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THE USE OF FEATHER ABRASION IN MOULT STUDIES

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Four stages of feather abrasion have been defined for fully grown feathers; they can be recognized in the remiges, rectrices, and primary and secondary coverts of most birds. A code is given for each abrasion stage, allowing abrasion to be recorded in conventional moult formulae. Systematic recording of abrasion condition may help establish when moult occurs in species for which few other data are available. Partial and arrested primary moults, staffelmausers and slow continuous primary moults all produce distinctive patterns of abrasion; all these types of moult need more study. Feather abrasion can be an indispensable ageing guide in birds in which we have some knowledge of the moult history.

A FEATHER ABRASION CLASSIFICATION SCHEME

Feathers undergo progressive damage as they are exposed to sunlight, accidental collisions and the forces exerted in flight. This process has been termed abrasion* (Ginn and Melville 1983). The extent of abrasion on a feather is related to the time elapsed since it grew; recording abrasion can therefore be very useful in moult studies.

A widespread convention in moult studies is to record fully grown feathers in one of two categories. These are old (●) and new (5). This practise was spread by Newton (1966), who found the codes useful when using regression techniques to analyse moult duration. There is much to be learned from applying a more refined abrasion classification.

*Mead (1985) pointed out that the term abrasion is unsuitable for describing a process that includes photo-degeneration of feather protein, since everyone but ornithologists believe abrasion to be a destructive process caused by friction. He preferred the term 'feather flaking'. I have not followed his example since 'abrasion' seems entrenched in ornithological literature.

The abrasion classification presented here was developed during passerine studies in Victoria. Essentially the same scheme has been devised independently for ducks (Braithwaite 1971), waders (Prater *et al.* 1977) and albatrosses (Brooke 1981). Although a few studies have involved recognition of more abrasion classes (Bartle and Sagar 1987; Prevost 1983; Rasmussen 1988), a four point scale seems to be the most refined that can be used consistently by different observers. Perhaps a considerably more detailed scheme could be based on microscopic examination of small feather clippings. Burt (1986) used this technique when studying the effect of colouration on abrasion.

Abrasion has two readily visible effects on feathers. Barbs, barbules and barbicels deteriorate (wear) at the edges and tips of feathers, giving them a distinctive frayed appearance. Sunlight makes pigmented feathers fade with age. In most birds, wing feathers fade most quickly in the sections exposed to sunlight when the wing is folded and pale 'shadows' form at their tips.

These two characters are used in the following classification scheme:

N (New) Feather fully grown, with no indication of abrasion. New feathers usually have a distinctive gloss, difficult to define, which is more easily recognized with experience.

S (Slight abrasion) A feather which shows traces of abrasion but cannot be classified as old. The distinctive gloss of brand new feathers is absent. Slight wear at the feather tip may be visible on close examination.

O (Old feather; abraded) Some fading over most of the feather, particularly on those feather tips not usually shaded by other feathers. Feather tips worn.

V (Very abraded) Feather faded and worn; wear is severe enough to affect measurements of feather length. Often the distal barbs wear away, leaving the shaft longer than the webs.

Feathers at these stages of wear are shown in Figures 1 to 3, which are described later in the text. The codes for these abrasion stages can be used in conventional moult formulae, as has been the custom with the codes 0 and 5. Descriptions of conventional moult formulae can be found in Newton (1966), Snow (1967), Ginn and Melville (1983), Roberts (1982), Rogers *et al.* (1986), Rogers (1989) and Marchant and Higgins (in press). When the abrasion classification is applied, the code N should be used rather than 5; the latter is readily confused with S in handwritten notes.

DIFFICULTIES IN USING THE ABRASION CLASSIFICATION

It should be stressed that this scheme has some limitations. Feathers of some birds may not show this abrasion pattern. Remiges of some terns have a silvery sheen which is lost with wear, making the feathers progressively darker (Dwight 1901; Ashmole 1963). It is probably impossible to detect slight abrasion in white feathers, in which fading cannot be detected.

