

THE ECOLOGICAL LIFE HISTORY

OF THE CAPE BULBUL

Richard Liversidge

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And David's Lips are lock't; but in divine  
High piping Pehleví, with "Wine! Wine! Wine!  
Red Wine!" - the Nightingale cries to the Rose  
That yellow Cheek of hers to incarnadine.

Verse 6. Rubáiyát of Omar Khayyám  
The Nightingale has been identified  
as *Pycnonotus barbatus*

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15. SUPPORTING PAPERS

Based on fieldwork on the Cape Bulbul in the study area.

- a) A preliminary study on Fruit Production in Certain Plants - submitted to Annals of C.P. Museums.
- b) The Biology of the Jacobin Cuckoo - *Clamator jacobinus* - in proof in Ostrich Suppl. 7. 1970.
- c) Pre-incubation development of *Clamator jacobinus*.
- d) Fluctuations in a breeding population in the Eastern Cape.
- e) Bird weights.

## 1. SUMMARY

## SUMMARY

The study of the ecological life history of the Cape Bulbul *Pycnonotus capensis* was carried out in 20 hectares of coastal dune forest near Port Elizabeth, South Africa. Results from four years 1959 to 1962 are given in detail and only the number of breeding pairs present in 1958 have been used from observations that year.

The Cape Bulbul is one of three closely related species of a predominantly tropical family. Intra specific breeding is rare and occurs only where man has altered the habitat. Distribution has altered slightly in 150 years where colonisation has occurred. Several conditions may influence distribution, the species is mainly limited to within winter or all year round zones of rainfall.

Population of breeding pairs varies from nine to 19 pairs. It is the commonest species in the area. There is a 25% annual adult mortality with life expectancy of an adult about three years. Competition for food is negligible. Predators concern mainly the nesting cycle. Clutch size which is two or three is not regulated by food supply or population changes. Main changes are due to emigration and immigration which is apparently influenced by density-independent factors.

The seasonal internal rhythms of moult and gonadial activity are shown to occur independent of each other. They show variation from year to year and both phenomena may occur together. Factors influencing these cycles and social changes are discussed.

The food eaten by the Cape Bulbul (90% fruit) was determined by observation and stomach analysis. By experiment with caged birds and natural food it was found 25% by dry weight food of the birds own weight was required daily. Botanical survey showed the number of fruits available for each month in study area. It was estimated that when food was minimal more than twice the quantity required by the highest observed population of Cape Bulbuls was present.

"French Mould" is recorded as well as an unidentified *Dypilidium* in natural populations of Cape Bulbul. Breeding by Jacobin Cuckoo *Clamator jacobinus* is given in detail -

39% of the host nests were parasitised - effecting a 7% loss to the host. Predators taking chicks eggs accounted for 60% of the nests - two snakes, three birds and five mammals were involved.

Breeding requirements are unspecialised as shown by Cape Bulbuls free use of exotic vegetation. Territory is for nesting only (feeding is social and wide ranging) and not actively proclaimed and defence in order of priority is for mate, nest site and song perch. Territory is effective in reducing predation upon the nest.

Cape Bulbul pairs for life and remain together at all times. The threat, appeasement and courtship displays are briefly described. The female locates the nest site and builds the nest. The male helped only when nest was built rapidly. Female only incubates but both sexes may brood and both feed chicks. There were 45 three-egg clutches from which 10 young fledged and 29 two-egg clutches from which 15 young fledged. There was no significant advantage in nesting success for the smaller clutch. Eggs from the smaller clutch had a significantly better fledgling success indicating quality of egg was more important than clutch size.

Incubation period varied from 11 to 14 days - mainly 12. Nestling period was 12 to 14 days mainly 13 days. The growth and development of the young is given. Mortality of hatched young is 20% in the nest, 20% in the first week and a further 62% in second to fourth week. The loss of fledglings to first breeding is 90%.

Discussion indicates the population is controlled by density-independent factors. Clutch size is variable with individual females and conservation of energy seems to influence this. Results indicate many aspects of the biology of passerine birds applied to north temperate conditions do not apply to the species studied.

