NEST-SITE SELECTION IN THE CAPE SUGARBIRD

A. E. BURGER, W. R. SIEGFRIED & P. G. H. FROST
Percy FitzPatrick Institute, University of Cape Town

We dedicate this paper to the memory of the late Dr G. J. Broekhuysen, our former mentor and friend, who did more than any other person in laying the foundations for an eco-ethological approach in scientific studies of the avifauna of the south-western Cape region of South Africa.

ABSTRACT

Cape sugarbirds, *Promerops cafer*, preferred certain protea bushes as nest-sites. These bushes were characterized by relatively large leaves and dense foliage. Nests were usually placed in the central parts of bushes Nest-sites were shielded from the cold night sky, and were associated with relatively favourable air temperatures and protection from wind in a season of unfavourable weather. Data on microclimate of nest-sites, together with those on heat loss from an incubating sugarbird, were interpreted in relation to nest-site selection as adaptive behaviour promoting breeding success through conservation of energy. Sugarbirds nesting relatively high off the ground and in dense vegetation were considered to be decreasing the risk of exposure to predators.

INTRODUCTION

Food availability, and shelter from predators and adverse weather are ultimate factors in habitat selection in bird species (Baker 1938; Hilden 1965). Nest-site selection is not a random procedure, and nest building will commence only when the summation of the heterogeneous stimuli of the micro-habitat exceeds the threshold for releasing nesting behaviour. This threshold depends on the internal motivation of the bird (Hilden 1965). Orians (1971: 525) predicted that 'there should exist a coevolution between fitness [of the bird] in different environments and the capacity of those environments to evoke settling behavior'. Thus, a bird would be stimulated to begin nest building in the most favourable site. Since birds are highly mobile, it may be assumed that they visit several potential sites to assess their quality before commencing to build a nest. The ontogeny of nest-site selection is considered to embrace a combination of innate and imprinted behaviour (Hilden 1965; Orians 1971).

A parent bird attending eggs or young tends to be restricted to one particular place for extensive periods. In those species which nest in the open, such temporary sedentariness may increase the parent's vulnerability to predators and the effects of harsh weather. Eggs and chicks are exposed to predators and weather when they are left unattended in the open. Since avian embryos and newly hatched altricial chicks lack thermoregulating mechanisms, they are vulnerable to the effects of harsh weather. Thus, weather and predators are important factors influencing a bird's behaviour in selecting a nest-site.

Zoologica Africana 11(1): 127–158 (1976)

Studies of sites actually used for nesting can contribute towards a better understanding of some of the selective pressures shaping nest-site selection behaviour. Nests of the Cape sugarbird, *Promerops cafer*, were chosen for study, since the species breeds chiefly during the austral winter when the climate is both cool and wet in the south-western Cape. The assumption was made that sugarbirds tend to respond positively to relatively sheltered microhabitats in selecting sites for their open, cup-shaped nests. This was examined by comparing certain characteristics of nest-sites actually used with those of sites available to the birds. Microclimatic conditions, in respect of wind, air temperature, nocturnal re-radiation heat loss and solar radiation, are described for nest-sites. These data, together with those on heat loss from an incubating bird, are interpreted in relation to nest-site selection as adaptive behaviour promoting breeding success through conservation of energy. The potential role of predators in shaping behaviour for nest-site selection is discussed.

THE BIRD AND ITS NEST

The Cape sugarbird is a passerine species endemic to the southern Cape region where it is common in protea-dominated, tall *fynbos* vegetation. Breeding territories of sugarbirds invariably include protea bushes. The ultimate determinant of the bird's breeding season is the availability of food, in the form of nectar and nectiferous insects and arachnids gleaned from the inflorescences of protea bushes (Broekhuysen 1959). The breeding season is synchronous with the peak time of flowering of most protea species. This occurs during the austral winter (Figure 1).

According to Broekhuysen (1959) the nest is built entirely by the female. Nests are built in bushes, and are normally placed between 90 and 160 cm above the ground. The nest is of the cupped and statant type, somewhat untidy on the outside (Figure 2). The internal depth of the cup is normally 5–6 cm and the diameter 6–7 cm. The bulk of the nest consists of dry twigs, invariably lined internally with a layer of protea seed pappi.

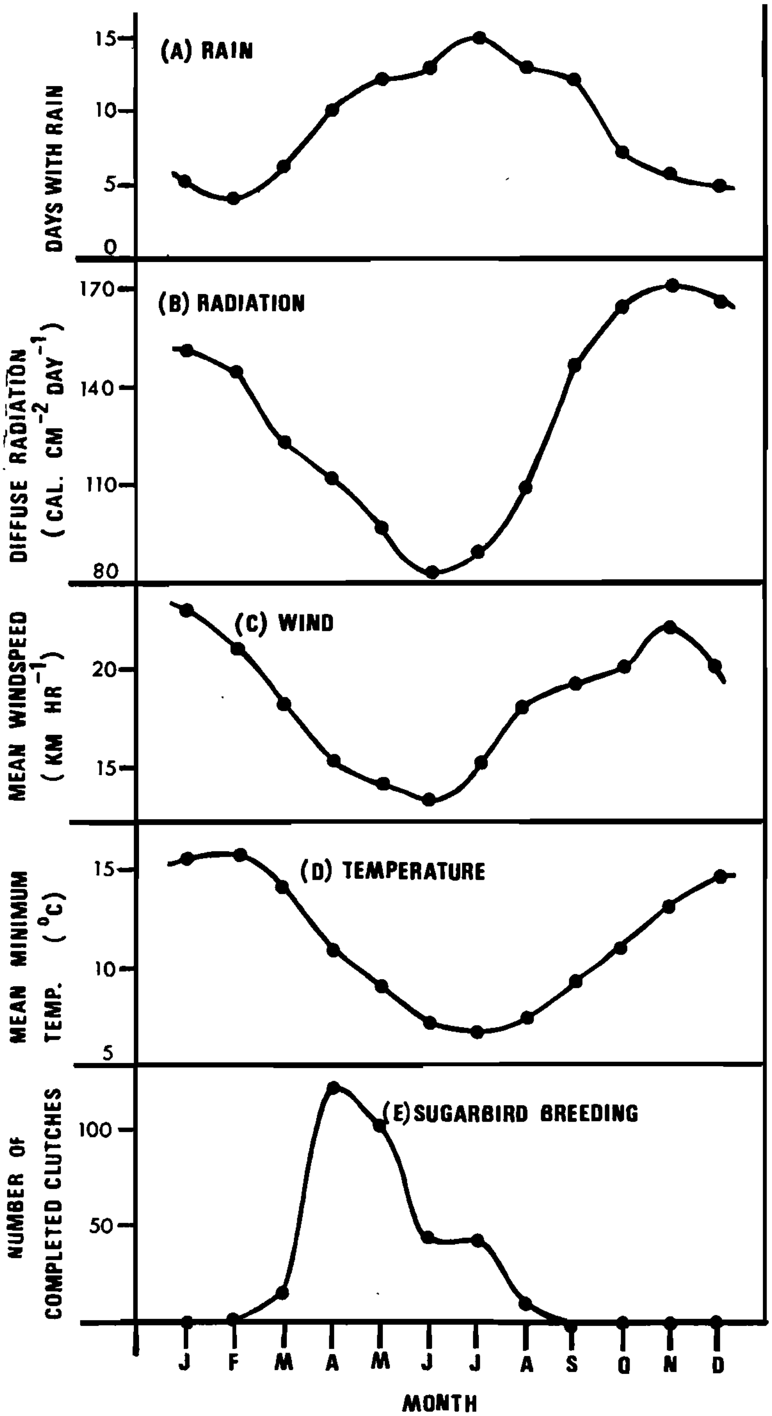
STUDY AREA

The study was carried out during 1975 at the Helderberg Nature Reserve (34°02′S/18°50′E) on the lower (500 m) southern slope of the Helderberg (1 010 m), near the town of Somerset West. The reserve embraces 15 ha of shrubs and thickets, characteristic of tall *fynbos* vegetation (Acocks 1975). The dominant shrubs are members of the family Proteaceae in which the genera *Protea* (20 spp.), *Leucadendron* (5 spp.) and *Leucospermum* (5 spp.) are common.

The climate is of the Mediterranean type, with hot, dry summers and cool, wet winters.

FIGURE 1

Mean monthly climate and the breeding season of the Cape sugarbird in the south-western Cape. Data for A–D taken from Schulze (1965), and for E from Winterbottom (1962) and this study.


(A) RAIN
DAYS WITH RAIN
0
5
10
15
(B) RADIATION
DIFFUSE RADIATION (CAL. CM^-2 DAY^-1)
80
110
140
170
(C) WIND
MEAN WINDSPEED (KM HR^-1)
15
20
(D) TEMPERATURE
MEAN MINIMUM TEMP. (°C)
5
10
15
(E) SUGARBIRD BREEDING
NUMBER OF COMPLETED CLUTCHES
50
100
J F M A M J J A S O N D
MONTH

Snow occasionally falls on the Helderberg. In the south-western Cape during winter the strongest and most frequent winds come from the north and north-western sectors of the compass (Figure 3). These are also the major rain-bearing winds (Schulze 1965).

METHODS

Data recording

Foraging, territorial and nesting behaviour of sugarbirds was recorded, and regular, systematic searches were made for nests in the study area during April–August 1975. Nests were grouped as those with eggs or chicks (classified as 'new' nests); and those found empty but in good repair (classified as 'old' nests). The latter class included some nests from the previous breeding season.

The distribution of plants in the study area was mapped with the aid of an aerial photograph and ground surveys. One or more 100 m^2 study plots were laid out in each vegetation type. The percentage ground cover of each of 22 plant species was estimated. These plants, considered most likely as sites for nests, comprised nearly all bush and tree species found in the study area. The total estimated vegetation cover of each of these plant species was computed. This provided an approximate measure of the availability of bushes in the study area.

Maximum heights and diameters of 30 bushes of each species were measured, and the ratio height: diameter was used in expressing bush shape. The mean leaf area of 30 mature leaves of each bush species was determined. The leaf density of each species was estimated, using a scale: zero (no leaves) to 10 (densely packed leaves).