This abrasion classification appears applicable only to the remiges, rectrices, and primary and secondary coverts. The remainder of this paper deals chiefly with primary moult, for which most data are available.

The scheme must be used carefully. When captured in mist-nets, birds may suffer slight damage to their feathers that is easily repaired by preening. This net-wear can make feathers appear more abraded than they really are. If this seems to have affected wing feathers, it is best to examine both wings.

Some feathers abrade faster than others. This can make interpreting the number of feather generations difficult. (A feather generation is a set of feathers grown in one moult period.) The tips of the primaries between the wing point (the longest primary) and the body are exposed to sunlight when the wing is closed, and in most birds they are one of the first areas to show abrasion. Most birds moult their primaries from the inside outwards. The inner primaries of a non-moulting wing are thus usually slightly older than the outer primaries, which may also make them appear slightly more abraded. It is not unusual to encounter birds with slightly worn inner primaries and new outer primaries, and it can be difficult to tell whether partial primary moult (discussed later in this paper) or differential abrasion has caused this condition.

The contrast in the amount of abrasion between the inner and outer primaries is greater in birds that have completed a partial moult, and with experience this distinction becomes easier to make. Sometimes partial moults can be detected because the abrasion condition of some primaries appears inconsistent with their position when the wing is closed. In cases where the distinction between partial moult and differential abrasion is difficult to make, I recommend that banders record the observed abrasion condition, and also note what they believe to be the cause of the abrasion anomaly. A simple code, such as G1 (one generation) or G2 (two generations) is usually sufficient.

Secondaries sometimes show traces of abrasion before primaries, especially for species in which the secondaries are paler. This problem can be treated in the manner described above.

APPLICATIONS: INDICATING ABSOLUTE FEATHER AGE

The abrasion class can be useful in determining when moult occurs. This is important in species for which it is difficult to catch birds in active moult. Such cases are common. Eleven families of birds, mostly waterbirds, moult their flight feathers practically simultaneously (Evans 1985). In the brief flightless period, these birds are wary and often difficult to catch. Some Caprimulgiformes and passerines also become flightless or secretive during wing moult (Haukioja 1971; Rowher and Butler 1977). In addition, it is difficult to monitor some sites, such as remote co-operative banding stations, throughout the year. Moult workers in museums are often hampered by a lack of specimens collected in active moult.

Braithwaite (1971) studied abrasion rates of the wings of captive Black Duck *Anas superciliosa* and Grey Teal *A. gibberifrons*. Some CSIRO reports have used his data as the basis for the following loose rules of thumb on duck feather age (Braithwaite and Norman 1974, 1976; Norman *et al.* 1984):

- 1 (equivalent to N) = 0 to 4 months old;
- 2 (equivalent to S) = 4 to 8 months old;
- 3 (equivalent to O) = 8 to 12 months old;
- 4 (equivalent to V) = more than 12 months old.

Catching ducks involves a good deal of work, and standard capture techniques may be skewed against flightless ducks (McKean and Braithwaite 1976). Most of the scanty data on wing moult of Australian ducks comes from examination of abrasion of wings obtained during the shooting season (CSIRO references above). Interesting differences between sites and years indicate that moult of ducks in southeastern Australia is not as regular as that in the Holarctic, where most duck moult studies have been done.

This finding (which remains unexplained) shows that the use of abrasion as an absolute indicator of feather age can provide fascinating information. It should be noted that Braithwaite's figures are probably only applicable to duck primaries. Differences in habitat, flight styles, and feather structure and colour (Palmer 1972; Ginn

and Melville 1983; Burt 1986) probably cause extensive interspecific variation in the rate of feather abrasion. Abrasion rates can also vary within species. Ducks in badly managed wildfowl collections can develop very abraded plumage in a short time (P. J. Fullager, pers. comm.). If stress also affects abrasion rates in wild ducks, then the findings in the CSIRO reports should be treated with caution.

APPLICATIONS: DESCRIBING RELATIVE FEATHER AGE

In a single bird

When three or more generations of fully grown feathers can be seen in a bird, or in a population of birds, it is misleading to record them simply as old (O) or new (N). There are several instances in which more than two feather ages may be seen in a bird, most of which are described by Rogers *et al.* (1986). A few are covered below.

