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ENVIRONMENTAL FACTORS INFLUENCING NEST-SITE PREFERENCE IN WHITE-BROWED SPARROW-WEAVERS (*PLOCEPASSER MAHALI*)[1]

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Abstract. Group-living White-browed Sparrow-Weavers (*Plocepasser mahali*) build their roost and breeding nests on one side of nest trees. The placement of nests correlates with the direction of the local prevailing wind. Birds gain a 35% increase in the useful life of a nest built on the leeward side of a nest tree, compared with a nest built on the windward side. Solar radiation, humidity, and thermal effects appear unimportant in influencing nest placement. Foliage density and other nearby cover does not affect nest placement. Hence, White-browed Sparrow-Weaver nest placement appears to be an adaptation for having large numbers of intact nests available for breeding and for roosting throughout the year.

Key words; White-browed Sparrow-Weaver; Plocepasser; *nesting; environmental physiology; heat loading; wind.*

INTRODUCTION

White-browed Sparrow-Weavers (*Plocepasser mahali* Smith) inhabit arid areas of northeastern and southwestern Africa (Mackworth-Praed and Grant 1963). They occur in stable, territorial groups of two to 11 individuals; a group consisting of a single breeding pair and additional nonreproductives (Collias and Collias 1978, Lewis 1982). Only a few of the many (10–60) nests built in the nest tree of each sparrow-weaver group are used for breeding or roosting (Earlé 1983, Collias and Collias 1984). Two types of nests are built: breeding nests and roosting nests, both of which have an inverted U-shaped form. Breeding nests have only one entrance, whereas roost nests have two entrances, one at either extremity of the nest (Earlé 1983). Breeding nests account for less than 10% of the total number of nests. Roost nests are often converted into breeding nests by the closure of one entrance, and vice versa (pers. observ.).

A conspicuous feature of these groups of nests is their location on one side of a nest tree (Fig. 1). Moreover, within a particular geographical area, White-browed Sparrow-Weavers tend to build their nests on the same side of nest trees. For instance, in the Bloemhof area, South Africa, nests are located on the southwest side of trees (see below). Several authors have commented on this phenomenon (Collias and Collias 1964, Mitchell 1966, Mendelsohn 1968, Ferreira et al. 1972, Burger and Gochfeld 1981), postulating explanations involving protection from exposure to solar radiation or from the prevailing wind. These studies demonstrated nonrandom nest placement but did not quantitatively relate it to any environmental parameter. The following hypotheses might explain the observed nest-site specificity:

(1) Nests are placed on the side of trees that receives the least sunshine. This should ameliorate the effects of heat loading during daytime when the birds make use of their nests, e.g., during incubation (Mendelsohn 1968, Burger and Gochfeld 1981). The function of nest placement would be to cool breeding nests.

(2) The nests are placed on the side of the tree that receives afternoon sunshine. This should warm the nests immediately before a cold night, resulting in the birds saving energy in thermoregulation. The function of nest placement would

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be to heat both roosting nests and breeding nests during early evening.

(3) The nests are placed on the side of the tree that receives least ultraviolet radiation, a factor that could be important in determining the rate at which nests weather and decompose. The function of nest placement would be to prolong the life of each nest.

(4) The nests are placed on the side of the tree that is least exposed to wind, another factor that could have an important influence on nest weathering and decomposition (Collias and Collias 1964, Mitchell 1966, Mendelsohn 1968). The function of nest placement would also be to prolong the life of each nest.

(5) The above hypotheses involve the designation of nest-placement behavior as an evolved adaptation that would have a direct effect on the fitness of the birds. A fifth hypothesis is that the nest-placement pattern is an incidental effect of unrelated processes (Williams 1966, p. 9).

We examine each of the above hypotheses in turn. The fact that nest placement of White-browed Sparrow-Weavers has been studied over a very large geographical area facilitates interpretation of the observed data. When results of the studies by Collias and Collias (1964), Mitchell (1966), Mendelsohn (1968), Ferreira et al. (1972), and Burger and Gochfeld (1981) are added to ours, data from eight localities, encompassing latitudes from the equator to 31° S are available.

