SOME FEEDING ADAPTATIONS AND POSTURES OF THE YELLOW WHITE-EYE (*ZOSTEROPS SENEGALENSIS*)

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ABSTRACT

Yellow white-eyes were observed in the Kivu Highlands of the Eastern Zaire both in the field and in an aviary.

Some feeding adaptations are described, among them the ability to reach most points of the feeding ground among twigs and leaves by clinging in almost every body position even to weak supports and by hovering, 'Zirkeln' (enlarging of crevices by introduction of the closed bill which then opens and presses its edges apart), intake of liquids by licking and examination of shallow cavities with the tip of the tongue.

Some aspects of the flock structure, clumping and allopreening are discussed.

The agonistic behaviour patterns are described. While fighting is still of a relatively general passerine pattern, threat and submissive postures are partly ritualized. Threat postures consist of bill-opening, pivoting, wing-dropping and bill-clattering, each of them manifesting increasing aggressive tendencies in this order. Submission is expressed by becoming motionless and, in higher intensity, by fluffing, whereby certain plumage areas, crown and back, are already fluffed maximally in low intensity displays and re-direct the aggressive tendencies of an eventual partner towards allopreening.

Only a few observations were made on courtship behaviour. Horizontal wing-quivering is the usual approach of males to their potential mates whose aggressive tendencies are cut off by the offer of the male's head and neck plumage for allopreening.

The described postures are compared with what is known of comparable behaviour of other *Zosterops* species.

INTRODUCTION

While systematic and ecological aspects of the white-eyes (Zosteropidae) have received considerable attention (Gill 1971, 1973; T. Harrison 1955; Mees 1957; Moreau 1957; Skead 1967; Skead & Ranger 1958; Stresemann 1931), there are still only a few accounts of their behaviour: that of *Zosterops borbonica* and *Z. olivacea* of Reunion Island by Gill (1971, 1973), that of *Z. lateralis* in New Zealand by Kikkawa (1961), that of captive *Z. palpebrosa* by Kunkel (1962) and that of several South African *Zosterops* species (summarized by Skead 1967). Most of the behavioural peculiarities described in the present article have been mentioned before only in *Z. lateralis* and *Z. palpebrosa*, *i.e.* two of about eighty species of the family. A short description of these peculiarities in a third species living at great geographical distance, may be welcome.

The birds studied belong to the population of the Zairian Kivu Highlands which is considered to be transitional between the races *Zosterops senegalensis stuhlmanni* and *Z. s. reichenowi* by Moreau (1957). The main area of observation was on the eastern, inner slope of the

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western rim of the Central African Rift Valley south-west of Lake Kivu. Here, most of the area between 1 460 m – the lake shore – and about 2 000 m above sea-level is intensively cultivated and does not offer habitats for white-eyes except in a few unarable places, *e.g.* around swamps, or on larger plantations which include secondary woodland. Fortunately the ground of the Institut pour la Recherche Scientifique en Afrique Centrale – IRSAC – at Lwiro (2°14'S/28°49'E) still includes numerous gardens, plots of secondary woodland and tree plantations, and supports a great population of yellow white-eyes. Most of the outdoor observations were made there. Further opportunities for observations were available a few km further west, in the Kahuzi-Biega National Park which includes most of the area above 2 000 m above sea-level south-west of Lake Kivu. This part is covered by mountain and bamboo forests where yellow white-eyes are frequent.

In addition to the outdoor studies, a small group of yellow white-eyes, ranging between three and nine individuals, has been kept in an aviary of dimensions: height 2,5 m, length 6 m, width 2 m, at Lwiro in order to observe some of the behaviour patterns more closely.

SOME FEEDING ADAPTATIONS

Like most other Zosteropidae, the yellow white-eye takes an extraordinary wide variety of food items: arthropods as staple food, but also nectar, berries and other fruits and occasionally small seeds.

The feeding ground of yellow white-eyes includes the smaller twigs and the leaves of trees and bushes. The birds avoid coming down to the forest floor except for drinking if no other liquid is available. Their ability to cling even to weak stems and twigs in almost every position of the body, supported by the feet alone, gives them access to most potential feeding places within their habitat. Besides, insects are taken occasionally in the air and can be picked from otherwise inaccessible leaves by hovering (Skead 1967). White-eyes thus have access to nearly all visible food items which they encounter, and some further behaviour patterns allow them to locate hidden ones as well or to use very small amounts of food-stuff.