Partial primary moult

Many birds undergo a partial moult of the flight feathers; an Australian example is the Curlew Sandpiper *Calidris ferruginea*, in which many overwintering juveniles moult a variable number of outer primaries from January to March (Paton *et al.* 1982; Barter 1986; Rogers *et al.* 1990). Presumably these moulted feathers are worn enough to impair flight, and are replaced at a time when the birds have insufficient energy reserves for a complete moult. The primaries of these Curlew Sandpipers are all replaced in the next complete moult. During this moult, one can see new feathers (N) on the inside of the wing, slightly abraded outer primaries (S) which grew during the partial moult, and between them, old to very abraded primaries (O to V) which have been retained for more than a year.

Arrested moult

Ginn and Melville (1983) defined an arrested moult as one which 'would normally have been "complete", which has stopped before all of the old feathers have been replaced. The old feathers, which have been retained, are then replaced in sequence at the time of the next complete moult...'. Before the next moult begins,

arrested moults cannot be told from suspended moults, in which moult is resumed at the point of interruption. Rogers *et al.* (1986) recommended the use of the term 'stopped moult' in such cases. In most birds which have arrested a moult, one can see three ages of feather during the next complete moult. In the primaries of most such birds, the innermost primaries (those between the growing feathers and the body) will show no abrasion (N); the outermost primaries, which have been retained for two years, will be very abraded (V), and the other fully grown feathers, which have been retained for one year, will be old (O).

Staffelmauser

This mode of flight feather moult has also been called wave moult (Brooke 1981), stepwise moult and serial moult (Prevost 1983). Staffelmausers are generally restricted to large volant birds (Prevost 1983). In most birds with a staffelmauser, moult of the primaries begins with a 'wave' of moult beginning on the innermost primary and heading towards the outermost. Before this wave of moult is complete, another begins at primary 1. In some large flying birds, several waves of moult may be active in the primaries at one time. Moult of the secondaries and tail often follows a similar pattern. Waves of moult can be interrupted; often the moult condition on each wing differs. Staffelmausers produce complex moult patterns that have sometimes been misinterpreted as irregular moults (Prevost 1983). They are likely to be confusing even when abrasion is taken into account. Discontinuities in feather abrasion indicate arrested moult waves and may be useful in identifying different feather generations.

Prevost (1983) suggested that staffelmausers are undertaken by large birds since they have high wing loadings and take a long time to grow a flight feather. They cannot complete a moult as rapidly as their environment dictates without shedding several feathers simultaneously, and they cannot shed adjacent feathers without seriously impairing their flying abilities. The staffelmauser appears to solve these problems.

Although sulphur amino acid availability may be a moult constraint (Murphy and King 1987), it seems likely that suspension of moult waves in

birds with staffelmausers occurs when there is least energy to spare from other activities. This may allow inferences to be made about energy constraints on a bird during a year. These clearly differ between albatrosses, which suspend moult when breeding (e.g., Furness 1988) and California Condors *Gymnogyps californianus*, White Storks and Black Storks *Ciconia ciconia* and *C. nigra*, which do so in the non-breeding season (Snyder *et al.* 1987; Bloesch *et al.* 1977; Bloesch *et al.* 1987). Staffelmauser also has interesting ageing applications. In species which always employ a staffelmauser, only juveniles will have a wing with uniform abrasion. Most staffelmauser studies have also revealed recognizable differences between moult condition of subadults and adults. If abrasion condition of opposite wings of albatrosses gets more out of kilter with age, as suggested by Brooke (1981), it might be possible to develop a technique for refined ageing of adults.