## 2. INTRODUCTION

## INTRODUCTION

When the author took up the post of Ornithologist at the Port Elizabeth Museum there were several interesting bird problems to tackle. One of these was the distribution of the Cape Bulbul *Pycnonotus capensis* and the Black-eyed Bulbul *Pycnonotus barbatus*. These two closely related species were separated by a simple geographic feature namely the Sundays River about twenty miles north of Port Elizabeth. The fact that these two species were very common and conspicuous birds provided the impetus to select the problem for a detailed study that would provide sufficient material for presentation as a thesis. There was a calculated risk in taking on an ecological study for a thesis for the task is not so clear cut as a morphological or anatomical problem. One can spend hours in the field, pages in the notebook for very little return in the line of facts and figures. However, the field was an untouched one in southern Africa and the prospect of working on a fruit eating bird was one that had not been studied in detail anywhere (at that stage).

The problem of a bird's distribution is not a matter of mere mapping of its occurrence along a line. To determine reasons why the one species did not fly a matter of twenty miles further requires a good deal of knowledge about its ecology and life history. Such an investigation would also show the importance of food and whether it was a limiting factor. It could also prove or confirm the author's belief that in southern Africa food for most bird species is not as important as a limiting factor as it appears to be in European and American species.

In this thesis, the results of an investigation of the ecology and life history are presented. Much of the observations were of a simple nature and much information had to be achieved by the time-consuming process of trial and error. For example to find out whether enough fruit was produced all the year round, a new technique had to be developed, as no previous work could give guidance on how to obtain the information. Similarly it was anticipated that there would be a simple formula to determine how much fruit would be required

by a frugivorous bird as there is for insectivorous and granivorous birds. This was not the case and simple experiments had to be carried out to obtain this basic information. Finally great care had to be exercised in the collecting of bird specimens so that the sampling would be sufficient to give the information on the birds of the study area without actually influencing the local population in any way at all. This with a study population not exceeding 38 birds.

In the presentation of the results I have followed Kendeigh (1961). There are nine sections in which the results of the work are presented and in each section discussion has been limited to the particular section only. This is followed by discussion which co-ordinates the findings of the several sections and deals with the points which originally instigated the work.

One final comment is a quote from Milne (1957) quoted by Lack (1966 p.296) "even the best field studies of the problem (the level about which fluctuations in populations occur) suffer from ecological deficiencies and statistical inadequacies which inevitably result in conclusions being matters of personal opinion and not of incontrovertible fact". Such comment applies to this present work and its presentation. This type of study cannot provide sufficiently convincing evidence, but only by several similar studies and expressions of opinion can progress be made - one small step at a time. At least the opinions expressed here are not biased by pre-conceived theories derived from experience confined to European and north American species. My experience and study of birds has been limited to the southern African scene with one short and stimulating sojourn in America.

The study was carried out in an area of coastal dunes (Figure 1) south east and halfway between the town of Port Elizabeth ( $33^{\circ} 58'S$   $25^{\circ} 37'E$ ) and Cape Recife. The boundary one side was the sandy beach (north) and on the other the Humewood Golfcourse. A road ran through the middle of the area and along the side of the road was a line of telephone poles. These poles were numbered and a system of field recording was based on these numbers and whether the site was to seaward or landward of the road. The study was started in 1958 and abruptly concluded in February 1963.



FIGURE 1. An aerial photograph of the study area showing the shrub covered coastal dunes. The limits of the study area are indicated by the dotted line. The suburb of Summerstrand can be seen in the background.

### 3. SYSTEMATIC POSITION OF THE CAPE BULBUL

## THE SYSTEMATIC POSITION OF THE CAPE BULBUL

### 1. THE BIRD

The Cape Bulbul is a dull brown bird, about 200 mm in length, almost thrush-like in appearance with similar soft plumage, and with three distinct field characters. The first is a bright yellow patch of undertail coverts from which the vernacular name 'geelgat' is derived. The second character is the white wattle around the eye of the adult bird. The third is the slight crest which is especially noticeable when the bird is alarmed or excited in anyway; this last character giving rise to the popular name 'toppie'. The name 'tiptol' is onomatopoeic. The bird is common throughout its range and is particularly noticeable because of its close association with man's own habitat.