STUDY AREAS AND METHODS

White-browed Sparrow-Weavers and their nests were observed in three areas: (1) immediately south of the Bloemhof Dam (27°40'S, 25°39'E) in the northwestern Orange Free State; (2) near Kimberley (28°40'S, 24°50'E) in the northern Cape Province; and (3) near Middelburg (31°28'S, 25°02'E), in the centraleast Cape Province, South Africa. Observations at Kimberley were localized to an area of about 16 km^2, while the other study areas covered approximately 300 km^2. The vegetation in these areas is similar, with *Acacia erioloba* or *A. karoo* being the dominant trees, and *Eragrostis* spp. being the common grasses.

Most of the work was carried out at Bloemhof. A survey of the placement and orientation of groups of nests and several other possible factors influencing nest placement was conducted as described below. The survey included 4,170 nests, built in 167 trees and belonging to 105 groups of birds. Similar surveys involving 376 and 568 nests were made at Kimberley and Middelburg, respectively.

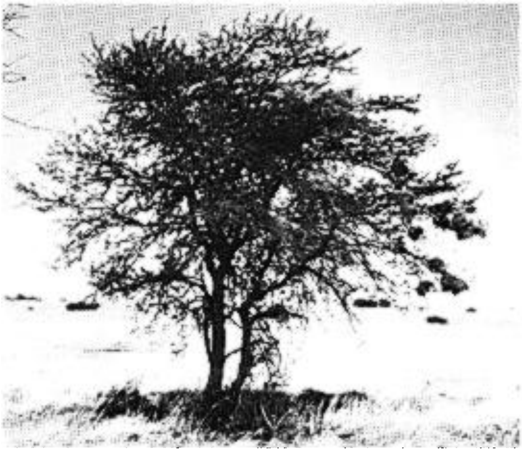

FIGURE 1. A nest tree of White-browed Sparrow-Weavers showing the clumped distribution of nests.

At Bloemhof, a systematic search was made for nest trees in an area where sparrow-weavers were relatively common. The following information was collected for each nest at every nest tree:

(1) Nest orientation, i.e., the direction in which the entrance pointed, relative to the center of the nest itself. For roost nests (with entrances at opposite ends of the nest) the most horizontally-situated entrance (most often used by the birds) was used as a reference point. Nest orientation was determined by means of a prismatic compass.

(2) Nest placement, i.e., the side of the tree on which the nest was located. The nest was aligned with the center of the nest-tree foliage, and the direction from the nest to the center of the foliage was determined using a prismatic compass. This reading was corrected by 180° and magnetic declination to give a true bearing from center of foliage to the nest.

(3) Height above ground, measured in decimeters.

(4) The condition of the nest on a scale of 1 to 5 (1 = very good condition, 5 = collapsed, disintegrated).

(5) The building stage of the nest on a scale of 1 to 5 (1 = being built, 5 = very old). A new, completed nest had a condition of 1 and a building stage code of 3.

The foliage density of each nest tree was assessed by means of a 6-m-long rod, graduated into 10-cm divisions. The number of junctions between adjoining 10-cm sections were counted, as viewed through the tree foliage from a point 20 m from the northern side of a nest tree. The mean number of visible 10-cm-section junctions per meter provided an index of foliage density. Tree-canopy foliage was classed as continuous or broken and disjunct. Measurements were made of tree height, canopy height, canopy width and the height of the densest canopy foliage. The direction to, number and distance of all trees within 100 m of each nest tree were recorded.

The deterioration of nests during a 2-year period was assessed at Bloemhof. Eighteen nest trees, displaying the widest variance in nest placement were used in obtaining a sample of nests placed relatively evenly around the circumference of the trees. These 783 nests were divided into two groups: north-facing (358 nests) and south-facing (424 nests). The condition of each nest was assessed as noted above. The survey was repeated 2 years later, noting the condition or disappearance of each nest.

Temperatures in and under nests were recorded in Bloemhof and Kimberley. At Bloemhof, four AD590 temperature sensors, connected to a Hewlett-Packard HP41C calculator and calibrated to 0.1°C accuracy at 0°C and at 30°C, were used. The calculator monitored the sensors and stored temperatures on magnetic cassette. The Kimberley data were collected using a YSI telethermometer and associated temperature probes. In both study areas, two nests on opposite (NE = sunny and SW = shady) sides of a nest tree were monitored simultaneously. One temperature sensor was placed inside the nest on the inner surface of the roof, while another was placed immediately below the nest in a permanently shaded position. Differentials between the internal and ambient temperatures of each nest and between the internal temperatures of the two nests were calculated. Nests on the NE side of trees were not exposed to the late afternoon sun, because of shade provided by the foliage. For determining the maximum effect of foliage on nest temperature, two breeding nests of similar construction were removed from their original sites. One nest was placed on an exposed branch on the north side of a nest tree where it was exposed to the sun for the whole day. The other nest was placed at an identical height below the tree's dense canopy, so that it would not be fully exposed to the sun at any time. The difference in the internal temperatures of these two nests was monitored from 10:00 to 14:00 on 2 days during which the ambient temperature reached 35°C. The two nests were switched around for measurements during the following day. Summer ambient temperatures often remain above 30°C for periods exceeding 8 hr day^{-1} at Bloemhof (Weather Bureau 1982).