The vegetation and topography of a 20 × 20 m area centred on each nest-site were recorded, following a method used by Sturman (1968). The percentage vegetation cover was estimated for three levels: (a) ground level to 0,75 m; (b) 0,75–1,5 m; and (c) above 1,5 m. Since most nests were located in the second level, the vegetation density at 0,75–1,5 m was used in distinguishing between 'dense' (ground cover > 50 per cent) and 'open' vegetation (ground cover < 50 per cent).

The height above ground of each nest and the maximum height of the bush containing the nest were measured. The nest was assigned to one of nine sectors described in the horizontal plane of the bush (Figure 9). A card marked out in 0,10 and 1 m^2 dimensions was placed on the cup of the nest, and the percentage vegetation cover was determined with the aid of photographs taken from north, south, east and west of the nest (Figure 4). The percentage overhead cover at 17 nests was determined, using an 18 mm 'fish-eye lens' camera placed facing vertically upwards in the nest.

The effectiveness of various bush species as barriers to wind was determined by measuring reduction of wind velocity through 1 m of bush. Wind-speed reduction was expressed as a percentage of the wind-speed recorded in the open, within 25 m of bushes. Casella mill anemometers were fitted with vanes designed to orientate into the wind. The anemometers were suspended 1 m above the ground. Anemometers sited within bushes were placed 1 m from the windward perimeter of the bush.

A female Cape sugarbird on her nest
Photo: G. J. Broekhuysen

Wind profiles in several vegetation types were determined with the aid of a Wallac-oy GGA 23S hot-wire anemometer. Readings were made at 25 cm intervals between ground level and 25 cm above the vegetation. The wind recorded at each height was expressed as a percentage of the wind-speed at 25 cm above the vegetation. Since the anemometer was extremely sensitive to fluctuations in wind-speed, an average value was determined for five readings of 20–30 seconds each at each point. This process was repeated several times in each vegetation type and the mean and 95 per cent confidence intervals were calculated for each interval.

Air temperatures were measured using a Grant automatic recorder. Thermocouples, shielded by aluminium foil, were placed 10, 50, 100 and 200 cm above ground in the open and in dense vegetation. Hourly mean temperatures were calculated from readings taken at two-minute intervals. Air temperatures were recorded during cloudless, relatively calm weather. Cloudy weather would have dampened the range of temperature fluctuations, and strong wind would have reduced temperature gradients (Geiger 1965; Lowry 1969).

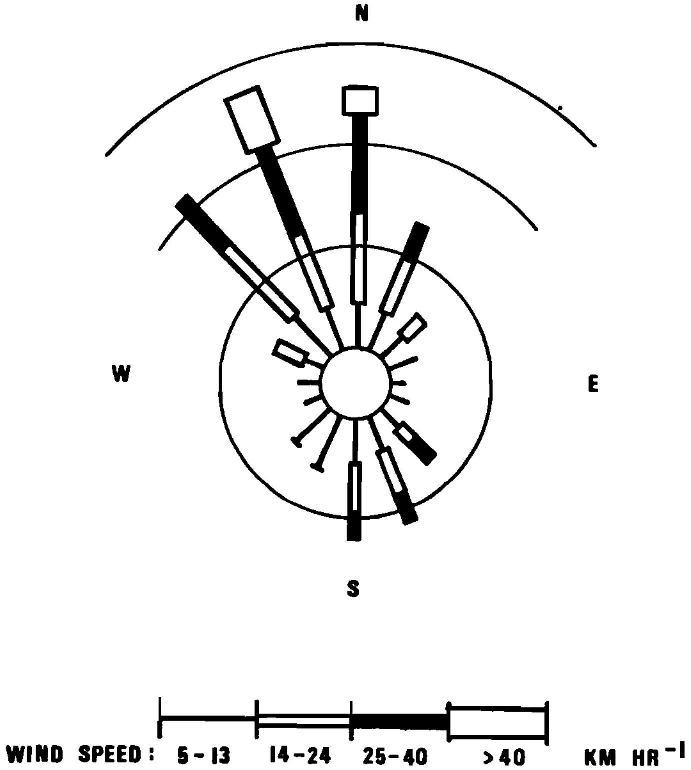


FIGURE 3

A wind rose for winter (July) showing direction and percentage frequency of winds of various speeds in the south-western Cape. Each arc represents a 5 per cent interval. Calms made up 12,4 per cent of the time. Data taken from Schulze (1965).

Radiation flux was determined at the same time and places as ambient temperature. Net radiation was measured using a Thornthwaite 603 miniature net radiometer. The radiometer was used in combination with a Barnes PRT 10-L infra-red thermometer to determine nocturnal radiation flux at actual nest-sites (Figure 5). Upward longwave radiation from the nest cup was derived through Stefan's Law (Monteith 1973) using the temperature of the surface of the cup of the nest, as measured by the infra-red thermometer.

$$R = E\delta Ts^4$$

where δ = Stefan-Boltzmann constant ($0{,}817 \times 10^{-11}$ cal cm^{-2} min^{-1} degK^{-4}), E = emissivity (*ca* 1 for vegetation and animals), and Ts = temperature (°K) of the body.

Downward radiation (Rd) was derived through

$$Rnet = Rd - Ru \text{ (upward radiation)}$$

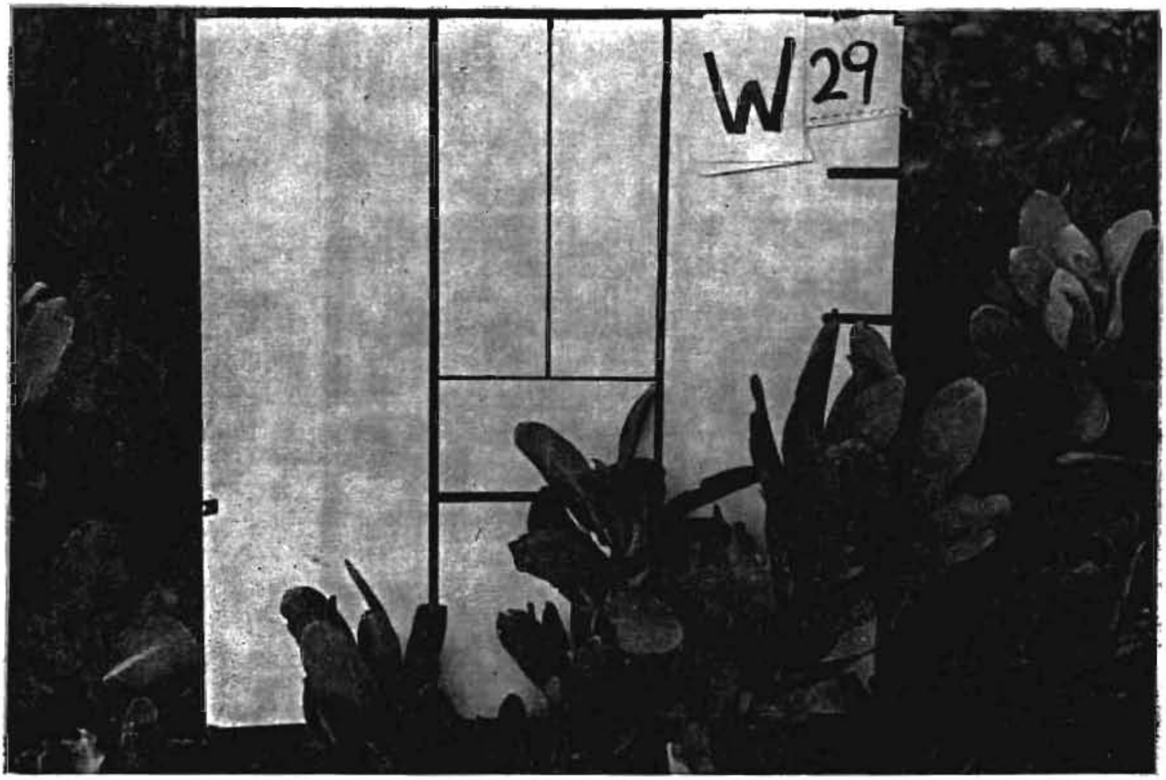


FIGURE 4

Method used in determining vegetation cover at Cape sugarbird nests. Percentage cover of vegetation was calculated for the 0,1 m² area (small lower square on card) and the 1,0 m² area (entire card area) on four sides of a nest.

Downward longwave radiation was determined for a nest artificially placed above the surrounding vegetation. Increase in downward radiation at the actual nest-site was calculated as a percentage of the downward radiation at the artificially exposed nest. The increase in downward radiation at the actual nest was then expressed as a function of the percentage leaf cover over the nest. Variations in downward radiation reflect more accurately the influence of overhead cover in moderating radiation energy loss. Values for net radiation are affected by variations in the upward radiation component which are dependent on nest surface temperatures. These differ according to nest-site.