One of these patterns is 'Zirkeln': the bird introduces its closed bill into a crevice, then opens it and presses the edges of the crevice apart in order to peer into it. Tame birds demonstrate considerable force when they try to open the 'crevice' between two fingers of the human hand. 'Zirkeln' has been seen to be used to examine the bark of twigs and dry rolled leaves which often contain insects and spiders, as well as to open certain flowers. It is also used during allo-preening to 'open' the offered parts of the plumage of the preened partner, but never seems to occur if the bird preens itself.

One morphological feature of the head seems to be correlated with 'Zirkeln': the lore of short dull-black feathers running down from the eyes towards the base of the bill. The feather stripe is straight and directed towards the tip of the slightly curved bill. This arrangement avoids all reflections which could disturb the bird when it peers binocularly on objects near the bill-tip in the opened crevice. It is not only the only black part of the whole plumage of yellow white eyes, but also the only structure which interrupts the conspicuous ring of white feathers around the eye. Very similar structures are present also on the heads of other birds which display

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'Zirkeln' (Lorenz 1949).

The heads of at least the majority of the species of the Zosteropidae show a similar configuration: a dull black lore interrupting the white eye-ring in front of the eye and running to the base of the bill. However, there are some published drawings of *Zosterops* heads (*e.g.* in Mees 1957) with entirely closed eye-rings, but these may be due to an erroneous arrangement of head feathers in the stuffed specimen from which the illustrations were drawn. The structure has, anyway, a wide distribution within the family which suggests a parallel distribution of 'Zirkeln', but this has been described until now in only one other species: the Indian white-eye (*Zosterops palpebrosa*) (Kunkel 1962), and apparently has escaped the attention of observers in other species.

The same is true of another feeding pattern: rapid examination of shallow holes by the tip of the tongue which comes out of the tip of the bill for one or two mm. This behaviour is frequent during the search of rough bark surfaces, leaf axils and flowers. Whether it occurs also during the examination of deeper cavities is uncertain although it is likely; it escapes observation by the deeper immersion of the bill-tip. Again, this behaviour has not yet been described in any Zosteropidae other than the Indian white-eye (Kunkel 1962).

The structure of the white-eye tongue (see Liversidge in Skead 1967 for summary) suggests that some intake of liquids is involved: the tip itself consists of a brush of horny papillae able to take up liquid by surface tension, but hardly able to taste. According to the present understanding of the function of the tongue, taste could only be detected after drawing back the tongue into the bill.

Thus, probing with the tip of the tongue may just represent a special case of the sucking technique of these animals. The main ecological advantage of the specialized function of the tongue apparatus may be that it enables the birds to take up liquids which are available in only very small quantities. It makes the white-eyes independent of water supply on the forest floor at most times and facilitates the use of nutrient liquids: flowers can be used even if they have a weak production of nectar, and the birds can take up exudations on twigs and leaves which are present in only small droplets.

Sunbirds (Nectariniidae) often display a similar set of feeding adaptations (Skead 1967), some of them also display 'Zirkeln' (Kunkel 1964). But they are apparently more dependent on nectar, and each species seems to be more restricted in its methods of obtaining arthropods (Kramer 1975). Compared with other insect-seeking birds in the same habitat, *e.g.* the Sylviidae, white-eyes have access to more food sources, especially to flowers and their nectar. Whether 'Zirkeln' is an advantage remains uncertain as so little is known about the distribution of such patterns. But, with their widely varied diet and their feeding patterns which ensure an intensive use of the food resources of the habitat, white-eyes obviously have a broader ecological niche than most other comparable small birds.

The ability to use many different food resources enables white-eyes to live in very varied habitats. The yellow white-eye with its wide geographical and altitudinal range furnishes an excellent example. This feature may also be at the base of the astonishing success of the colonization of the most remote tropical islands around the Old World. It seems also to be the decisive factor for the survival of white-eyes within the continental bird faunas: specialization does not occur in Zosteropidae except on islands with a restricted avifauna and 'unoccupied niches'.

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Continental species tend to be very similar and to exclude each other geographically (Mees 1957, Moreau 1957).