Because White-browed Sparrow-Weavers occur in semi-arid areas, humidity effects might be important in their water balance. At Kimberley, data were collected using a YSI telethermometer connected to dry-bulb, wet-bulb, and black-bulb thermometers in each nest. The humidity in a north-facing nest was compared with that in a south-facing nest on a day when the ambient temperature rose to 40°C.

RESULTS

NEST PLACEMENT AND ORIENTATION

At both Bloemhof and Kimberley, nests tended to be located on the southwest side of trees (Fig. 2), with an average placement of 210° with respect to north. This distribution differed significantly from random ($\chi^2 = 1{,}145$; df $= 2$; $P < 0.002$). The location of roost nests did not differ significantly from that of breeding nests ($\chi^2 = 22.2$; df $= 35$; $P < 0.5$). The locations of newly-built nests also did not differ significantly from the overall pattern at Bloemhof. Indeed, nests at all conditions of deterioration and at all stages of completion occurred in significantly larger numbers on the southwest side of trees (Fig. 2). A nocturnal survey of 16 nest trees was made to determine the location of the roost nests actually used for roosting. A total of 64 actual nests was found, and their sites had a significantly more southerly to southeasterly bias when compared to the placement of all nests ($\chi^2 = 23.2$; df $= 11$; $P < 0.05$). Nest orientation did not have a similar bias: each nest tended to be built transversely to the direction of the branch on which it was located.

The placement of 568 nest sites at Middelburg was measured during January 1986. The nests were distributed bimodally, being mostly situated on the southeast side, but many were also placed on the northern side of trees (Fig. 3).

SHELTER AFFORDED BY NEARBY FOLIAGE

At Bloemhof, nests tended to be about 3 m above ground level. There were no significant differences between the height distributions of roosting nests, breeding nests, defunct nests, or newly-built nests. Although many smaller trees were available, nests were only built in *A. erioloba* trees taller than 3 m.

A multiple correlation was performed on the foliage and nest-placement data collected at each nest tree. Neither the placement nor the variance in nest placement were significantly correlated with either the foliage density of the nest tree itself or the proximity of nearby trees. Nest placement was also not significantly correlated with any of the physical dimensions of the nest tree. Nests tended to be sited 1.5 to 2 m below the level of the densest foliage of the nest tree.

DIURNAL NEST TEMPERATURES

The greatest amount of diurnal thermal stress on birds in breeding nests could be expected to occur in summer (December to February) when ambient temperatures are highest (Weather Bureau 1982). During this period the temperatures inside breeding nests on different sides of a nest tree differed very little, usually being within 2°C of one another (Fig. 4). The data from Kimberley were recorded on an exceptionally hot day when the ambient temperature rose to 40°C, and even then the nest-to-ambient differential of a north-facing nest remained within 3°C of that of a south-facing nest. There was no significant regression between the ambient temperature and differential temperature of north- and south-facing breeding nests (t = 0.34, df = 1 for intercept; t = 1.46, df = 1 for slope). During the nest relocation experiment, the temperatures in the breeding nests placed below the tree canopy and on totally exposed branches differed by a mean of only 0.96°C during the period 10:00 to 14:00, when the ambient temperature exceeded 34°C.

Although large variation in the internal roost nest temperatures at Bloemhof makes interpretation of the data difficult, no evidence was found to indicate that northeast-facing roost nests cool at a faster rate than southeast-facing nests.

DIURNAL NEST HUMIDITY

The differential in relative humidity between two breeding nests located on opposite sides of a nest tree did not exceed 7% (Fig. 5). If solar radiation affected relative humidity through increased nest temperature, the relative humidity in the north-facing nest should have been lower than in a south-facing nest. From the few data available (Fig. 5) this expectation was not fulfilled.