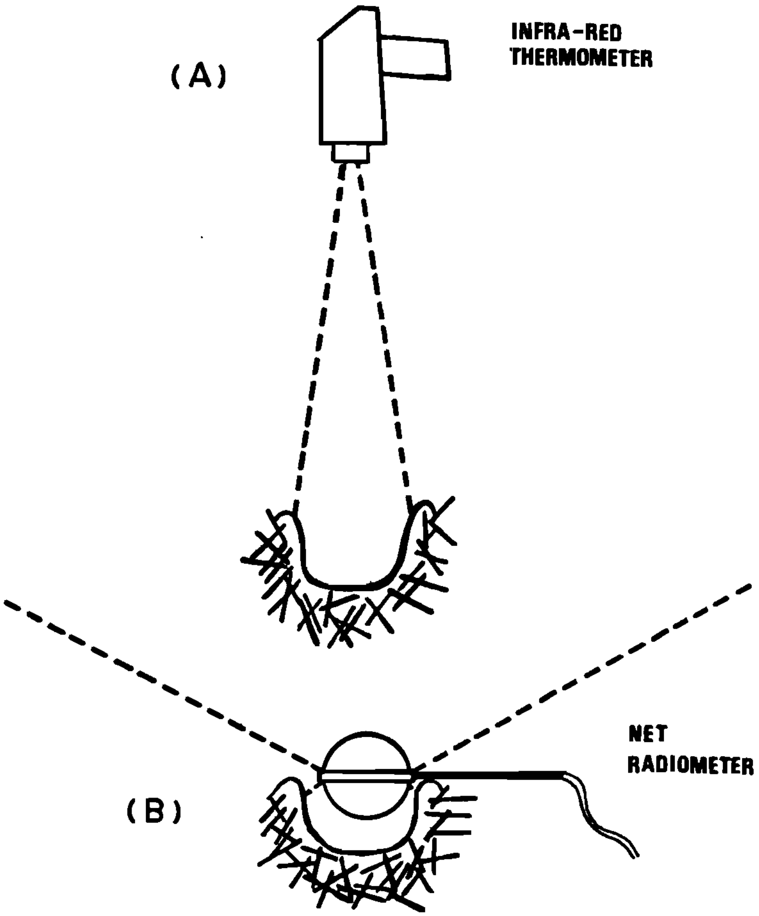


FIGURE 5

Method used in determining longwave radiation flux at Cape sugarbird nests. The dashed lines show approximate fields measured.

Ambient temperature and radiation flux were measured at 20 nests. These nests had been occupied earlier in the 1975 season, but were empty when the measurements were made.

No apparent change in the condition of the vegetation had taken place between time of occupancy by the birds and the measurement of radiation flux. The radiation observations were made during cold, cloudless nights when the effective radiation temperature of the sky was recorded. Because of the low temperatures encountered, it was necessary to off-set the zero-setting of the infra-red thermometer (Calder 1973a). Since the scale was not linear below the calibrated range of the infra-red thermometer, the results obtained by the off-setting procedure are approximate to within about 10 per cent. The surface temperature (radiation temperature) of an incubating sugarbird was recorded during a cold, cloudless night, using the infra-red thermometer; wind velocity, wind temperature and net radiation were recorded during the same period.

Data analyses

Correlations were drawn and tested between the characteristics of bushes and the density of nests (number of nests per unit area of vegetation) for each plant species, using the method advocated by Sturman (1968) and the assistance of a multiple regression programme (BMD 02R) available through the Health Sciences Computing Facility, UCLA, California. Correlations were drawn between microclimatic conditions and the height, shape, leaf area and leaf density of bush species. Step-wise multiple regression analysis identifies the variable, or set of variables taken together, that correlated most strongly with the dependent variable (Sokal & Rohlf 1969).

Heat lost by convection from an incubating female sugarbird was calculated using the formula given by Calder (1973b).

$$Hc = (k\,V^{1/3}/D^{2/3})\ (Ts - Ta)$$

where k is a constant ($6{,}17 \times 10^{-3}$) having units so that Hc is in cal cm^{-2} min^{-1} (Porter & Gates 1969), V = wind velocity (cm sec^{-1}), D = diameter of bird (cm), Ts = surface temperature of bird (°C), and Ta = air temperature (°C). The diameter of the bird was taken as the mean internal diameter of the nest cup.

Heat lost through net radiation from the incubating bird was calculated using the formula given by Monteith (1973).

$$Rnet = Ru - Rd$$

The surface area of a female sugarbird was derived from the bird's body mass (W in grams) using Meeh's formula given by Drent and Stonehouse (1971).

$$S = 10W^{2/3}$$

One-quarter of the bird was taken to be exposed above the rim of the nest cup. Basal metabolic rate was calculated from the empirical formula:

$$M = 0,867\ W^{0,724}$$

where M is metabolic rate in kcal bird^{-1} day^{-1} and W is body mass in grams (Kendeigh 1970).

TABLE 1

Plant species used as foraging and nesting sites by Cape sugarbirds at Helderberg.

Species	*Plant cover (m^2)*	*Number times sugarbirds recorded feeding*	*Number nests*			*Number nests per 1 000 m^2*
			New	*Old*	*All*	
Protea eximea	5204	91	29	32	61	11,8
P. grandiceps	1769		11	7	18	10,2
P. neriifolia	1554	85	2	10	12	7,7
P. compacta	6676	18		6	6	0,9
P. longifolia	4460	16		6	6	1,4
P. lorifolia	161		3	3	5	31,1
P. laurifolia	534		3	1	4	7,5
P. longiflora	1311	58	2	2	4	3,1
P. pulchra	4450	9	1	3	4	0,9
P. barbigera	777		1	3	4	5,2
P. repens	3527	71	1	3	4	1,1
P. lepidocarpodendron	2554	31		3	3	1,2
P. cynaroides	919	2		2	2	2,2
P. lanceolata	1135			2	2	1,8
P. suzannae	228	3		1	1	4,4
P. lacticolor	6856	30	1		1	0,2
P. macrocephala	1824	161				
Leucospermum sp.	782				1	1,3
Rhus spp.	762					
Brabeium sp.	2213					
Acacia spp.	500					
Totals	49773	575	55	85	140	

RESULTS

Plant species

Of the 22 plant species considered most likely as sites for sugarbird nests, 17 were actually used and some were used more often than others (Table 1). The three most frequently used species (*Protea eximea, P. grandiceps* and *P. neriifolia*) represented only 17 per cent of the total bush cover, but supported 65 per cent of all nests found.

Table 2 lists physiognomic properties of each of the 22 plant species. Linear correlation co-efficients between the variables listed are given in Table 3. Leaf area and leaf density were correlated significantly with nest density. There was no significant correlation between nest density and bush height or bush shape. Only leaf area and leaf density significantly increased the multiple regression correlation (Table 4). Plant availability, not a physiognomic property of the plant species, was not included in the regression analysis.

TABLE 2

Mean physiognomic characteristics of plant species at Helderberg.

Species	*Mean plant height (m)*	*Plant 'shape' (height/diameter)*	*Leaf area (cm)*	*Leaf density**
Protea eximea	1,7	1,5	28,5	7,0
P. grandiceps	1,1	0,5	50,8	9,0
P. neriifolia	2,0	1,5	20,1	6,0
P. compacta	3,0	2,0	21,4	6,0
P. longifolia	1,1	0,7	12,6	6,0
P. lorifolia	1,4	0,7	56,0	9,0
P. laurifolia	3,1	1,1	26,0	7,0
P. longiflora	3,5	1,5	14,3	5,0
P. pulchra	1,3	0,6	15,1	5,0
P. barbigera	1,7	0,6	52,5	9,0
P. repens	2,5	1,2	7,8	4,0
P. lepidocarpodendron	2,4	2,5	9,4	5,0
P. cynaroides	1,1	0,6	47,1	3,0
P. lanceolata	1,8	2,0	3,3	3,0
P. suzannae	2,3	0,8	16,9	7,0
P. lacticolor	2,8	2,8	17,9	3,0
P. macrocephala	3,0	1,1	18,2	1,0
Leucospermum sp.	1,2	0,6	4,9	2,0
Leucadendron sp.	1,5	1,0	6,5	5,0

*See text for derivation.

The last regression equation does not fully explain nest-site preference, since only 53 per cent (Table 4) of the variation of the equation can be accounted for by the variables added. This suggests that sugarbirds are somewhat catholic in their selection of nest-sites and/or that some factor or factors important in nest-site selection have not been considered.

In sum, nest-site selection appears to be independent of the availability of plants and in fact those species which were used most often as nest-sites were generally less abundant than others. Leaf area and leaf density appear to be the most important common factors at sugarbird nest-sites.

TABLE 3

Linear co-efficients of correlation of nest-bush characteristics.

	Nest density	*Bush height*	*Bush shape*	*Leaf area*	*Leaf density*	*Plant availability*
Nest density	1,000	—0,247	—0,265	0,675*	0,642*	—0,306
Bush height		1,000	—0,577*	—0,307	—0,200	0,159
Bush shape			1,000	—0,366	—0,298	0,500†
Leaf area				1,000	0,636*	—0,144
Leaf density					1,000	—0,159
Plant availability						1,000

*Correlation significant, $P < 0,01$.
†Correlation significant, $P < 0,05$.

TABLE 4

Multiple regression of physiognomic characteristics of plant species where nest density is the dependent variable (y).

Variables	R_1	R_2	R_3	*Regression equations*
Leaf area (x_1)	0,6745	0,6745	0,4550	$-1,56 + 0,27\ x_1$
Leaf density (x_2)	0,7287	0,0542	0,5311	$-5,31 + 0,18\ x_1 + 1,10\ x_2$
Bush height (x_3)	0,7298	0,0011	0,5326	$-4,40 + 0,17\ x_1 + 1,10\ x_2 + 0,39\ x_3$
Bush shape (x_4)	0,7305	0,0007	0,5336	$-4,65 + 0,17\ x_1 + 1,11\ x_2 - 0,58\ x_3 + 0,42\ x_4$

R_1 Multiple correlation co-efficient.
R_2 Increase in R with the addition of extra variable.
R_3 Square of R: the amount of variation in y accounted for by the x variable(s) added.

Vegetation density

Of 140 nesting territories studied, 61 per cent were in dense vegetation and the remainder were in open vegetation. Of 4,99 ha of bushes in the study area, 57 per cent were in dense vegetation and the balance in open vegetation. The number of nests found in dense vegetation was not significantly higher than expected ($\chi^2 = 0{,}79$ $P > 0{,}05$). Thirty-nine (71 per cent) of the nests in the open vegetation were, however, located in bushes with dense foliage.

Nest height

There was no significant correlation between nesting density and bush height (Table 3). The data also indicate that sugarbirds do not prefer bushes of any particular height. However, they appear to prefer to place their nests at a particular height above the ground.