FLOCK STRUCTURE

Outside the breeding cycle, yellow white-eyes occur in small flocks of about four to ten birds. The big assemblies reported of other *Zosterops* species in regions with pronounced winters – New Zealand (Kikkawa 1961) and South Africa (Skead 1967, Skead & Ranger 1958) – do not occur in the Kivu Highlands, not even in the three months of the great dry season when the white-eyes roam far outside their normal habitats and appear *e.g.* at Lwiro in greater numbers than during the rest of the year.

Within these flocks, birds keep together in 'pairs', or more exactly allopreening and clumping alliances. In most cases, one white-eye allopreens and clumps with only one other partner at a given moment, but occasionally a bird is allopreened by two other individuals, one from either side, which try to avoid each other. We did not observe the composition of a flock over a longer period in the wild, but caught an entire one, banded the birds with colour rings and put them in our aviary. Here 'pairs' revealed themselves as unstable and clumping partners were often exchanged. This has also been found in the Indian white-eye (Kunkel 1962) and differs strongly from the behaviour of other small passerines which keep together in pairs and flocks, *e.g.* the Estrildidae. An interpretation of both behavioural types has been tried elsewhere (Kunkel 1974). It was thought that the frequent exchange of partners serves to secure a partner in equal gonadic condition and that the close coherence of the flocks assures the necessary frequency of such meetings.

There is a constant high level of aggressiveness inside the small flocks of yellow white-eyes. To maintain the coherence of the flock in spite of this aggressiveness, an elaborate advertising of aggressive tendencies and an effective appeasement behaviour had to develop. These patterns will be described in the following sections.

CLUMPING AND ALLOPREENING

Clumping and allopreening are such prominent features in the behaviour of many, if not most, white-eyes that they have been described in most of the species which have been studied (*e.g.* Gill 1973, C. I. O. Harrison 1965, Kunkel 1962, Skead 1967) and even documented by sketches for the South African forms by Skead (1967) and by photographs for the Indian white-eye by Kunkel (1962). These behaviour patterns do not differ essentially in the yellow white-eye and therefore need no detailed description here. Only a few general aspects should be discussed.

In white-eyes, it is particularly evident that allopreening is due to 'sublimed' or re-directed agonistic tendencies (Goodwin 1956, C. I. O. Harrison 1965), aggressive ones in the allopreener, submissive ones in the preened bird. It is the means of turning these tendencies into innocent ones and of ensuring the social contact within a pair or an allopreening alliance. Therefore it is not astonishing that a great deal of the appeasement as well as the courtship display is derived

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from postures which offer parts of the plumage to be allopreened (see below), and that it thus serves also to maintain the flock coherence.

As shown elsewhere (Kunkel 1974), allopreening may have an even higher importance outside than inside the breeding cycle. In the latter period, mutual attraction is ensured by sexual tendencies which do not counterbalance agonistic ones outside of it when these may be overcome by the re-direction into allopreening alone.

AGONISTIC BEHAVIOUR

Serious fights which result in damage of plumage or worse, have not been observed in flocks of the yellow white-eye. They do not even occur if a new, strange bird is introduced into the aviary which contains only members of a 'natural' flock caught together in the wild. But there is a constant 'quarreling' within the flock involving chasing and various threat displays similar to those described by Kikkawa (1961) for the winter flocks of *Zosterops lateralis*.

A short pecking into the plumage, especially of neck and sides, is common if two yellow white-eyes approach too near to each other in a feeding place. It may be repeated after a while if the pecked bird does not retreat, but it does not lead to fight or pursuit. It is frequent also in pairs and allopreening alliances when one of the partners tends to avoid the other which is drawing near to clump and/or to allopreen; often the pecking bird hops a few cm aside after having pecked. The behaviour often turns into allopreening if the partner insists on clumping. The quite similar pecking in *Z. lateralis* has been considered as ritualized by Kikkawa (1961).

Higher levels of aggressive tendencies manifest themselves in pecking on the head, especially the crown. But this has been seen very rarely: either the attacking bird is superior to the attacked one which flees upon its approach, or the birds are more or less on the same level of aggressiveness. Then they erect in front of each other and peck mutually on their bill-tips. After a few pecks, fight is given up; one or both of the opponents fly away.