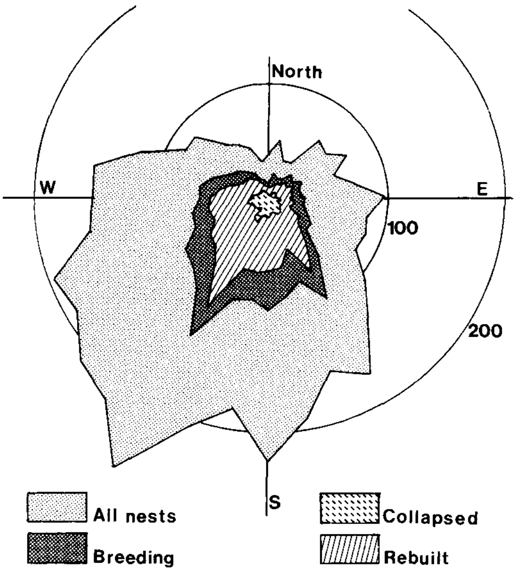

FIGURE 2. Placement of 4,170 nest sites of White-browed Sparrow-Weavers at Bloemhof. The number of observations in each direction is indicated relative to the concentric scale and indicate that the placement of all categories of nests are biased to the southwest.

NEST DETERIORATION

The 2-yearly survival rate of 40.9% for 358 north-facing (windward-placed) nests differed significantly from the comparable value of 54.1% for 424 south-facing nests (Wilcoxon's $C = 57$, $n = 6$, $m = 6$, $P < 0.002$). Sparrow-weavers therefore lengthen the useful nest life by 35% when building nests on the leeward side of trees as opposed to the windward side.

DISCUSSION

The fact that newly built nests were placed very similarly to those of old nests, suggests that sparrow-weavers actually prefer to build their nests on the southern side of the trees in our study areas. If a high proportion of collapsed nests had been found on the northeast side, it would have meant that differential, weather-induced erosion was responsible for the observed uneven distribution.

If nest placement was a response to solar radiation, one could expect that the observed pattern would differ between localities with different characteristics of solar radiation. Data from the

