding biology and ecology. This paper reports on results obtained during the first three years of the study.

## Materials and Methods

### *Study site and general methods*

Fieldwork began in July 1999 and remains ongoing; data collection for the results presented ceased in January 2002. The study site is situated approximately 35 km south-west of Melbourne, at the Western Treatment Plant, Werribee (38°0′S, 144°34′E), adjacent to Avalon Airport (38°2′S, 144°28′E) and small areas of surrounding private land, a total area of approximately 15 000 ha. Additional details of the study site have been described elsewhere (Baker-Gabb 1984*a*). The study site was visited regularly (6–7 days per week during late winter to early summer, 2 days per week at other times), with bal-chatri and modified goshawk traps (Bloom 1987) utilised to capture falcons. All birds were fitted with a unique combination of colour bands and a service band supplied by the Australian Bird and Bat Banding Scheme (ABBBS). Following data collection, birds were released at the point of capture. Nestlings raised in the study area were also colour-banded at an appropriate age (McDonald 2003). At all times when present on the study site I actively searched for banded birds and plotted their location on maps to identify territorial and pair relationships. Attempts were made to capture all unbanded birds and offspring returning to the study site.

### *Assigning age and sex*

Following capture, markings on flank feathers were used to assign relative age (Weatherly *et al.* 1985). In adult birds (4–6+ years old) of both sexes these feathers appear with numerous cream spots either side of the midrib, in immature birds (2–4 or 6 years old) these feathers are normally mottled with buff blotches or occasionally a mixture of buff spots and blotches. Novel juveniles (unbanded birds hatched the same year they were captured) from outside the study area were easily identified by their buff front, buff undertail coverts and dark upperparts (Weatherly *et al.* 1985). The terms 'adult', 'immature' and 'juvenile' refer to birds aged in this manner. The sex of captured free-flying individuals was determined on the basis of behavioural observations and a variety of morphometric characters that show little overlap in fully-grown Brown Falcons (Baker-Gabb 1984*b*; McDonald 2003). Molecular data were used to confirm the accuracy of this procedure; in a sub-sample of 20 males and 20 females sex was correctly assigned in every case (McDonald 2003).

### *Plumage and bare part descriptions*

Throughout the following, on first use of a colour (except black and white), descriptions are followed by a number and name in parentheses, corresponding to standard colours in Smithe (1975). Following capture, detailed descriptions of plumage characteristics were obtained and a photograph taken of each falcon. Before release, each bird's upperparts, cap and underwing coverts were scored as one of four colours, in order of increasing lightness: dark chocolate brown (21; Fuscous), chocolate brown (33; Cinnamon-brown), rufous-brown (~38; Tawny) and rufous (~140–40; Pratt's/Cinnamon-rufous). Markings on either side of the rachis of underwing coverts were also recorded as either cream (~54; Cream) or buff (124; Buff) spots or blotches, the latter being imperfect irregular markings in comparison with the regular circles of spotted feathers. Ventral plumage colouration was scored according to the percentage of various shades of brown present in both the breast and belly region. Birds that completely lacked brown on these feathers (i.e. ventral plumage was white) were given a score of 0, whereas birds with completely brown feathers were given a score of 100. Variations in between were assigned an appropriate value to the nearest 10%. Facial bare parts were assigned a value between 0 and 3 based on the degree of yellow present in the cere and orbital ring – 0, both cere and orbital ring blue-grey (86; Pale neutral grey); 1, lower half of orbital ring pale yellow (157; Sulfur yellow); 2, Both cere (usually top half) and orbital ring partially pale yellow; 3, both cere and orbital ring completely bright yellow (55; Spectrum yellow).

### *Statistical analyses*

Falcons captured on multiple occasions were included in analyses using data from their initial capture only. Differences in plumage and facial bare part colouration according to sex and age were assessed with generalised linear models (McCullagh and Nelder 1989). In analyses, the explanatory factors 'age' and 'sex' were assessed for statistical significance, as was 'adultmale', a factor that compared adult males with all other falcons sampled. Significance of terms was assessed as they were added in a step-wise fashion using the change in deviance statistic. This statistic approximates a Chi-square distribution (McCullagh and Nelder 1989). Where necessary, differences between two ages and/or sexes were determined using $z$ statistics. Ventral plumage colour was assessed using an ANOVA with 'age' and 'sex' as factors. All statistical tests were carried out using Genstat 5, release 6.1. Means are reported ± one standard deviation. The methodology utilised in this work was approved by the Australian National University Animal Experimentation Ethics Committee (Registration No. F.BTZ.02.99).