The most frequent aggressive behaviour in yellow white-eyes consists of 'supplanting attacks' (Hinde 1952): a superior bird pursues an inferior one by a rush on its temporary resting place, the latter flees, and the challenger 'supplants' its adversary for an instant on its former resting place before rushing on its victim again. Long series of such supplanting attacks are common, and often a flock of yellow white-eyes moves quickly through a piece of woodland, its members pursuing each other all along by supplanting attacks.

Fighting behaviour itself has remained relatively simple and corresponds to that of most passerine birds. Some of the threat and appeasement postures which accompany it, have taken, on the other hand, a rather peculiar form.

Bill opening is the threat posture with the obviously weakest motivation of aggressive tendencies. The threatening bird crouches, sleeks its plumage and opens its bill widely towards the threatened individual, following its movements by turning the head. No sound is uttered during this display. If the threatened bird draws nearer, fluffing of the crown feathers, a submissive posture (see below), is often combined with bill opening (Figure 2A).

Bill opening occurs in birds which are obviously in a conflict between two opposite tenden-

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cies: the tendency to flee from an approaching superior individual and the tendency to stay where they are. In most cases, this is near a feeding source. The behaviour sequence which follows depends on the movement of the bird which is displayed to: if it moves off without having drawn too near to the displaying bird, the latter remains on the spot and takes up its former occupation, usually feeding, again. But a closer move of the superior bird towards the displaying one, and particularly its touching the plumage of the latter, results invariably in the flight of the displayer.

Pivoting (Figure 1A) consists of slow turning movements from one side to the other in a rather narrow angle of about 30°. There is no short stop at the lateral turning point as in similar displays of numerous other passerines (Andrew 1961, Blume 1967), but an instantaneous reversal. The body is held stiff during the movement and kept in a position slightly more horizontal than in the normal relaxed state, the head and bill remaining strictly in the longitudinal body axis, but pointing downwards at an angle of about 45° below the horizontal. The plumage is slightly fluffed, but still forms a coherent cover all over the head and body. The displaying bird does not utter a sound, but in the intervals between bursts of pivoting, loud calls, falling in pitch, are given.

Such pivoting, without wing displays, has been seen infrequently in the yellow white-eye. The bird then either proceeds with an actual attack or turns away from the threatened bird, and sometimes attacks another individual. Pivoting occurs more often in combination with wing-dropping. The behavioural sequences following such a display show a hesitation to attack. Pivoting in courtship, combined with horizontal wing-quivering, often leads to an attack on the courted bird.

The situations in which pivoting occurs suggest a nearly balanced conflict between tendencies to attack and to avoid the threatened bird. This conflict corresponds to the origin of the posture: it is derived from the change between the positions of taking off either to the right or to the left

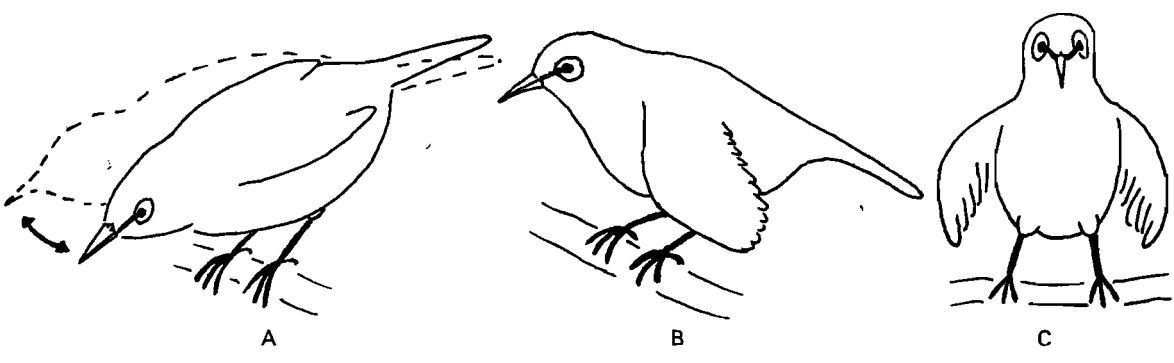

FIGURE 1

Threat postures (schematic): A, pivoting; B, wing-dropping (lateral view); C, wing-dropping (frontal view).

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of the threatened individual (Daanje 1950). The most prominent features of the ritualization are the stiffness of the posturing bird and the slowness of the movement which differ strikingly from the normal rapid behaviour of the agile yellow white-eyes.