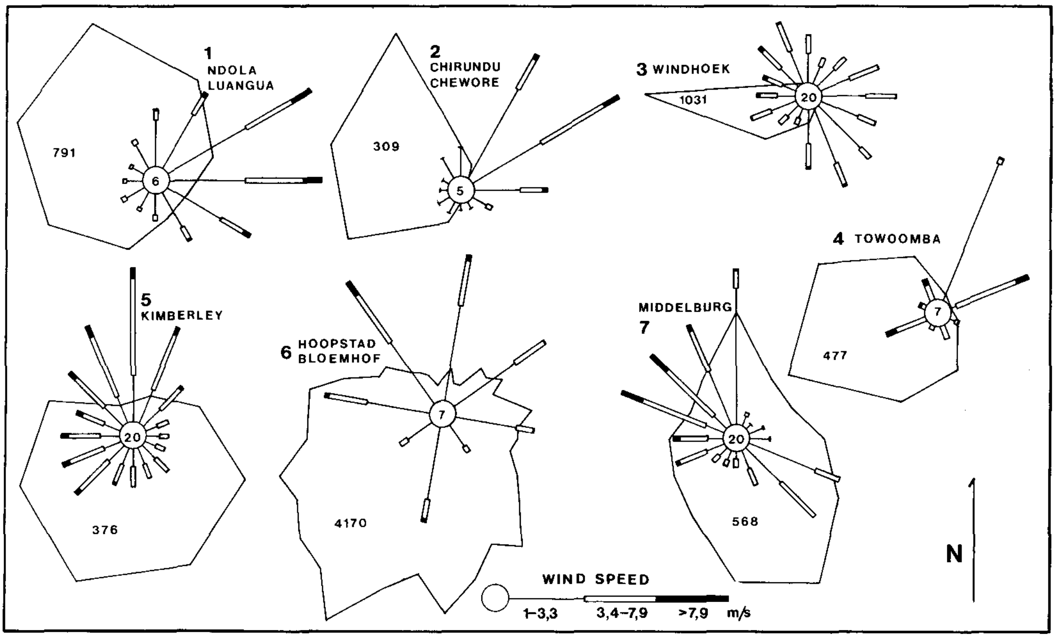

FIGURE 3. White-browed Sparrow-Weaver nest placement at various localities with different wind regimes. The polygons represent the number of nests located on different sides of the nest tree at each locality, while radial bars constitute wind roses that depict the relative frequencies and wind velocities from various directions. Except for Hoopstad and Towoomba, all wind data were recorded by means of anemographs. Where two localities are given for a diagram, the top one indicates where wind data were recorded, while nest data were collected at the lower locality. Numbers inside polygons indicate the number of nests measured at each locality. Numbers in the center of each diagram indicate number of years over which wind data were collected. Nest data were obtained from the following localities and sources: 1. Luangua, Zambia, 12°40'S; 30°45'E. Mitchell (1966); 2. Chewore, Zimbabwe, 15°45'S; 29°50'E. Ferreira et al. (1972); 3. Gamsberg, SWA/Namibia, 23°20'S; 16°20'E. Burger and Gochfeld (1981); 4. Towoomba, South Africa, 24°55'S; 28°19'E. Mendelsohn (1968); 5. Kimberley, South Africa, 28°40'S; 24°50'E. This study; 6. Bloemhof, South Africa, 24°40'S; 25°39'E. This study; 7. Middelburg, South Africa, 31°28'S; 25°02'E. This study.

above five studies and from the present study indicate that nest placement correlates negatively with latitude (Kendall's $\tau = 14$; $n = 7$; $P < 0.035$). Nests at localities closer to the equator are situated on the northwest and western side, whereas nests at localities farther from the equator are situated on the southwest side of trees. This suggests that the trajectory of the sun does correlate with nest placement. If nests are situated on the sides of trees that receive the least sunshine, one would expect nests to be placed around the circumference of trees at the equator (Kenya) where all sides of a tree receive an equal amount of solar radiation. However, according to Collias and Collias (1964) the nests of White-browed Sparrow-Weavers in Kenya have a very pronounced tendency for being situated on the western side of trees: this strongly contradicts the solar radiation hypothesis. The observed correlation between nest site and latitude cannot be related to any known geographical effect apart from solar radiation. Consequently one should consider the possibility that the above correlation is a fortuitous effect of unrelated processes (see below).

The effect of solar radiation on nest temperature appears to be minimal (Fig. 4). Three points suggest that the preferred placement of nests does not conform to the hypothesis of nest placement reducing diurnal nest temperature: (1) The observed diurnal nest temperatures fall within the thermoneutral zone of White-browed Sparrow-Weavers (10°C–35°C: Ferguson 1986), so that even if the temperature differential between north-facing and south-facing nests was larger, the energetic cost due to thermoregulation would be minimal. (2) The highest ambient temperatures normally occur after 12:00 (Weather Bu-

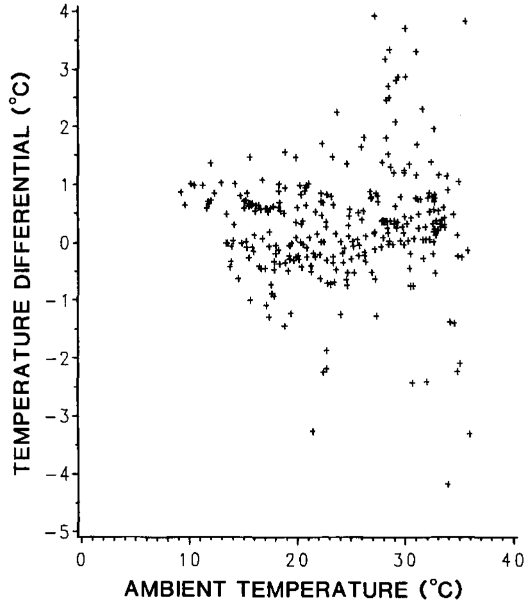

FIGURE 4. Daytime temperatures of breeding nests of White-browed Sparrow-Weavers during summer. The temperature differential between a north-facing and a south-facing nest is shown as a function of the ambient temperature. Temperature differential = temperature in north-facing nest minus temperature in south-facing nest.