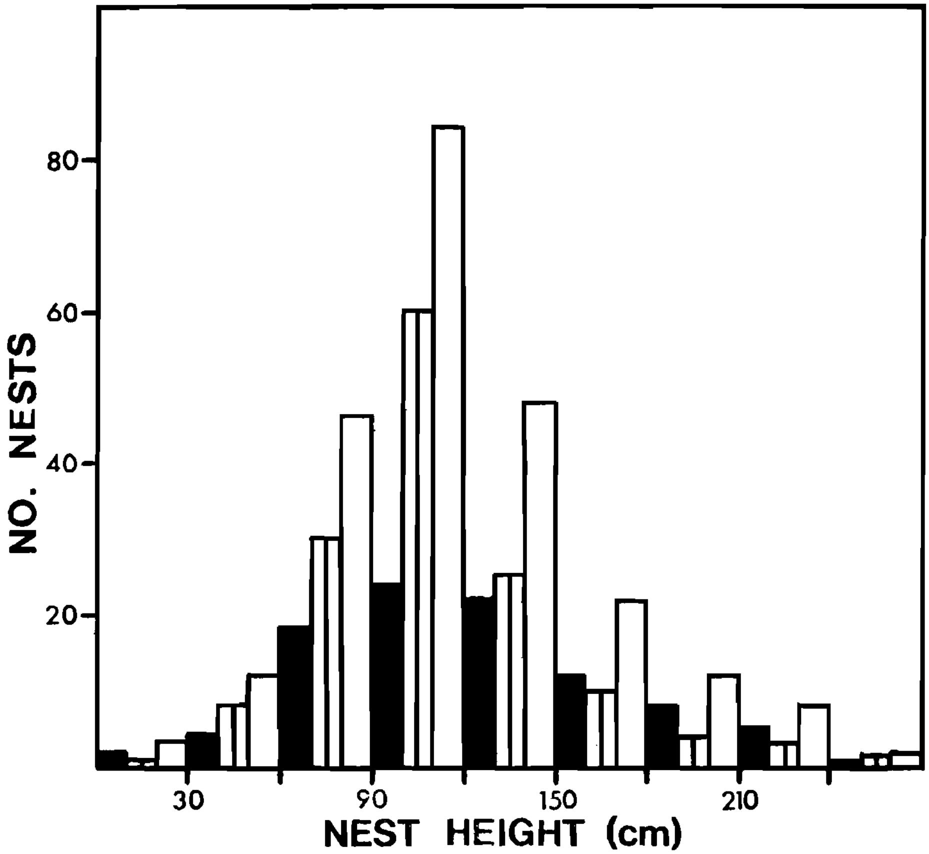


FIGURE 6

Number of Cape sugarbird nests grouped into 30 cm intervals above ground level. Solid columns (A) based on data in Broekhuysen (1959), hatched columns (B) nests recorded for this study, and clear columns (A) and (B) combined.

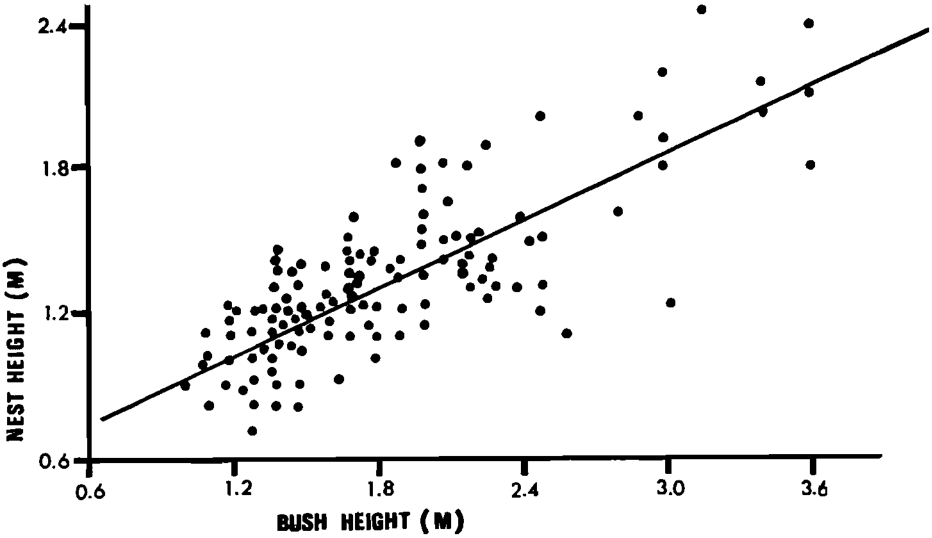


FIGURE 7

Height of Cape sugarbird nests in relation to height of bushes.

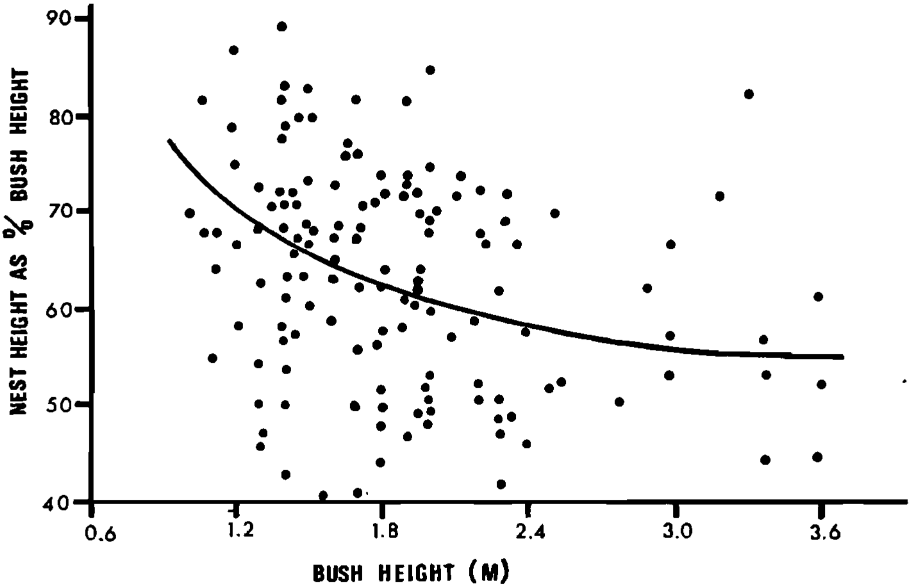


FIGURE 8

Height of Cape sugarbird nests as a percentage of bush height.

Most nests (67 per cent) were located between 90 and 140 cm above the ground, which agrees with Broekhuysen's (1959) data (Figure 6). Since no significant difference (paired *t*-test, $t = 0{,}01$ $P > 0{,}05$) was found between our data and Broekhuysen's, they have been pooled to indicate a preferred nest height at about 1 m above ground level. Nests were located at slightly higher elevations in relatively tall bushes (Figure 7). The relationship is represented by

$$y = 0{,}47\,x + 0{,}28 \; (y = \text{nest height}, x = \text{bush height}).$$

Using this equation, nest heights were expressed as a percentage of bush height to indicate that in low bushes nests tended to be placed near the top of the plant, and in taller bushes nests tended to be located at about half the height of the plant (Figure 8).

Bush sector

Forty-nine per cent of the nests in dense vegetation and 47 per cent of the nests in open vegetation were placed in the central sectors of bushes (Figure 9). Of the remaining nests, some preference was shown for the three south-facing sectors. No significant difference ($t = 0{,}08$ $P > 0{,}05$) was found between nests in dense and open vegetation.

Nest cover

Percentage vegetation cover did not differ significantly ($P > 0{,}05$) between directional aspects at either 0,1 or 1 m above nests (Table 5). Percentage cover for each aspect was, however, significantly different ($P < 0{,}01$) between the two areas above nests (Table 5). This indicates that (a) nests were not sited randomly, since cover was greater at 0,1 m than 1 m above nests;

TABLE 5

Mean ± one S.D. percentage vegetation cover on sides of Cape sugarbird nests (n = 47 nests).

	Percentage vegetation cover		
Cover aspect	*0,1 m² above nest*	*1 m² above nest*	t-*value*
North	76,3 ± 21,6	48,4 ± 20,4	6,44*
South	72,1 ± 19,6	39,5 ± 19,0	4,11*
East	66,3 ± 21,4	41,5 ± 20,0	5,80*
West	68,7 ± 21,0	45,3 ± 20,1	5,52*
Average	70,9 ± 20,8	43,7 ± 19,5	13,05*
ANOVA (*F*-value)	1,80	1,85	NS ($P > 0{,}05$)

*Difference significant, $P < 0{,}01$.

and (b) nest-sites had been selected without regard to some critical influence prevailing laterally from a particular direction. The mean overhead vegetation cover for 17 nests was 63 per cent (Appendix 1).

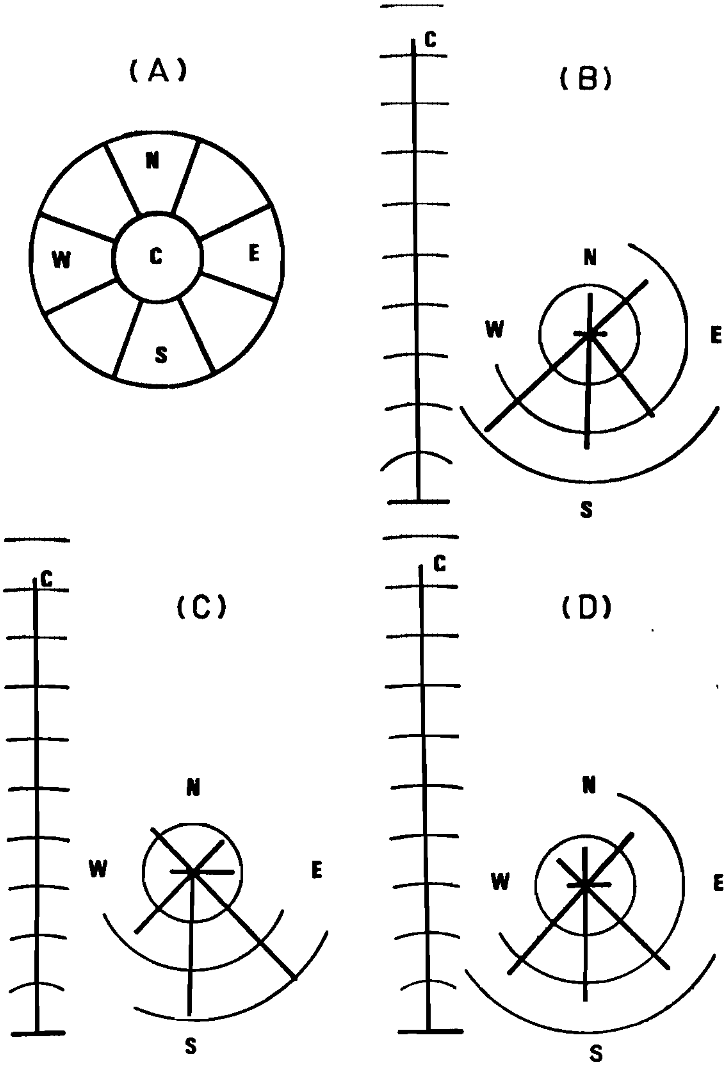


FIGURE 9

Selection of sectors in bushes as sites for Cape sugarbird nests. (A) Eight peripheral and one central sector, all of equal area, were considered. (B) Bushes in dense vegetation. (C) Bushes in open vegetation. (D) B and C combined. Each arc represents a 5 per cent frequency interval.