## Results

In total, 187 falcons were captured, consisting of 48 adult, 43 immature and 9 juvenile females and 41 adult, 28 immature and 9 juvenile males. Eight adult and seven immature females and three adult and four immature males were also recaptured during the course of the study. A total of 209 plumage descriptions were therefore recorded, including eight recruited offspring and three birds banded by others prior to this study; both of these latter groups were of known age.

**Table 1. Distribution of colours of upperpart, cap and underwing covert plumage recorded in Brown Falcons of different sex and age**
Significantly different ($P < 0.05$) groups are shown with different superscript letters

| Age and sex class | Dark chocolate brown | Chocolate brown | Rufous-brown | Rufous |
|---|---|---|---|---|
| Colour of upperparts | | | | |
| Adult males$^{A}$ | 1 | 4 | 8 | 26 |
| Adult females$^{B}$ | 4 | 28 | 10 | 3 |
| Immature males$^{B}$ | 8 | 11 | 8 | 1 |
| Immature females$^{C}$ | 19 | 22 | 1 | – |
| Colour of cap | | | | |
| Adult males$^{A}$ | – | – | 9 | 29 |
| Adult females$^{B}$ | 3 | 16 | 7 | 4 |
| Immature males$^{B}$ | 7 | 8 | 12 | 1 |
| Immature females$^{B}$ | 12 | 19 | 6 | 2 |
| Colour of underwing coverts | | | | |
| Adult males$^{A}$ | 1 | 2 | 2 | 24 |
| Adult females$^{B}$ | 3 | 13 | 9 | 13 |
| Immature males$^{C}$ | 5 | 15 | 1 | 3 |
| Immature females$^{C}$ | 13 | 19 | 1 | 5 |

### *General plumage descriptions*

Plumage descriptions of each bird fitted the very broad range given in Marchant and Higgins (1993). Falcons with dark chocolate brown upperparts were similar to the 'dark' morph, birds with chocolate brown or rufous-brown upperparts were similar to the 'brown' morph and falcons with rufous upperparts the 'rufous' morph (Marchant and Higgins 1993). Plumage of juveniles closely conformed to that provided by Weatherly *et al.* (1985) and, as such, is not considered further here.

### *Upperpart, cap and underwing covert plumage*

Adult male falcons had significantly lighter upperpart plumage than all other groups ($\chi^2_1 = 77.2$, $P < 0.001$) (Table 1); 86.7% of birds scored as rufous were adult males. In addition, significant age ($\chi^2_1 = 12.0$, $P < 0.001$) and sex effects ($\chi^2_1 = 7.4$, $P = 0.01$) were apparent when added to the model. When these relationships were examined further, immature females were significantly darker than immature males ($z = 2.7$, $P < 0.01$) and thus adult females (Table 1); 59.4% of dark chocolate-brown birds were immature females. Adult females and immature males tended to be intermediate in colour between the other groups and did not differ significantly from each other ($z = -1.0$, $P > 0.05$).

Cap colouration tended to be similar to upperpart plumage, in that 80.6% of rufous falcons were adult males and 54.5% of dark chocolate brown birds were immature females (Table 1). Cap colours of adult males were significantly lighter than in all other groups ($\chi^2_1 = 82.3$, $P < 0.001$) (Table 1); however, no additional age $\chi^2_1 = 2.5$, $P > 0.05$) or sex ($\chi^2_1 = 2.75$, $P > 0.05$) effects were apparent.

Adult males had significantly lighter underwing coverts than all other groups ($\chi^2_1 = 38.6$, $P < 0.001$) (Table 1); 53.3% of falcons with rufous underwing coverts were adult males. The addition of age to this model was also significant ($\chi^2_1 = 17.2$, $P < 0.001$), indicating that adult females had lighter underwing coverts than immature birds (Table 1) but darker coverts than adult males ($z = 3.5$, $P < 0.001$). The addition of sex to this model was not significant ($\chi^2_1 = 0.7$, $P > 0.05$), as both male and female immature birds had chocolate brown to dark chocolate brown underwing coverts (Table 1).