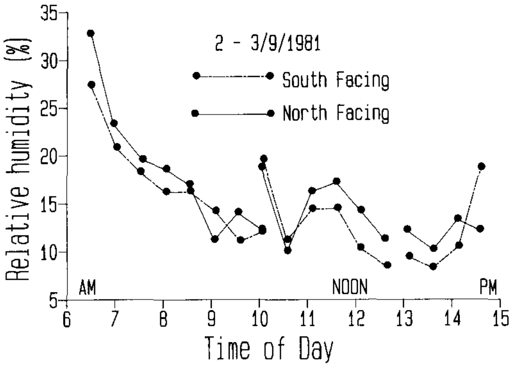

FIGURE 5. Relative humidity measurements in north-facing and south-facing nests of White-browed Sparrow-Weavers at Kimberley.

reau 1982). If any nests were to become overheated, it would be those with a western aspect (where nests are actually situated) because they are exposed to solar radiation during the relatively high ambient heat of the afternoon. (3) In the Bloemhof study area, breeding commenced during July when the supposed limitation of high nest temperature would not apply. Unless extreme selective forces operated during speciation, the evolution of an adaptation that effectively lowers the breeding nest temperature during part of the breeding season only, seems improbable. There is no evidence of such forces operating at present. For these reasons the hypothesis concerning lowered breeding nest temperatures is rejected.

Winter measurements indicated that the temperatures in roost nests facing southwest did not differ significantly from those facing northeast, immediately before entry of the sparrow-weavers in the evenings. There was also no evidence that a southwest-facing nest cooled at a slower rate than a southeast-facing nest. The hypothesis concerning elevated roost nest temperatures is thus also rejected.

All the hypotheses involving nest placement as a response to the thermal environment have been discarded. The hypothesis concerning ultraviolet radiation appears unlikely because of the observed westerly placement of nest sites near the equator; the arguments relating to solar radiation, mentioned above, apply here as well. Because of the significant correlation between latitude and nest location, another effect of solar radiation coupled with latitude may operate. No such effects are, however, known. Thus, it would serve no purpose to explain nest placement as a consequence of radiation. The correlation between nest placement and latitude is probably an indirect expression of a strong correlation between latitude and prevailing wind direction, discussed next.

The placement of the dominant south Atlantic high-pressure system situated southeast of southern Africa (Taljaard 1972) predicts that if White-browed Sparrow-Weavers place their nests away from the prevailing wind, nests on the northern periphery of the high-pressure system should be placed on the western to northwestern side of trees, whereas nests on the western periphery of the system should be placed on the southern side. Data on velocities and directions of wind at localities close to the study sites of Mitchell (1966), Mendelsohn (1968), Ferreira et al. (1972), and Burger and Gochfeld (1981) were obtained from various weather offices in southern Africa (Zambia Meteorological Department 1974, Weather Bureau 1975, Zimbabwe Department of Meteorological Services 1981). The predictions of the effect of wind on nest placement are met at the seven localities where studies have been conducted: nests are placed on the leeward side of the tree (Fig. 2, Kendall's $\tau = 10$; $n = 7$; $0.11 > P > 0.06$). Figure 3 also shows that nest placement is not related to the direction from which the strongest winds blow. The most meaningful comparison would be between the observed nest placement and the annual kinetic wind energy from various wind directions. Such data are, however, not available for the observed sites and we assume that the kinetic energy from various wind directions is related to the prevailing wind directions. Particularly useful data were obtained at Middelburg, where the bimodal wind direction pattern predicts a minor nest-site preference for the northwestern, and a major preference for the southeastern sides of trees. Although the minor peak has a more northerly aspect than expected, the resultant data fitted the prediction remarkably well. None of the above alternative hypotheses allows such a close fit between predictions and observations.

WHY BUILD NESTS ON THE LEEWARD SIDE OF TREES?

Of the five hypotheses explaining nest placement by White-browed Sparrow-Weavers, the wind direction hypothesis best fits the observed data. The advantage gained by building nests on one side of the tree could result either from a preadaptation or an evolved adaptation in a situation where many nests were critical for the survival of a group. This study revealed no adaptation that has the incidental effect of causing White-browed Sparrow-Weavers to build nests on the side of trees away from the prevailing wind. The need for nests which survive for a long period of time is evident when taking into account that sparrow-weavers use roost nests throughout the year (Ferguson 1986), whereas other sympatric weaver species only use their nests for breeding activities during the breeding season. In contrast to most other weaver species, sparrow-weavers use dry grass stems for nest building. This would predispose these nests to rapid deterioration. Moreover, the rate of nest deterioration on the side of trees exposed to the prevailing wind is 35% higher than for nests on the leeward side, pointing to the strong adaptive reason for the observed nest placement. It therefore appears that placement in White-browed Sparrow-Weavers is an adaptation that prolongs the life of nests, thus increasing the number of intact nests available for roosting and breeding. Such large numbers of nests appear to be crucial for the birds' survival (Ferguson, unpubl.).

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