Wing-dropping (Figures 1B, C) is a very frequent threat pattern. Body and head position as well as the degree of fluffing of the plumage resemble those already described for pivoting. The wings hang down symmetrically on the sides of the body in a bowl-like manner, still held parallel to the body axis, but as far off the body as possible. In low intensity, they are only slightly moved out of their normal resting position, but in full intensity dropped down to the level of the tarsi. The effect, particularly if the bird is seen from the front as the threatened individual will see it, is a strong enlargement of the body silhouette. The dropped wings are quivered in short bursts. The display is sometimes combined with pivoting (see above) and usually accompanied by the loud calls with falling pitch already mentioned. Very superior birds utter these in tremolo, *i.e.* regularly interrupted by short pauses.

Wing-dropping is obviously an expression of high aggressive tendencies in conflict with weak tendencies not to attack: it leads almost always to heavy attacks on the bird to which it is displayed, and is the normal display which is interspersed between series of supplanting attacks. Only superior individuals display in this way.

Bill-clattering is heard during every challenge. It may also be heard at feeding places if superior or equally motivated individuals come in contact with other white-eyes or almost so. It is the display with the highest aggressive level. How exactly it is done, remains open.

Pivoting and wing-dropping are highly ritualized and conspicuous among the threat patterns of the yellow white-eye. They advertise very clearly the mood and intentions of the displaying bird to its partner; so does bill-clattering. This advertisement allows the challenged individual to give way in time and thus avoids the high level of general aggressiveness of the species resulting in serious damage among flock members.

Becoming motionless – '*freezing*' – is the very first reaction to threat or low intensity pecking. The plumage is sleeked at the first instant. While birds in which tendencies to peck back and to retreat are fairly balanced stretch up their body in front of the pecker before freezing, submissive birds crouch before they freeze. They often react to the next movement of the superior pecker or threatening individual by fluffing of the crown or, in higher intensity, of crown and back feathers, the head and body still remaining motionless.

Freezing occurs in all kinds of low intensity pecking encounters, but is especially frequent in pecking contacts between the members of a pair or an allopreening alliance. In this case, one partner may peck the other, which then freezes, whereupon the pecker freezes too. The pecking bird may then peck again or be pecked by its partner, and again a short freezing of both takes place. Such pecking and freezing sequences may go on for a while and finish up in clumping and allopreening in most cases. During the formation of a pair or an allopreening alliance, the bird which tries actively to get into contact with the other freezes more often than its partner, a behaviour which obviously facilitates the contact and often 'cuts off' a tendency to fly away in the more passive partner. Finally, freezing is the usual response of inferior birds to an outburst of

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supplanting attacks within the flock. Such attacks are, indeed, more often directed towards active birds, and the attacker tends to overlook freezing inferior individuals.

The situations under which freezing occurs, indicate again a conflict between opposite tendencies: the bird tends to fly away, but also to stay where it is. In some of the described situations aggressive tendencies also become overt, but only in low intensity patterns. The tendency to take off manifests itself also in the postures adopted when freezing takes place: they are starting positions to fly off (Daanje 1950).

There is no doubt that freezing has a signal function, especially during the formation of a pair or an allopreening alliance, and that, at least in short distance displays, it has become ritualized by extension of the time of presentation.

Fluffing is the main submissive posture. Figure 2 shows different stages which correspond to different degrees of intensity. The type with the lowest threshold involves the fluffing of only the crown feathers (A) which cease to form a coherent cover, but are lifted one from the other. This display is often combined with bill-opening as shown in the drawing, but has also been seen often