Clear age effects were apparent in the colours and shape of underwing covert markings (Table 2). Immature birds of both sexes tended to have buff blotched markings whereas adults had cream spots. In every bird that did not conform to this pattern a mixture of both markings was observed; these birds probably reflect individuals that have either just obtained, or were on the verge of obtaining, adult plumage. Once again, adult males had markings of a significantly different colour ($\chi^2_1 = 37.3$, $P < 0.001$) and shape ($\chi^2_1 = 5.0$, $P = 0.03$) from those of the other groups. Adult males always had cream markings, 78.6% of which were spots (Table 2). Significant age effects were also apparent for both colour

**Table 2. Distribution of colours and patterns of markings on underwing covert feathers in Brown Falcons according to sex and age**
Significantly different ($P < 0.05$) groups are shown with different superscript letters

| Age and sex class | Buff | | Cream | |
|---|---|---|---|---|
| | Blotches | Spots | Blotches | Spots |
| Adult males$^{A}$ | – | – | 6 | 22 |
| Adult females$^{B}$ | 1 | – | – | 37 |
| Immature males$^{C}$ | 20 | 1 | 2 | 1 |
| Immature females$^{C}$ | 31 | 2 | – | 5 |

($\chi^2_1 = 80.7$, $P < 0.001$) and shape ($\chi^2_1 = 5.0$, $P = 0.03$), indicating that adult females differed significantly from both immature sexes. All but one adult female possessed cream spotted underwing covert markings. Immature falcons did not differ significantly from each other in colour or shape of markings, tending to both be buff blotched (colour: $\chi^2_1 = 1.3$, $P > 0.05$; shape: $\chi^2_1 = 1.3$, $P > 0.05$) (Table 2).

*Ventral plumage*

There was a significant age and sex interaction in the total proportion of brown evident in the ventral plumage of falcons ($F_{1,156} = 5.0$, $P = 0.03$). This interaction arose as males had lighter fronts than did females of the same age; however, immature males did not have lighter fronts than adult females (Fig. 1). The same interaction and patterns were evident when the percentage of brown in the breast alone was examined ($F_{1,156} = 4.4$, $P = 0.04$) (Fig. 1). In contrast, the interaction between sex and age was not significant for belly scores ($F_{1,156} = 3.5$, $P > 0.05$); however, there were significant age ($F_{1,156} = 86.9$, $P < 0.001$) and sex ($F_{1,156} = 37.6$, $P < 0.001$) effects (Fig. 1). Thus, immatures of both sexes (relative to adults) and females of both ages (relative to males) were the darkest birds.

Every adult female except one had a broad band of chocolate or rufous-brown across the breast (Fig. 2). This breast band led to the breasts of adult females being significantly darker than their bellies ($t_{0.05(2),47} = 5.5$, $P < 0.005$) (Fig. 1), an effect that was conspicuous in the field in comparison with the more evenly coloured ventral surfaces of the other groups.

*Bare part colouration*

Facial bare part colouration of adult males was significantly brighter than in other groups ($\chi^2_1 = 92.1$, $P < 0.001$); only adult males developed fully yellow ceres and orbital rings and every adult male had at least some yellow in both these areas (Table 3). Both age ($\chi^2_1 = 19.2$, $P < 0.001$) and sex effects ($\chi^2_1 = 43.0$, $P < 0.001$) were significant when added to this model. Further examination of this pattern showed that immature females had darker, more blue-grey facial bare parts than immature males ($z = 5.8$, $P < 0.001$) (Table 3). However, while immature males tended to have brighter facial bare parts than adult females this difference was not significant ($z = 0.5$, $P > 0.05$) (Table 3). Leg and feet scales were a blue-grey colour in all birds examined.