Wind

Certain plant species were more effective than others as barriers to wind (Table 6). Reduction of wind speed through plants was correlated significantly with leaf area and leaf density (Table 7). These two features were the only ones to correlate significantly with nest density (Table 3). This suggests that a need for shelter from wind may be an important factor influencing nest-site selection.

Figure 10 shows wind-speed profiles in different vegetation types and in the open. The profile in the open area conformed to the expected pattern of wind over bare ground (Geiger 1965). Thickets of certain protea species reduced wind-speed more effectively than others. Bushes with large leaves and dense foliage permitted nests to be placed relatively high above the ground, without loss of protection from the cooling and shaking effects of wind. In general, the

TABLE 6

Effectiveness of plant species as barriers to wind, measured 1,0 m above ground level.

	Wind velocity		
Species	*In bush cm/sec*	*In open cm/sec*	*Per cent reduction over 1 m*
Protea eximea (dense)	6,6	32,8	80
P. eximea (open)	44,1	100,1	56
P. grandiceps	0,2	20,9	99
P. grandiceps	27,8	106,8	74
P. compacta	72,1	100,1	28
P. longifolia	62,4	222,8	72
P. longifolia	27,0	85,6	82
P. loriflora	86,2	132,7	35
P. longiflora	142,6	222,8	36
P. longiflora	47,6	132,2	64
P. pulchra	61,0	132,7	54
P. barbigera	7,1	54,1	87
P. barbigera	3,1	61,4	95
P. repens	15,6	20,9	25
P. repens	65,1	85,6	24
P. lepidocarpodendron	22,3	33,8	33
P. lacticolor	40,6	106,8	62
P. macrocephala	24,3	33,8	28

top quarter section of most bushes provided least resistance to wind. The unusual and 'reversed' profile for *Protea grandiceps* (Figure 10F) can be explained in terms of the plant's distribution and physiognomy. It occurred as solitary bushes, not in thickets, and leaves were relatively sparse in the lower third portion of the bushes.

Air temperature

An air temperature inversion or negative lapse-rate (Lowry 1969) was found at night in both dense and open vegetation (Figures 11 & 12). Thus, at night the coldest air occurred closest

TABLE 7

Lineai co-efficients of correlation of wind speed reduction in bushes and physiognomic properties of bushes.

Variable	*Correlation coefficient with wind speed reduction*
Leaf area	0,792*
Leaf density	0,746*
Bush height	0,423
Bush shape	0,391

*Difference significant, $P < 0{,}01$.

TABLE 8

Calculated downward longwave radiation (cal cm^{-2} min^{-1}) at night at three sites.

	Height (cm) above ground		
	10	100	200
Dense vegetation	0,464	0,449	0,413
Open area with ground cover	0,432	0,433	0,424
Open area with bare ground	0,423	0,424	0,413

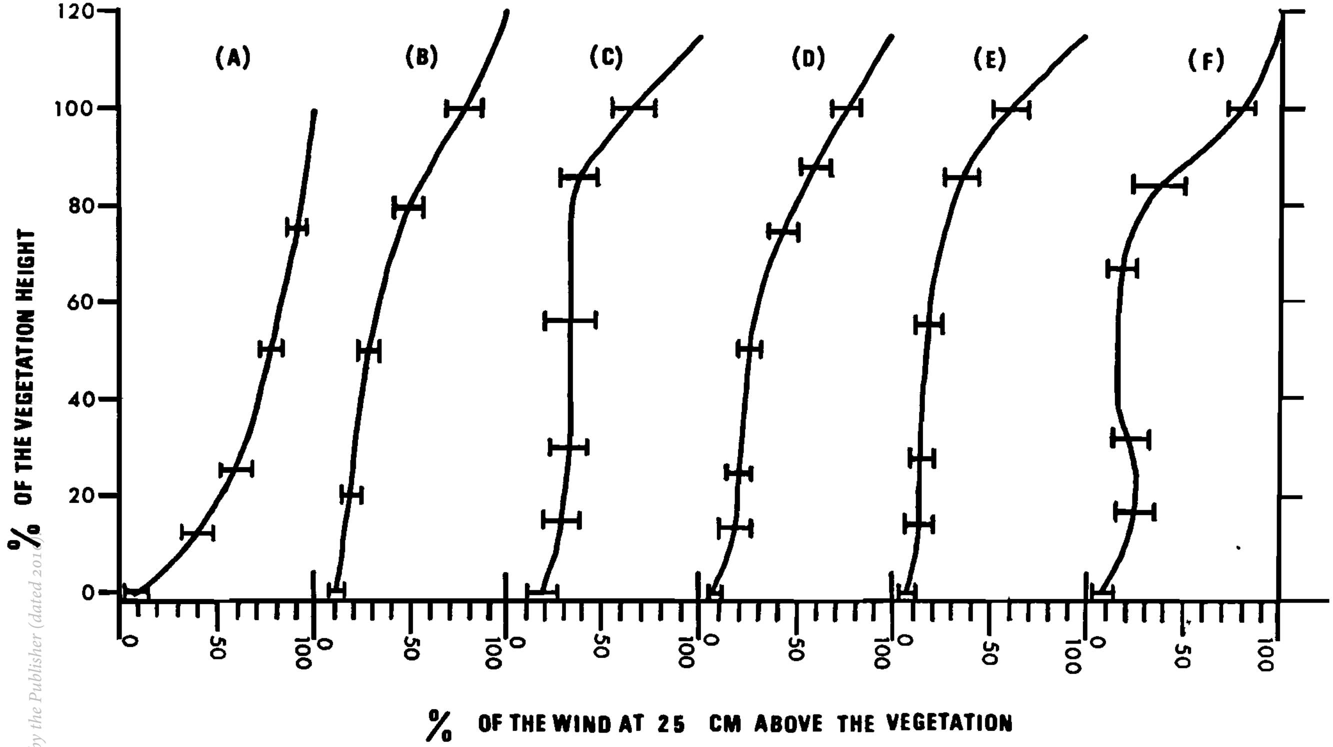


FIGURE 10

Wind profiles in an open area (A) and in protea thickets. (B) *Protea compacta* and *P. lacticolor*, (C) *P. neriifolia* and *P. lepidocarpodendron*, (D) *P. longifolia*, (E) *P. eximea*, (F) *P. grandiceps*. Wind speeds in the open area are given as percentages of the wind at 2,0 m above the ground level. Wind speeds in vegetation are given as percentages of the wind at 25 cm above the top of the vegetation. Mean values and 95 per cent confidence intervals are shown.

to the ground. Nests placed relatively high above ground in both dense and open vegetation were protected best from cold air at night. The inversion in the open vegetation broke down in the morning, as the sun heated the ground, and a strong positive lapse-rate was formed between 11h00 and 15h00. In the dense vegetation, however, the ground was shaded, and below 50 cm an inversion persisted all day.

Radiation

Most of the incoming solar radiation was shielded from the ground in dense vegetation. At night the net radiation loss was low in places shielded from the night sky by leaves. There was less downward radiation and greater upward radiation loss near the upper storey of the vegetation (Figure 13). Downward longwave radiation varied little with height in the open at night (Table 8). The relationship between vegetation cover over a nest and the nocturnal radiation at the nest is shown in Figure 14.

TABLE 9

Heat loss through convection and radiation from incubating Cape sugarbird* nesting† at different elevations in dense *Protea eximea* thickets. See text for further particulars.

	Height (cm) of nest above ground		
	10	100	200
Air temperature Ta (°C)	6,4	7,1	7,7
Bird surface temperature Ts (°C)	19,0	19,0	19,0
(Ts—Ta) (°C)	12,6	11,9	11,3
Mean wind speed (cm sec^{-1})	6,0	10,8	36,0
Convection coefficient hc (cal cm^{-2} min^{-1} $°C^{-1}$)	$4,5 \times 10^{-3}$	$6,1 \times 10^{-3}$	$11,1 \times 10^{-3}$
Heat loss through convection (cal hr^{-1})	93,8	119,0	206,0
Radiation from bird (cal cm^{-2} min^{-1})	—0,578	—0,578	—0,578
Radiation from sky and vegetation (cal cm^{-2} min^{-1})	0,464	0,449	0,413
Net radiation (cal^{-1} cm^{-2} min^{-1})	—0,114	—0,129	—0,165
Heat loss by radiation (cal hr^{-1})	188,1	212,9	272,3
Combined radiation and convective heat loss from bird (cal hr^{-1})	281,9	331,9	478,3
Estimated basal metabolic rate BMR‡ (cal hr^{-1})	489,0	489,0	489,0
Per cent BMR lost through radiation and convection	58,0	68,0	98,0

*Mean mass of female bird = 36,5 g (± 2,40 S.D. n = 6).

†Mean internal diamter of nest = 6,12 cm.

‡BMR estimated from M (kcal bird $^{-1}$ day^{-1}) = 0,867 W $(g)^{0,724}$ (Kendeigh, 1970).