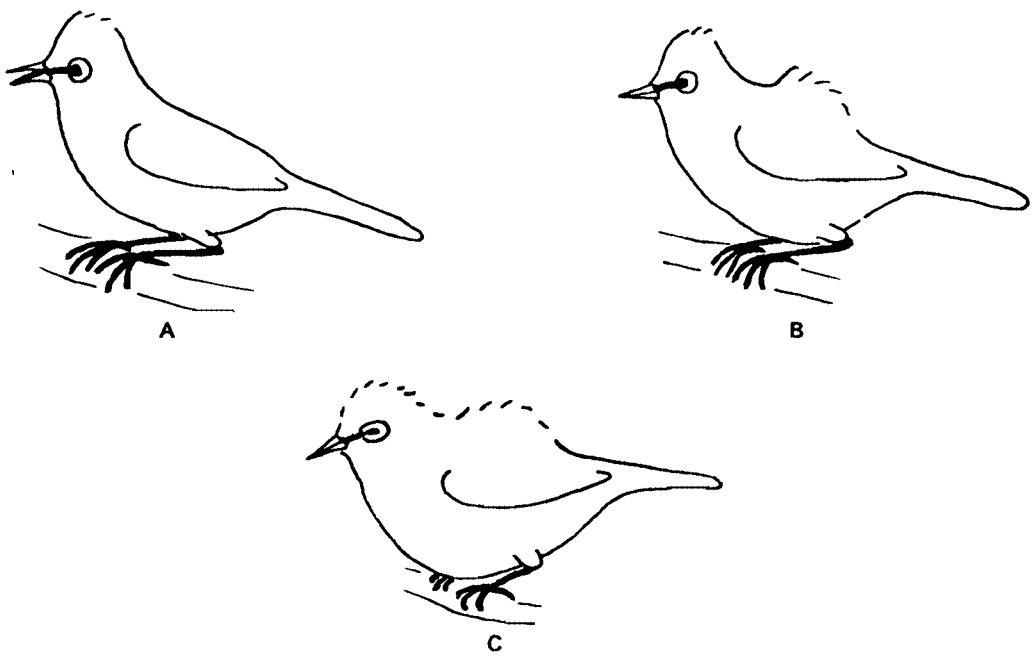

FIGURE 2

Submissive fluffing (schematic): A, crown-fluffing (low intensity form); B, crown- and back-fluffing (medium intensity form); C, full fluffing of head and body plumage (full intensity form).

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in birds which were menaced by the presence of a superior bird on the feeding place, but continued to feed eagerly. In medium intensity, the feathers of the central back are fluffed and raised in addition to the crown feathers (B), forming a distinct 'hump'. The high intensity form (C) consists of the fluffing of the whole head and body plumage which gives the bird a rounded and 'woolly' appearance; the eyes are half closed in this display so that the ring of white feathers around the eye is flattened, a trait typical of sleeping or dozing birds and certainly of signal value here. This posture is always adopted in a crouched position.

Fluffing of head and back feathers occurs under similar circumstances as does freezing. It seems to have a somewhat higher threshold: it follows regularly on freezing if the menacing individual draws nearer and the freezing bird does not take off. Fluffing of the crown has often been observed in pecking encounters also; almost invariably the fluffing bird retreats a few instants later. Both forms also make part of the display given by an individual which actively tries to form a pair or an allopreening alliance with another, and it is in this context alone that full intensity fluffing has been observed in our aviary which was big enough for inferior birds to avoid continual persecution by superior ones. Full intensity fluffing closely resembles the submissive postures of numerous other passerines (Andrew 1961, Blume 1967). But the fluffing of crown and back feathers is peculiar: only a few parts of the plumage are raised, but these fully, and although these parts are neither limited by a sharp line during fluffing nor accentuated by colour or texture, the pattern is clearly ritualized into a social signal.

Superior birds and particularly those sought for the formation of a pair or allopreening alliance react in many cases to these fluffing postures by allopreening. Their pecking is re-directed into preening of the fluffed bird, passing through numerous transitional forms. Most likely allopreening has been the selection pressure which led to the peculiar ritualization of fluffing in the yellow white-eye.

To sum up, the agonistic behaviour of the yellow white-eye resembles in its basic pattern that of most passerine birds, but includes several ritualized elements such as pivoting, wing-dropping and bill-clattering in threat and full fluffing of some plumage parts as an appeasement display 'inviting' to allopreen the displaying bird. This ritualization must have taken place under the pressure of the necessity to maintain the coherence of the flocks and to reduce the tensions within a flock by advertisement and re-direction of aggressive tendencies. The relatively high degree of ritualization underlines the importance of flock formation.

COURTSHIP

Only fragmentary observations were made on courtship behaviour. No entire breeding cycle has been studied. Courtship in the form of horizontal wing-quivering is frequent and has been observed often in the field as well as in the aviary. No normal copulation has ever been seen, only rape when new birds were introduced into the aviary which already contained well-established males.