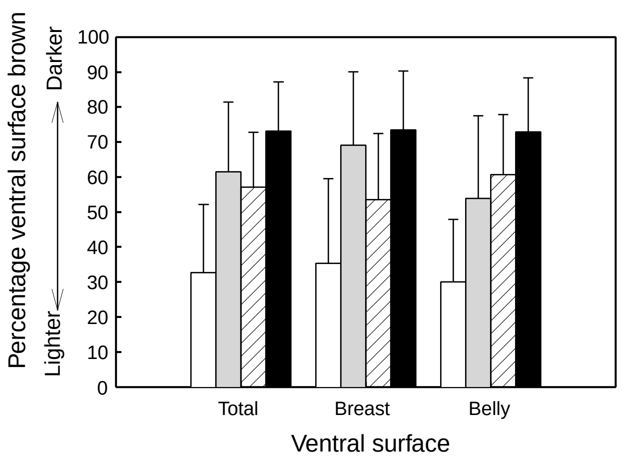


**Fig. 1.** The percentage of brown present in two regions (breast, belly and total) of the ventral plumage of Brown Falcons. Mean scores for adult males (white bars, $n = 41$), adult females (grey bars, $n = 48$), immature males (striped bars, $n = 28$) and immature females (black bars, $n = 43$) are displayed. Error bars indicate one standard deviation.

*Tail characteristics*

Incomplete barring of rectrices was observed in immatures significantly more often than in adults ($\chi^2_1 = 19.8$, $P < 0.001$), with just one adult female (2.1%) and no adult males showing the character. There was also a weak sex effect, with more immatures females (27.9%) having incomplete barring of the rectrices than immature males (10.7%) ($\chi^2_1 = 4.0$, $P = 0.045$). Moreover, barring of rectrices in immatures tended to begin ~20% of the way along the rachis; in adults, barring usually began at the base of the feather.

In contrast, barred undertail coverts were more frequently recorded in adults (46.1%) than in immatures (25.4%) ($\chi^2_1 = 7.4$, $P = 0.01$), with adult females 60.4% significantly more likely than adult males (29.3%) to show the character ($\chi^2_1 = 8.8$, $P = 0.003$).

*Characteristics of known-aged falcons*

The plumage colour of the eight nestlings recaptured on the study site at two years ($n = 7$) or one year (1 male) of age followed the patterns described above, with females tending to be darker (Table 4). As proposed by Weatherly *et al.* (1985), the inner flank feathers of these immatures were never fully spotted, although some individuals had developed spots in a few feathers, verifying the ageing technique used in this study. In a similar pattern to flank feathers, all but one male had buff blotched underwing coverts.

The broad patterns identified above indicate a progressive lightening of plumage and brightening of facial bare parts with increasing age, particularly in males. Excluding returned offspring and falcons recaptured without moulting, multiple descriptions were obtained for 14 birds. Of these, eight had lighter ventral plumage (Fig. 2*a*, *b*) and six (all adults) received the same score as on initial capture. On the basis of the photographs taken at capture, many birds that were not recaptured also lightened considerably during the study. Again, this effect was more prominent in males, although these differences could not be quantified. Some adult females, however, did not change appreciably after moult (Fig. 2*c*, *d*). Similarly, facial bare part colouration either remained the same ($n = 12$) or was scored as more yellow ($n = 10$) in recaptured birds. In no case was the reverse, a loss of yellow colouration, observed.


**Fig. 2.** (*a*) Adult female 111-25115, 15 September 1999, and (*b*) 9 November 2000, 420 days later. (*c*) Adult female 111-25122, 4 October 1999 and (*d*) 19 November 2000, 411 days later. (*e*) Adult male, 100-86344, 13 November 1999, 16 years and 23 days old.

The three older birds that were banded prior to the commencement of this study supported this pattern. One adult female was recaptured at 13+ years of age with plumage typical of other adult females on the study site: a chocolate brown breast band, white belly and chocolate brown upperparts (e.g. Fig. 2*c*). Two males were recaptured, at 16 and 18 years of age. Both had bright yellow facial bare parts, rufous upperparts and over 90% of their ventral plumage was white, the lightest recorded in the study. Underwing coverts of these individuals were also white with only a few rufous markings (Fig. 2*e*). This further supports the result that, as falcons age, particularly males, ventral and upperpart plumage became lighter and the proportion of yellow in facial bare parts increased.