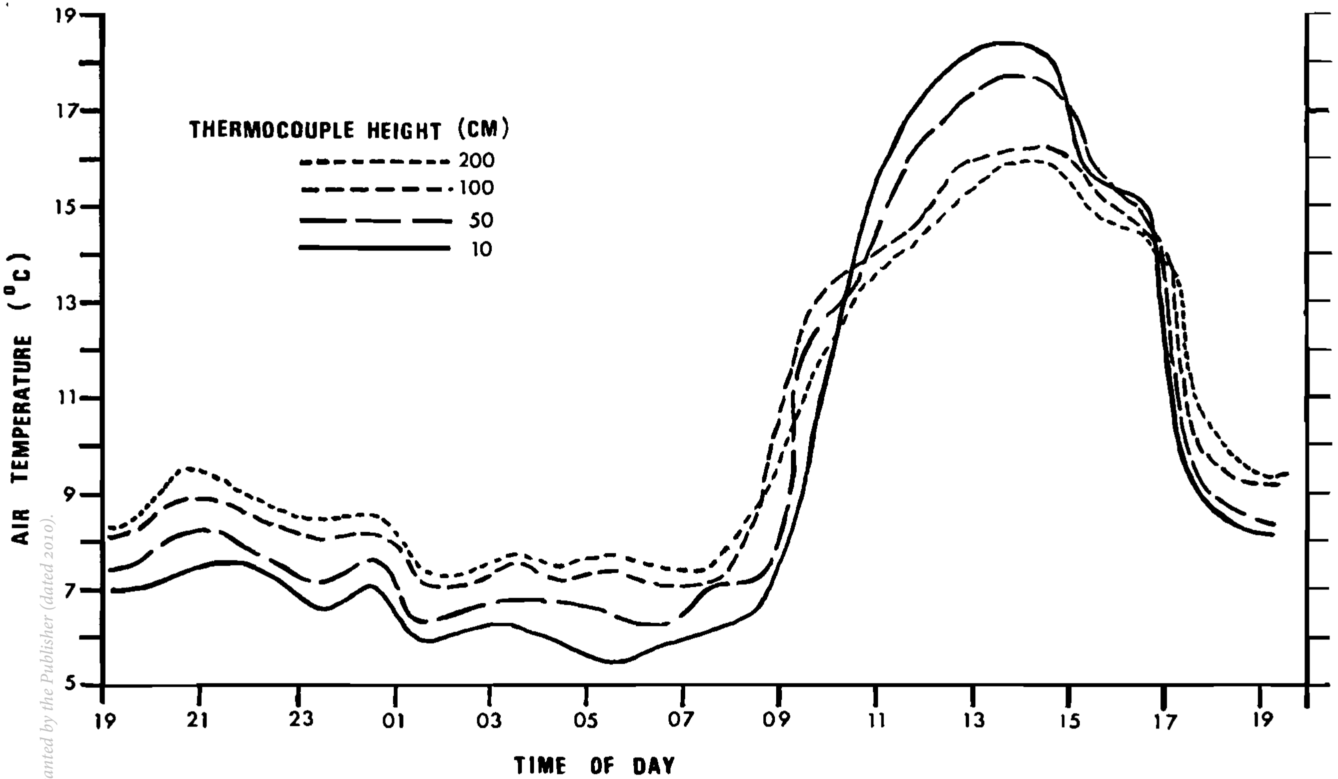


FIGURE 11

Air temperature according to time of day in open vegetation. Thermocouples were placed at 10; 50; 100 and 200 cm above ground level.

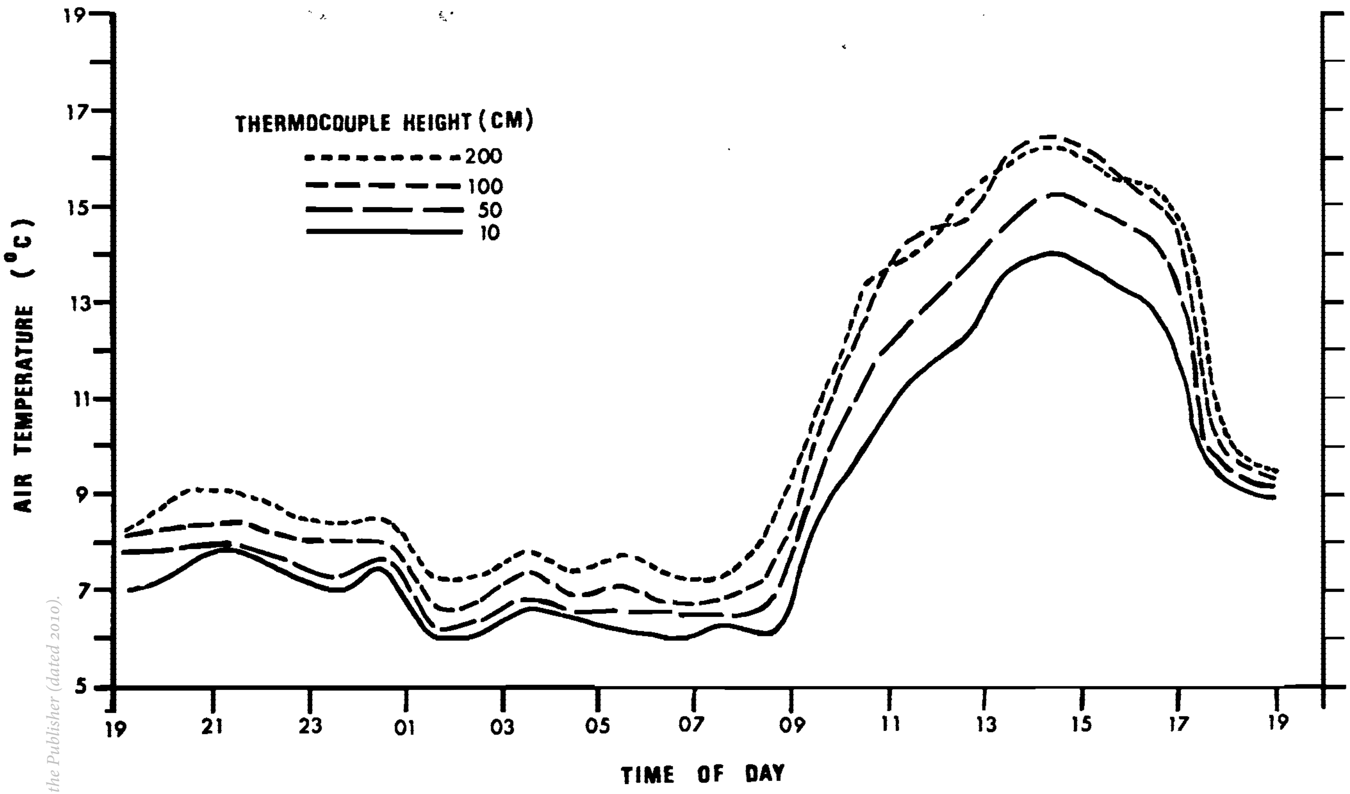


FIGURE 12

Air temperature according to time of day in dense vegetation. Thermocouples were placed at 10; 50; 100 and 200 cm above ground level.

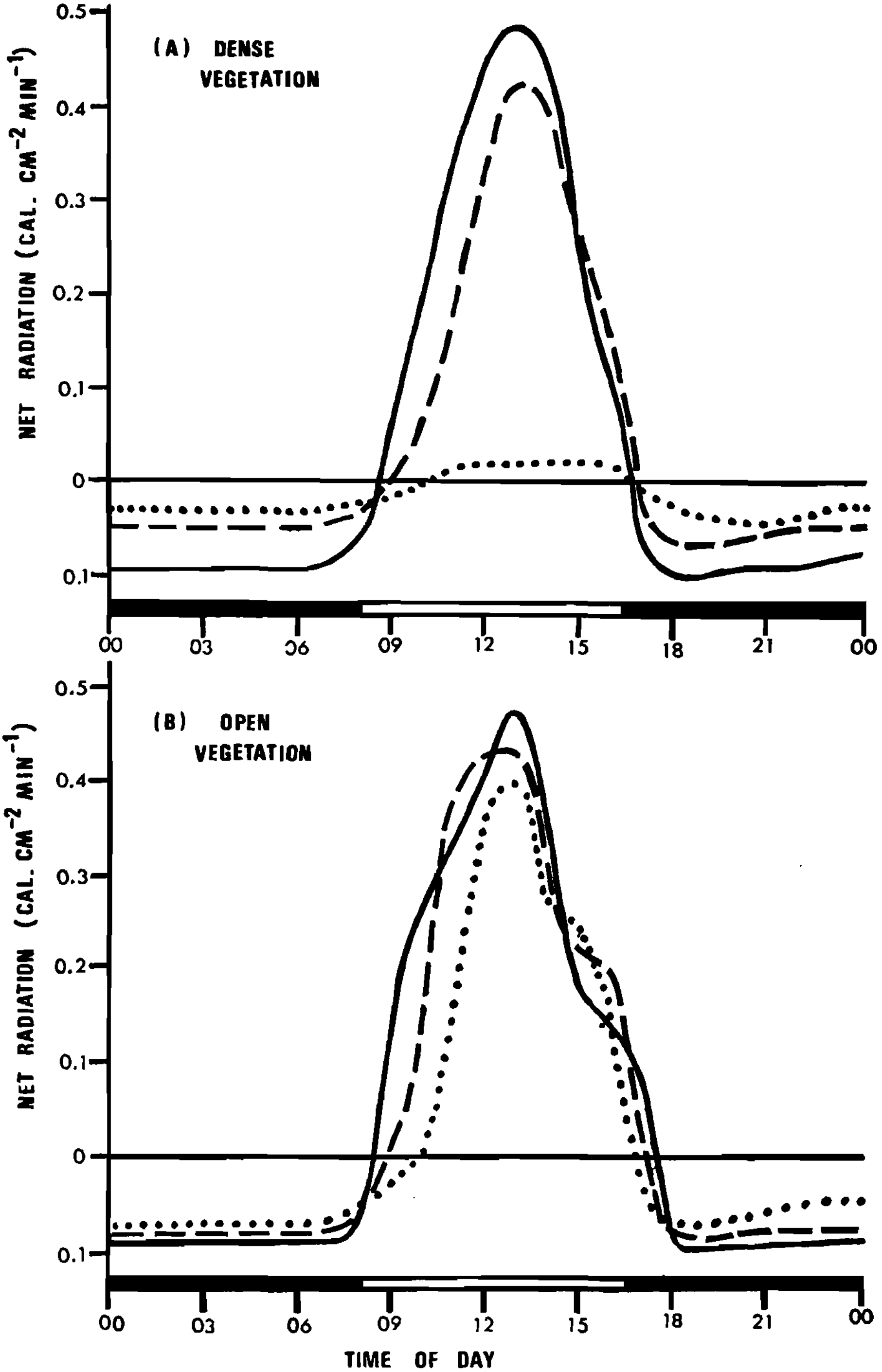


FIGURE 13
Net radiation flux according to time of day at two neighbouring sites: (A) in a dense thicket of *Protea eximea*, and (B) in an open area with grassy substrate. Measurements made at 10 cm (dotted line), 100 cm (dashed line) and 200 cm (solid line) above ground level.