Horizontal wing-quivering (Figure 3) is the usual and frequent display of males during pair formation. The bird adopts a normal posture, but fluffs its plumage slightly so that the silhouette

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becomes somewhat more rounded. In low intensity versions of the display, the crown is often moderately fluffed (see above). Both wings are raised symmetrically into the horizontal, but, at low intensities, not spread, and quiver continuously (A). In higher intensities, more plumage is fluffed according to the sequence described in the previous chapter, the eyes half-shut and the wings spread more and more. Figure 3B shows the maximum spreading of the wings which has been seen only once.

The response of the courted female to horizontal wing-quivering consists mostly of flight or low-intensity pecking. The latter induces the male to freeze and to fluff its plumage more strongly, upon which the female reacts by more pecks or flight again, until, after a few sequences of these mutual responses, she begins to allopreen the male. The initial stages of the re-direction of the female's tendencies to peck into allopreening are marked by a transitional pattern in which the female pecks at the male, but stops just short of his plumage and begins to preen it in a hurried and rough way. The acceptance of the male as an allopreening partner completes the pair formation, and horizontal wing-quivering then disappears.

Horizontal wing-quivering in a very low intensity often accompanies the short-distance song (Kunkel 1974) which lonely males give some distance from the flock. These males then also fluff the plumage of the head and back, often to the point that the feathers are lifted one from the other, and sing with half-closed eyes. In higher intensity all the plumage may be fluffed a little bit. Often this song with horizontally quivering wings is interrupted by 'games' with nesting materials and nest-building movements not yet directed to a fixed nest site, but executed on twigs which are often unfit for the support of a nest.

While, in this case, horizontal wing-quivering is accompanied by short distance song, the courting male utters a series of short, high-pitched contact calls in rapid sequence. These are also weak in volume and can only be heard for a short distance. This is important in order not to

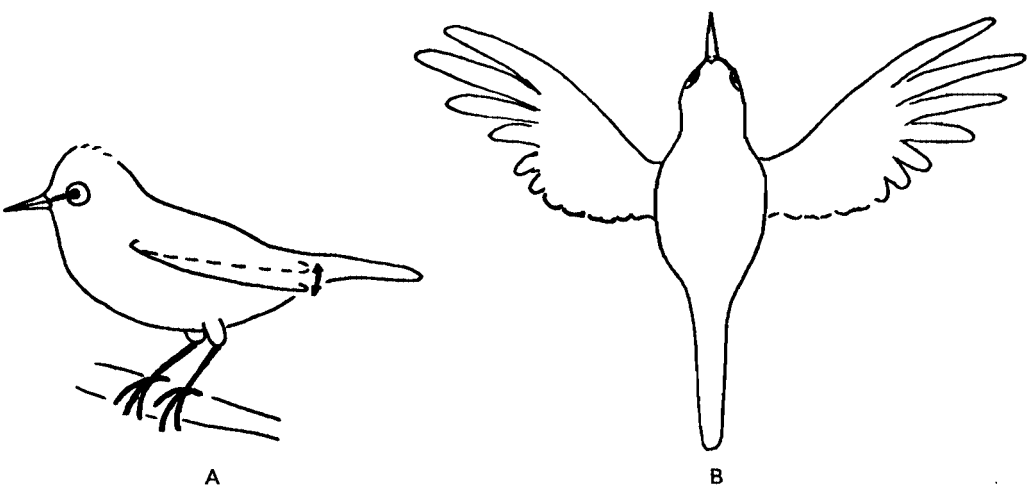

FIGURE 3

Horizontal wing-quivering in courtship (schematic): A, low intensity form; B, high intensity form.

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attract other flock members which could intervene and disturb the formation of the pair.

Horizontal wing-quivering, again, is a widespread courtship pattern among passerines (Andrew 1961, Blume 1967). In many of these, the pattern closely resembles the wing movements of begging fledglings; this is the case also in the yellow white-eye, and the two patterns are doubtless homologous in this species. Originally a locomotory intention movement, it has become an expression of hindered appetitive tendencies in both functions. The same holds true for the vocalizations in front of the courted female or the feeding parent which also resemble each other closely.

Courtship resembles the general passerine pattern but for one peculiarity: the offer of plumage to be allopreened serves to facilitate social contact.