Slow continuous moults

Zann (1985) described a pattern of moult in the Zebra Finch *Poephila guttata* that is very similar to a staffelmauser. Zebra Finches replace their primaries in slow outward moving waves. Only one growing primary can be seen in a moult wave at one time, and each wave of moult takes about seven months. Another wave of moult begins at about the time that the previous wave of moult is completed. Moult is slowed, but not stopped, by energetic inconveniences such as breeding. Similar moult patterns appear to occur in the Squatter Pigeon *Petrophassa scripta* (Crome 1976) and the Budgerigar *Melopsittacus undulatus* (Wyndham 1981).

This moult sequence appears to be a simple staffelmauser, but Prevost's (1983) theory explaining staffelmausers can not apply to such small birds. Wyndham (1981) suggested that the slow continuous moult permitted opportunistic breeding in birds living in arid, unpredictable areas. Very few moult studies have been done in such environments, and the theory cannot be tested without more information about the moult sequences employed by birds in these areas. A gradual transition from new to old primaries can be expected on birds that do a slow continuous moult.

In a population

As a rule, the feathers of same aged birds in a population show similar abrasion conditions. Exceptions to this generalization have been reported, and it should be remembered that slight differences in the moult schedule of individuals, such as those between sexes (Ginn and Melville 1983), may not produce obvious differences in abrasion. Differences in abrasion condition between age classes can be a valuable ageing

character, especially in species in which the first plumage is very similar to that of the adult.

In most species from temperate climates, adults have rather worn plumage at the time when their young fledge into a fresh juvenile plumage. The juvenile plumage appears less abraded until the adults finish their next complete moult. This can be seen in Lesser Golden Plovers *Pluvialis fulva* (Figs 1 and 2). In some species, the post-juvenile

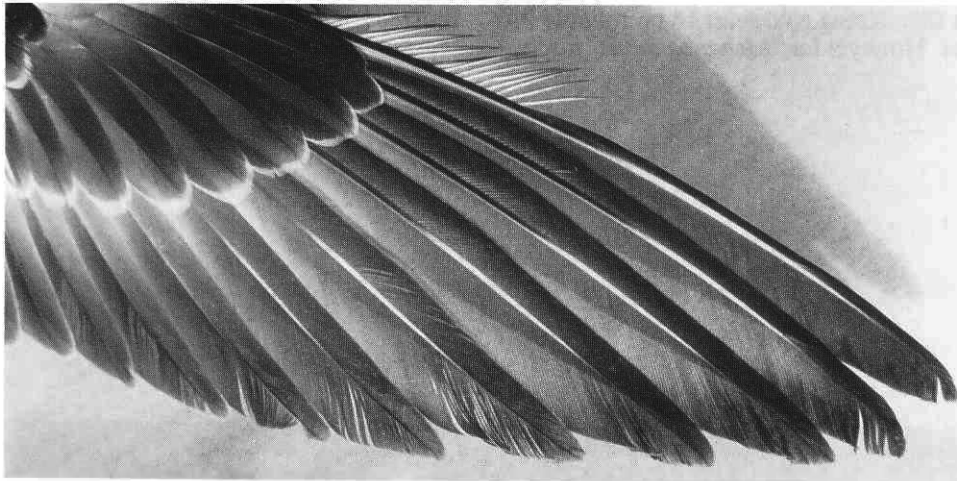


Figure 1. Outstretched wing of juvenile Lesser Golden Plover *Pluvialis fulva*, with moult formula S^{10} . Photographed at Yallock Creek, Victoria, 15 November 1986.