During the day the greatest gain in solar radiation would occur at a nest placed either in open vegetation or in the top storey of dense vegetation. Heat lost through radiation during the night would be least at a nest placed low in dense vegetation.

Heat loss from an incubating bird

Heat lost through convection and radiation from an incubating female sugarbird on a cold clear night (19h00–08h00) was calculated in relation to three nest-sites in a dense stand of *Protea eximea* bushes (Table 9). Basal metabolic rate was calculated to be 11,73 kcal bird^{-1} day^{-1} or 489 cal bird^{-1} hr^{-1}.* Thus the amount of energy lost by incubating sugarbirds through radiation and convection at night varied from about 58 per cent of BMR at 10 cm nest height above ground to 98 per cent of BMR at 200 cm nest height above ground. A progressive increase in vegetation cover above a nest resulted in a reduction of the heat lost through radiation from the bird (Table 10).

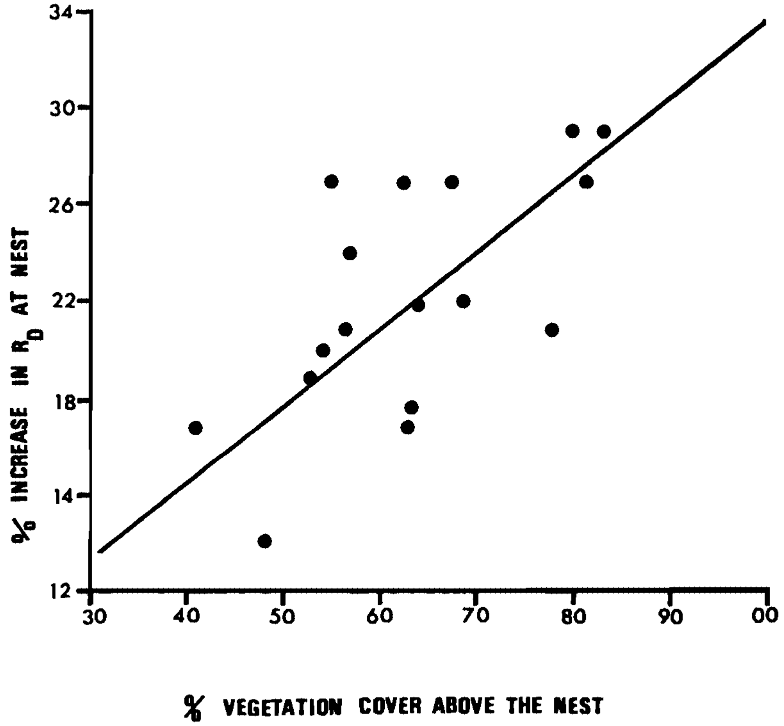


FIGURE 14

Percentage increase in downward longwave radiation with increase in vegetation covering nests of Cape sugarbirds. Based on data in Appendix 1.

---

*1 kcal = 4 186,8 joule.

TABLE 10

Radiation heat loss from an incubating Cape sugarbird according to overhead vegetation cover.

Per cent vegetation cover over nest	*Downward radiation cal cm^{-2} min^{-1}*	*Upward radiation cal cm^{-2} min^{-1}*	*Radiation energy loss by bird cal hr^{-1}*
0	0,343	—0,578	775,5
20	0,372	—0,578	679,8
40	0,394	—0,578	607,2
60	0,416	—0,578	534,6
80	0,434	—0,578	485,1
100	0,460	—0,578	389,4

DISCUSSION

The plants preferred as nest-sites by Cape sugarbirds were neither the most abundant nor the species most used as food sources. Most birds which nest in vegetation select for density of foliage at different levels above the ground; other features of the vegetation appear less important (Orians 1971). The Cape sugarbird conforms to this trend, in respect of its preference for bushes with large and densely packed leaves correlated with enhanced shelter from wind. Most of the plant species preferred as nest-sites form robust bushes, not readily disturbed by wind. Wind, possibly together with rain, appears important in influencing selection of nest-sites.

In certain bird species, nests tend to be situated on the leeward side of bushes and trees in areas where prevailing winds affect nesting success (Mitchell 1966). Most sugarbird nests were located in the central parts and to a lesser extent in the southern sectors of bushes. We expected to find many more nests in the southern sectors of bushes, since the prevailing, rain-bearing wind in the south-western Cape is from the north. However, the local topography at Helderberg diverts wind so that strong gusts are experienced at times from all directions. Thus, the central part of a bush would offer maximum shelter. Nests situated in the northern sectors of bushes, while receiving most solar radiation in winter, would be most exposed to wind and rain. Nests exposed to rain and wind were prone to disintegration.

Most sugarbird nests were surrounded by dense vegetation, and were shielded from wind and rain. Large leaves and dense foliage over a nest reduced heat loss from the incubating bird, and presumably also helped in hiding the bird from aerial predators. The mean percentage cover over nests was, however, relatively low (63 per cent). The birds may not have been able to improve on this, because of constraints set by the morphological characteristics of the plant species available as nest-sites. The forks of protea bushes have branches radiating horizontally, thus reducing the amount of foliage directly above nest-sites. Overhead cover shields incubating birds from the radiation 'heat sink' of the cold night sky. Calder (1973a & b) considered overhead shielding to be of primary importance in promoting energy savings by nesting hummingbirds (Trochilidae) in a cold climate. Our calculations suggest that heat loss by radiation is an important pathway for energy loss from nesting sugarbirds at night.

From work on several species Preston (1946) suggested that birds are 'conscious' of height above ground when selecting nest-sites. He found that most species had a characteristic, 'preferred' height for placing nests. Sugarbirds most often place their nests in the upper half of bushes. However, in these situations, night-time convective and radiative energy losses from incubating birds are increased. Conversely, birds incubating lower in the vegetation, though subject to relatively lower convective and radiative energy losses, are exposed to lower ambient temperatures. Furthermore, in dense vegetation, this thermal inversion persists throughout the day. Low ambient temperatures increase the metabolic costs of maintenance and incubation.

Diurnal incoming radiation at an elevated nest would be relatively great, depending on the amount of overhead cover. Local solar radiation in winter is approximately 231 cal cm^{-2} day^{-1} (Fuggle 1970). The absorbtivity of a dark passerine bird is high (Porter & Gates 1969), and a sugarbird exposed to this radiation would gain heat. This could be advantageous in reducing metabolic heat production of the incubating bird, providing the heat gained was not excessive. Incubating sugarbirds have been observed to pant while exposed to direct sunlight. Water is freely available during the sugarbird's breeding season. Evaporative heat loss could reduce the disadvantage of direct exposure to sunlight without itself being disadvantageous through reducing the bird's water balance.

Nests of the cactus wren *Campylorhynchus brunneicapillus* situated in spinescent vegetation tended to be avoided by predators, but these sites were not the most suitable ones available for avoiding excessive heat in the desert (Ricklefs & Hainsworth 1969). Little is known about the effects of predators on the Cape sugarbird. Broekhuysen (1959) found that mortality of eggs and nestlings was high, and he thought that predation was an important contributory factor. Broekhuysen listed some of the potential predators, including ants, snakes, birds and mammals. All were present in the Helderberg study area.

The boubou shrike *Laniarius ferrugineus*, which takes young sugarbirds (personal observation), normally forages on the ground and in the lower regions of bushes (McLachlan & Liversidge 1970). Most of the potential mammalian predators are ground-dwellers. It is likely that most predators on sugarbird nestlings and eggs approach and detect nests from below. Thus, the probability of detection could be reduced for nests placed high above ground. A sugarbird, through nesting relatively high above the ground, might conceivably improve its chances of escaping an actual attack by a predator from below. Preston & Norris (1947) suggested that predators constitute a major force limiting birds nesting on or near the ground. It seems likely that nests which are surrounded on all sides by dense cover tend to escape detection by predators. Such cover may, however, hinder the nest-owner's rapid escape when attacked.

SYNTHESIS

Table II summarizes negative and positive properties of Cape sugarbird nests in relation to their situation in bushes. Nest-site selection can be regarded as the product of a behavioural matrix for optimization of energy budgeting and breeding success. Figure 15 shows some of the relationships between environment, nest-site and breeding success of the Cape sugarbird. Time and energy are the two most important resources affecting parental behaviour and breeding success (Drent 1973). Sufficient energy must be available to meet the cost of normal existence and the extra cost of breeding. The parent bird must collect sufficient food, but cannot leave the nest too frequently to feed. The relationship between the parent's energy requirements and its time budget is a complex one, but reproductive success will be affected adversely should either time or energy be limiting.

The energy balance of an organism is given by the following equation (Smith, Roberts & Miller 1974), modified from Porter & Gates (1969)

$$HM = HE \pm HR \pm HC \pm HK,$$

where HM represents metabolic heat production; HE is evaporative heat loss; HR is net radiational energy exchange between the organism and the environment; HC is convective heat exchange; and HK is heat exchange by conduction.