**Table 3. Distribution of facial bare part colouration scores of Brown Falcons according to sex and age**

Significantly different ($P < 0.05$) groups are shown with different superscript letters. Higher scores indicate brighter (more yellow) facial bare parts, see Methods for details

| Age and sex class | Facial bare part score 0 | 1 | 2 | 3 |
|---|---|---|---|---|
| Adult male$^{A}$ | – | – | 24 | 17 |
| Adult female$^{B}$ | 1 | 21 | 26 | – |
| Immature male$^{B}$ | 3 | 7 | 18 | – |
| Immature female$^{C}$ | 27 | 14 | 2 | – |

## Discussion

Based on quantified data, as opposed to more usual qualitative descriptions, the results clearly indicate that much of the variation in Brown Falcon plumage and facial bare part colouration in southern Victoria can be attributed to differences according to sex and/or age (Table 5). Birds with the darkest plumage were generally immature females and the lightest were adult males. The plumage colours of these birds closely matched what others (e.g. Marchant and Higgins 1993) have termed dark (immature females) and rufous

**Table 4. Colours of upperpart, cap and underwing covert plumage and colour and pattern of underwing covert markings of immature Brown Falcons either two years (four females, three males) or one year old (one male)**

| Sex and age class | Females | Males |
|---|---|---|
| Colour of upperparts | | |
| Dark chocolate brown | 1 | – |
| Chocolate brown | 3 | 2 |
| Rufous-brown | – | 2 |
| Colour of cap | | |
| Dark chocolate brown | 2 | – |
| Chocolate brown | 2 | 3 |
| Rufous-brown | – | 1 |
| Feather colour of underwing coverts | | |
| Dark chocolate brown | 2 | – |
| Chocolate brown | 1 | 3 |
| Rufous-brown | – | – |
| Rufous | 1 | 1 |
| Underwing covert feather markings | | |
| Buff blotches | 4 | 3 |
| Cream spots | – | 1 |

morphs (adult males). Immature males and adult females tended to be intermediate and of similar colouration to these two extremes, closely matching plumage descriptions of the 'brown morph' (Marchant and Higgins 1993). Facial bare part colouration followed a similar pattern: immature females tended to have blue-grey facial bare parts lacking yellow colouration; immature males and adult females usually had pale yellow in portions of both the cere and the orbital ring; adult males always had some yellow and, in many cases, completely bright yellow facial bare parts. Adult females could be readily distinguished from immatures by a distinct breast band, cream ventral plumage in areas that were not brown, lighter underwing coverts and cream (not buff) markings on these feathers (Table 5).

Age effects on the frequency of incomplete barring in rectrices were also found (*contra* Marchant and Higgins 1993). However, these differences were not consistent enough to utilise as the sole criterion for assigning age, as suggested by Condon (1951). The preponderance of barring in the undertail coverts of adult females was unexpected and has not been noted elsewhere. This barring led to adult females having generally darker undertail coverts than adult males, as fitted the trend for other plumage characteristics, whereas in both sexes of immatures barred undertail coverts were encountered in similar frequencies.

In Brown Falcons both sexes defend territories and breed in immature plumage (author's unpublished data), engaging in 'side-slipping' displays (Baker-Gabb 1982; Debus 1991; Marchant and Higgins 1993), alternatively displaying their ventral and dorsal surfaces. While both sexes regularly perform this display, only males regularly do so alone (author's unpublished data). The lighter ventral surface of males of both ages compared with females results in greater contrast between dorsal and ventral surfaces during these displays. Further, the lighter (almost white) ventral and underwing coverts and rufous upperparts of the apparently oldest males maximises this effect, leading to these birds performing displays of the greatest contrast to my eye. White feathers reflect much greater amounts of ultra-violet light than do reddish-brown feathers while both buff and brown feathers reflect similar, comparatively small, proportions of UV light (Burkhardt 1989). Therefore, differences in the contrast between dorsal and ventral plumage of Brown Falcons evident to humans are also likely to be apparent throughout the entire spectrum visible to the birds. Moreover, facial bare parts of adult birds contain more yellow, and are brighter, than those of their younger counterparts, particularly in males, a feature that could quickly and easily be assessed by either sex. As these features appear age-related and are likely to be difficult to 'fake', ventral plumage and facial bare part colouration may be honest signals of quality (Zahavi 1975; Simmons 1988; Palokangas *et al.* 1994), particularly as adult raptors are usually better breeders than younger birds (see Newton 1989; Sæther 1990; Martin 1995 for reviews). These aspects will be investigated elsewhere.