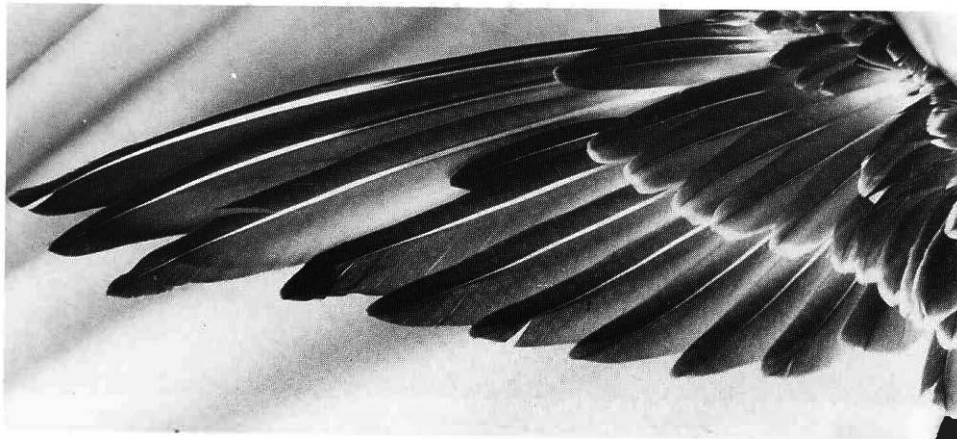


Figure 2. Adult Lesser Golden Plover *Pluvialis fulva*, age 2+, with moult formula $N^{63}O^3$. Photographed at Yallock Creek, Victoria, 15 November 1986.

moult is complete and occurs at the same time as that of the adult (Ginn and Melville 1983; Rogers *et al.* 1986).

In many other species, the juvenile wing and tail are not moulted until the second summer/autumn at about the same time as the annual adult moult. The first plumage of such birds is more abraded than that of the adults during the first winter and spring and the second summer. Age 2 birds (Australian Bird and Bat Banding Schemes' Age Code; Rogers *et al.* 1986; Rogers 1989) can often be identified in their second summer because their feathers are very abraded. Retraps have shown this ageing character to be reliable in the Fuscous Honeyeater *Lichenostomus fuscus*

(Rogers *et al.* 1986) and the Red-necked Stint *Calidris ruficollis* (Forest 1982; Rogers *et al.* 1990). The wing of an age 2 Lesser Golden Plover is shown in Figure 3.

These generalizations do not apply universally, and many birds have different moult histories which also make abrasion a useful ageing character. The moult histories of most Australian birds are undescribed; such birds can be difficult to age. When more information on the moult of such birds becomes available, banders who have recorded moult and abrasion condition systematically on little known species may be able to correct or refine age codes assigned to birds they captured some time ago.

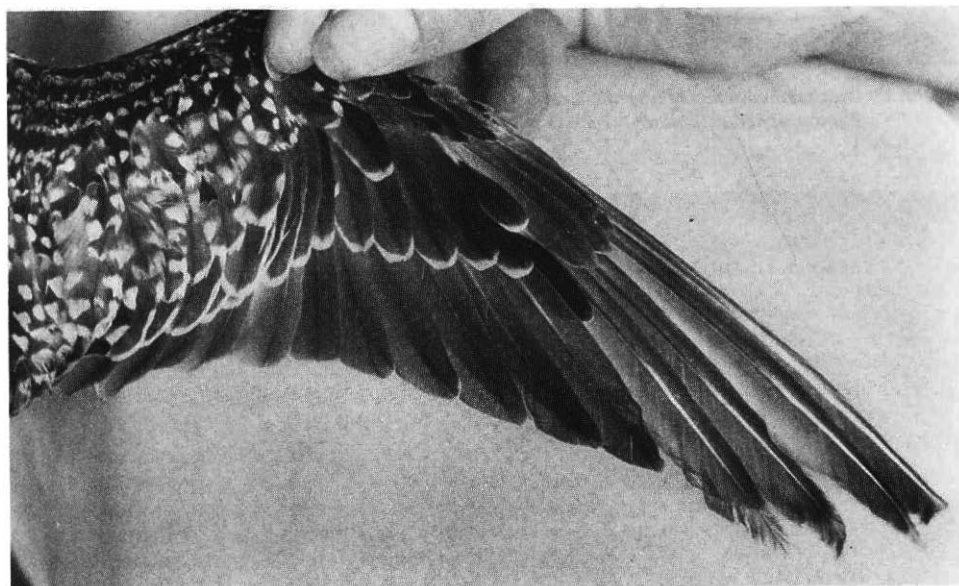


Figure 3. Immature Lesser Golden Plover *Pluvialis fulva*, age 2, with moult formula $N^53^1V^4$. Photographed at Yallock Creek, Victoria, 15 November 1986.

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