TABLE 11

Properties of Cape sugarbird nests in relation to situation in protea bushes. Advantageous (+), disadvantageous (—), little or no effect (O).

	Rigid base for nest	*Dense vegetation*	*Increased elevation of nest*	*Orientation of nest*	*Increased foliage around nest*
Reduced effects of wind and rain	+	+	—	+	+
Escape from predators	O	—	+	O	—
Avoidance of detection by predators	O	+	+	O	+
Reduced nocturnal radiation heat loss	O	+	—	O	+
Increased solar radiation gain	O	—	+	+	—
Increased nocturnal air temperature at nest	O	O	+	O	+

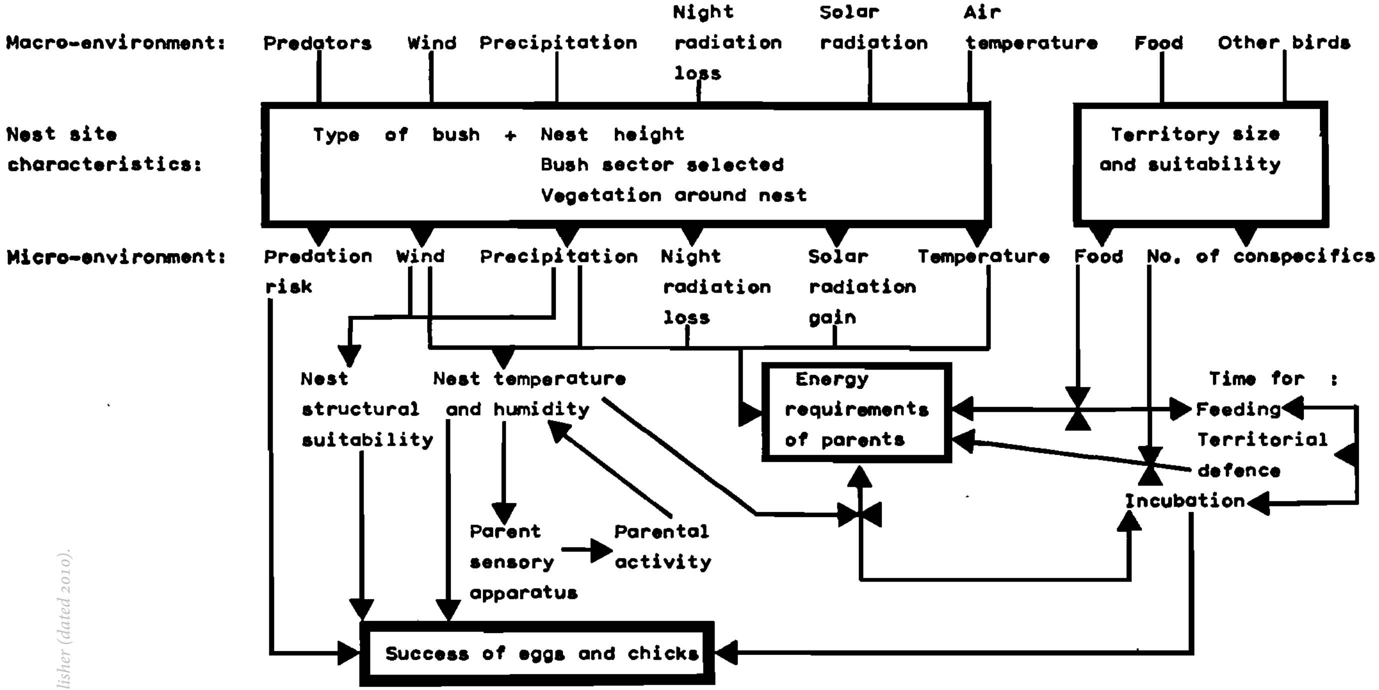


FIGURE 15

Relationships between properties of nest-sites and factors influencing breeding success of Cape sugarbirds. Arrows indicate direct effects and valves indicate moderating factors between properties or quantities.

Our current data are insufficient to complete an energy balance for the Cape sugarbird. We have, however, shown that the incubating bird loses considerable energy at night. For convection and radiation alone, the values for energy loss represent between 58 and 98 per cent of the estimated basal metabolic rate. These values are higher than those derived from incubating broad-tailed hummingbirds *Selasphorus platycercus* (Calder 1973b). However, the value for basal metabolic rate is likely to be considerably less than that for actual metabolism. No data are available at present to improve the estimate. Air temperature and humidity, wind velocity, exposure to radiation and the cold night sky are all determinants of energy exchange. These can all be modified by optimal nest-site selection, nest composition and construction (Calder 1973b; Smith *et al.* 1974).

Our results show that the nest-sites preferred by Cape sugarbirds have favourable microclimates in a season of unfavourable weather. A favourable microclimate at the nest has many selective advantages. Reduced heat loss from the parent results in energy savings for incubation and brooding. The parent would thus require to spend less time feeding. A favourable microclimate reduces heat loss from eggs and nestlings, decreasing their risk of thermal stress during parental inattentiveness. The parent could thus spend longer periods feeding. The situation of the nest may also be important in reducing disturbance from predators and conspecifics. This would result in enhanced efficiency in incubation and brooding, allowing the parent more time for maintenance activities.

ACKNOWLEDGEMENTS

We thank Donella Banks, Val Canty, Bruce Campbell, Toni Milewski and Nico Myburgh for their assistance. Richard Fuggle and Eugene Moll contributed advice and information. The Council for Scientific and Industrial Research and the University of Cape Town provided financial support for the study.

REFERENCES

ACOCKS, J. P. H. 1975. Veld types of South Africa. *Mem. bot. Surv. S. Afr.* 40: 1–128.

BAKER, J. R. 1938. The evolution of breeding seasons. In *Evolution, essays on aspects of evolutionary biology presented to G. B. Goodrich*, ed. G. R. de Beer: 161–177. Oxford.

BROEKHUYSEN, G. J. 1959. The biology of the Cape sugarbird, *Promerops cafer* L. *Ostrich*, Suppl. 3: 180–221.

CALDER, W. A. 1971. Temperature relationships and nesting of the Calliope hummingbird. *Condor*, 73: 314–321.

CALDER, W. A. 1973a. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. *Ecology*, 54: 127–134.

CALDER, W. A. 1973b. An estimate of the heat balance of a nesting hummingbird in a chilling climate. *Comp. Biochem. Physiol.* 46: 291–300.

DRENT, R. H. 1973. The natural history of incubation. In *Breeding biology of birds*, ed. D. S. Farner: 262–311. Washington, D.C.: Nat. Acad. Sciences.

DRENT, R. H. & STONEHOUSE, B. 1971. The thermoregulatory responses of the Peruvian penguin, *Spheniscus humboldti*. *Comp. Biochem. Physiol.* 40: 689–710.

FUGGLE, R. F. 1970. A computer programme to determine the direct shortwave income on slopes. *Clim. Bull. McGill Univ.* 7: 8–16.

GEIGER, R. 1965. *The climate near the ground.* Cambridge: Harvard Press.

HILDEN, O. 1965. Habitat selection in birds. *Ann. Zool. Fenn.* 2: 53–75.

KENDEIGH, S. C. 1970. Energy requirements for existence in relation to size of bird. *Condor*, 72: 60–65.

LOWRY, W. P. 1969. *Weather and life.* New York: Academic Press.

MCLACHLAN, G. R. & LIVERSIDGE, R. 1970. *Roberts birds of South Africa*, 3rd ed. Johannesburg: C.N.A.

MITCHELL, B. L. 1966. Orientation of nests of the white-browed sparrow weaver. *Puku*, 4: 167–170.

MONTEITH, J. C. 1973. *Principles of environmental physics.* London: Arnold.

ORIANS, G. H. 1971. Ecological aspects of behaviour. In *Avian biology*, eds. D. S. Farner & J. R. King, 1: 513–546. New York: Academic Press.

PORTER, W. P. & GATES, D. M. 1969. Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* 39: 227–244.

PRESTON, F. W. 1946. Nesting heights of birds building in shrubs. *Ecology*, 27: 87–91.

PRESTON, F. W. & NORRIS, R. T. 1947. Nesting heights of breeding birds. *Ecology* 28: 241–273.

RICKLEFS, R. E. & HAINSWORTH, F. R. 1969. Temperature regulation in nesting cactus wrens: the nest environment. *Condor*, 71: 32–37.

SCHULZE, B. R. 1965. *Climate of South Africa, Part 8, general survey.* Pretoria: Weather Bureau.

SMITH, W. K., ROBERTS, S. W. & MILLER, P. C. 1974. Calculating the nocturnal energy expenditure of an incubating Anna's hummingbird. *Condor*, 76: 176–183.

SOKAL, R. R. & ROHLF, F. J. 1969. *Biometry, the principles and practice of statistics in biological research.* San Francisco: Freeman & Co.

STURMAN, W. A. 1968. Description and analysis of breeding habitats of the chickadees, *Parus atricapellus* and *P. rufescens*. *Ecology*, 49: 418–431.

WINTERBOTTOM, J. M. 1962. Breeding season of the long-tailed sugarbird *Promerops cafer*. *Ostrich*, 33: 77.

APPENDIX 1

Vegetation cover and radiation (cal cm^{-2} min) at Cape sugarbird nests at night.

		Radiation		
Nest number	*Percentage Leaf cover*	*At nest*	*In open*	*Increase at nest*
H20	53	0,50	0,42	0,08
H8	80	0,53	0,41	0,12
H19	63	0,48	0,41	0,07
H25	55	0,52	0,41	0,11
H26	57	0,51	0,41	0,10
H32	63	0,50	0,41	0,09
H29	54	0,49	0,41	0,08
H21	57	0,51	0,42	0,09
H2	41	0,48	0,41	0,07
H24	62	0,52	0,41	0,11
H22	67	0,50	0,41	0,11
H6	83	0,53	0,41	0,12
H15	48	0,46	0,41	0,05
H7	78	0,51	0,42	0,01
H10	64	0,49	0,42	0,07
H12	69	0,50	0,41	0,09
H5	81	0,52	0,41	0,11