The frequency of yellow in facial bare parts of Brown Falcons was far greater than the 1% of birds suggested by Weatherly *et al.* (1985). In this study every adult male and

**Table 5. Summary of the main differences in Brown Falcon plumage and facial bare part characteristics according to age and sex**

| Character | Adult | | Immature | |
|---|---|---|---|---|
| | Male | Female | Male | Female |
| Orbital ring and cere | Both at least some yellow, often completely bright yellow | Usually some yellow in both, never completely yellow | Usually some yellow in both, never completely yellow | Blue-grey, occasionally some yellow in lower half of orbital ring |
| Upperparts | Rufous to rufous-brown | Chocolate to rufous-brown | Chocolate to rufous-brown | Dark chocolate to chocolate brown |
| Underwing coverts | Rufous with cream spots | Chocolate to rufous-brown with cream spots | Dark chocolate to chocolate brown with buff blotches | Dark chocolate to chocolate brown with buff blotches |
| Ventral plumage | Breast and belly with similar, limited amounts of brown, mainly cream | Cream belly with distinct brown breast band | Brown markings with irregular buff blotches | Brown markings with irregular buff blotches |

98% of adult females had at least some yellow and 41% complete bright yellow in their facial bare parts. While age differences in facial bare part colouration have been observed in most falcons, sexual differences are far less frequently reported (e.g. Marchant and Higgins 1993; Negro *et al.* 1998; Ferguson-Lees and Christie 2001), perhaps due to poor recording of facial bare part colour on museum labels and the rapid fading of this character following death (Condon 1951). In any case, the supposition of Weatherly *et al.* (1985) that the presence of yellow in facial bare parts of Brown Falcons increases with age was confirmed by this study. Despite this, for both age groups, males exhibited more yellow in their facial bare parts than did equivalent-aged females and only adult males had fully bright yellow ceres and orbital rings. Seasonal variation in the colouration of these areas was not observed, in contrast to patterns reported for finches (Burley *et al.* 1992) and the American Kestrel, *Falco sparverius* (Negro *et al.* 1998), although repeated intensive sampling of individuals over a season is required to confirm this result.

The fact that adult birds had significantly lighter ventral plumage in comparison with same-sexed immatures also supports the findings of Weatherly *et al.* (1985). Weatherly and colleagues suggested that this process was faster and more complete in males, on the basis of their observations of captive birds. Quantified data from this study support this: adult females nearly always had a breast band whereas in most males the entire ventral surface was of a uniform colour. The extreme condition of an entire white ventral surface was found in only the oldest adult males. Marchant and Higgins (1993) rejected differences in plumage according to sex; however, the concurrence of this study and previous work indicates, at least for falcons in Tasmania and southern Victoria, that sexual differences in plumage are considerable and repeatable. Weatherly *et al.* (1985) found that breast bands were yellow in some females and were eventually lost as birds aged. In this study, breast bands of females were a variant of brown in colour over cream to white ventral plumage, and were present in all but one female, including a bird over 13 years old. Further, recaptured adult females retained breast bands over multiple moults, indicating that it is unlikely that breast bands are routinely lost in older females.

As the exact ages of all birds sampled were not known, it is possible that the sexual differences in adult plumage described have arisen through biased sampling, that is, comparatively older, and thus lighter, males were assessed in comparison with females. This appears extremely unlikely, however, because of the large numbers of falcons scored and the fact that recruitment of both sexes occurred at the same age (two years for four females and three males) or even younger for males (one male one year old).

Despite the progress in understanding variation in plumage outlined above, the age at which adult plumage is attained in Brown Falcons remains unclear, as recaptured nestlings had yet to acquire adult plumage. Further assessment of known-age falcons will provide clues to this process. Descriptions of the sequence of plumages exhibited by birds until the attainment of adult plumage, and the precise timing of this event, remain the last stumbling blocks to a more complete understanding of plumage variation in this species, at least for populations in southern Victoria.

Distinct differences in the proportion of colour 'morphs' of the Brown Falcon have been reported in other areas; for example, the preponderance of 'red' morphs in central Australia and 'dark' morphs in the tropical north (Amadon 1941; Marchant and Higgins 1993). Despite this, at least for the large population studied, most variation in plumage colouration observed could be attributed to differences resulting from sex- and age-specific influences, not the presence of different colour morphs within the population. Indeed, each age and sex class resembled the colour 'morphs' described by others (Amadon 1941; Marchant and Higgins 1993). This relationship casts doubt upon descriptions of races and morphs based solely on collections of falcons of uncertain age, sex and provenance. Clearly, further research of known individuals from other parts of the falcon's range is warranted. This information is critical to our understanding of the supposed marked plumage variation in this species, and thus the interpretation of the validity of proposed subspecies.

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