The *rapes*, which have been observed several times, consisted generally of mere hopping on the back of a newly introduced female which then fled away from under the male. There was no introductory soliciting pattern except in one case when a male pecked rapidly several times on the lore of one side of the female's head before he mounted. This behaviour has been seen before in the Indian white-eye (*Zosterops palpebrosa*) as the normal soliciting pattern before copulation (Kunkel 1962), and the isolated observation in the yellow white-eye suggests the same function in this species.

COMPARISON WITH SOCIAL BEHAVIOUR PATTERNS OF OTHER SPECIES OF *Zosterops*

As already mentioned in the introduction, comparable observations on the numerous other species of *Zosterops* are rare, and more detailed reports are restricted to three species: the New Zealand white-eye (*Z. lateralis*) in which the agonistic behaviour has been studied in winter flocks (Kikkawa 1961), the Indian white-eye (*Z. palpebrosa*) (Kunkel 1962), and the Mascarene white-eye (*Z. borbonica*) for which Gill (1973) gives some details of the behaviour patterns in a study dedicated mainly to other aspects of the biology of this species.

Even the most striking and frequent behaviour of white-eyes, clumping and allopreening, seems to have been reported in only a few species, *e.g.* the Indian white-eye, the Mascarene white-eye, *Z. japonica* (Eddinger 1967), *Z. virens* (Kunkel 1962, Skead 1967) and *Z. pallidus* (Skead 1967). It would be of interest to know more about the distribution of this pattern, particularly in the less social forms and those which diverge to a higher degree from the general 'white-eye type', especially the forms living on high mountains and small islands, and to learn more about the relation of this pattern to the ecology of the species.

The agonistic behaviour is known in more detail only in the New Zealand white-eye and the Indian white-eye. The fighting technique – types of pecking, postures and supplanting attack – of both species seems to be the same as that of the yellow white-eye or nearly so. Among the agonistic postures, bill-clattering and head-fluffing have been described for the two species in an almost identical form and in identical situations. Bill-opening has been described in the Indian white-eye only; but here again it is almost identical in form and motivation to that of the yellow white-eye.

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Differences exist in regard to pivoting and wing-dropping. Wing-dropping occurs in the New Zealand white-eye apparently in the same form and under the same circumstances as it does in the yellow white-eye. In the Mascarene white-eye, Gill says that 'aggressive individuals often prominently displayed their white axillary tufts and rump patch' which implies a sort of wing display most likely homologous to the wing-dropping of the yellow white-eye and the New Zealand white-eye, strengthened by particular morphological signals in this species. Wing-dropping is absent in the Indian white-eye, a species which has been observed for about four years and which is certainly the best-studied of all the forms mentioned here, so that wing-dropping would not have been overlooked if it had been present.

Apart from the yellow white-eye, pivoting has been described for the Indian white-eye only, where it is the most frequent threat posture and is even displayed before imminent attacks, *i.e.* replaces wing-dropping as an expression of predominant aggressive motivation.

Horizontal wing-quivering has been described for the Indian white-eye where it occurs in the same form and has the same function. This seems to be the case also in the Mascarene white-eye although it was misinterpreted by Gill. He writes that, in the early breeding season, 'certain apparently subordinate individuals often quivered their wings even when not being chased'. That it has not been described for the otherwise accurately studied New Zealand white-eye, results from the fact that Kikkawa observed his birds during the winter, outside the breeding season.

With the exception of pivoting and wing-dropping, the postures as far as they are known seem to be very uniform in the different species of *Zosterops* even if these live in widely separated geographical areas. This is in accordance with the close morphological resemblance of all the species of the genus.

The only marked difference is apparently due to the disappearance of one posture and a change in the threshold of aggressive motivation of another display: while, in the Indian white-eye, even the strongest participation of aggressive tendencies in a motivational conflict manifests itself in pivoting, this posture is suppressed by higher aggressive tendencies in the yellow white-eye. From a geographical point of view, it is puzzling that two species living in the outer parts of the total area of distribution of the genus, the yellow white-eye and the New Zealand white-eye, resemble each other more closely than they resemble a species living in most of Southern Asia, *i.e.* the whole intermediate area settled by *Zosterops*. Furthermore, detailed studies on the causation of the postures of white-eyes as well as observations on more species of this family may contribute to an understanding of this strange distribution.

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