### 2. THE GEOLOGICAL PAST

There are few fossil remains of the passeriformes. We are therefore fortunate that there is a single record of *Pycnonotus barbatus* as a fossil, recorded from the mid pleistocene deposits in Israel (Fisher & Peterson 1964).

Swinton (1964) states that most passerines are geologically speaking very modern in development. By the mid-tertiary period most of the higher families were established. The fossil family Palaeosciniidae is associated by Wetmore (1960) with the Pycnonotidae. Palaeoscinis is described from Miocene limestone deposits in California. If Pycnonotidae are related to the miocene Palaeoscinis as suggested, then the family is probably rightly considered of fairly old stock in the passeriformes and probably pre-pleistocene.

The origins of the family Pycnonotidae are uncertain. Many authors (Ivanov 1964, Delacour 1943, Austin 1961, Fisher & Peterson 1964, Rand & Deignan 1960) express the opinion that it is probably Ethiopian in origin. Such opinions can only be conjecture.

### 3. THE FAMILY PYCNONITIDAE

Generally, bulbuls have dull olivaceous or dull brown

brown colouring with some shading to a darker head. Many species have brightly coloured undertail coverts, red, orange, yellow or white depending upon the species. A few species have bright facial patterns with white and or red and several have fleshy, coloured lobes around the eye. All bulbuls possess a few hair-like nape feathers; these may be easily seen in *Andropadus importunis* or difficult to detect even after fresh moult as in *Pycnonotus capensis*. Sexes are alike and the juvenile plumage is similar to that of the adult. The majority of species are forest dwellers and thus arboreal in habits but a few are terrestrial. Except the terrestrial species which are insectivorous, bulbuls are predominantly fruit or berry feeders. Most species are resident, they pair for life and except for a few species which includes the *Pycnonotus* group, they show little tendency towards social associations.

Delacour's (1943) remarks as regards the family Pycnonotidae being one of the most clearly defined groups of perching birds, is most misleading. The Passeriformes are subdivided into the so called 'sub-oscines' (with four or fewer pairs of syrinx muscles) and the 'oscines' or 'songbirds' (with five to eight pairs of syrinx muscles). Of the latter, only two families can be defined by anatomical features, Alaudidae and Hirundinidae. For the remainder, the evidence of relationship is hard to define, definitions frequently use functional rather than phyletic characters. Lack of definitive characters can well be illustrated by the genus *Nicator*. *Nicator* is considered by most workers to belong to the family Pycnonotidae. Several workers, however, are not convinced that this is the correct family and express doubt but few go as far as Bannerman (1953) to place the genus in the Laniidae (shrikes), a family which is not considered to be closely related to the bulbuls.

The heading 'Bulbuls and allies' used by Mayr and Amadon (1951) refers to the three families Campephagidae (cuckoo-shrikes), Pycnonotidae and Chloropseidae (or Irenidae the leaf-shrikes). Wetmore (1951) did not enter the Chloropseidae in his earlier world classification although he did discuss it in the text. Later Wetmore (1960) included the family placing it next to the Pycnonotidae. These

relationships are generally agreed upon. Some novelty and much speculation was thrown on the scene by Fisher & Peterson (1964). They indicate a possible ancestry in the old world warblers which gave rise to five branches. One of these branches being the bulbuls that in turn gave rise to seven families, including those listed above. I consider this highly speculative guesswork. It seems highly unlikely that the wattled crows, birds of paradise and bower birds, which differ so markedly in colour patterns, behaviour patterns, breeding habits and numerous other ways from the bulbuls, should be related.

The bulbuls are typically an Afro-Asian family with representatives throughout Africa, Malagasi, and its associated islands, southern Asia from Syria east to Korea and Japan and south to the Philipines and Java. (Figure 2) The distribution of the family as shown by Fisher & Peterson (1964) includes Australia and other oceanic islands as well as the countries mentioned above. Such a family distribution includes several groups whose affinity is not yet clearly understood and for the moment these doubtful groups should not be included with the bulbuls. Figure 2 shows a somewhat modified distribution of the family from the one mentioned above.

The majority of bulbul species are found in tropical Africa with a secondary less important area of abundance in south eastern Asia.

There is little agreement on the sub-division of the family into genera and species. Rand & Deignan (1960) in their section of the Check List of the Birds of the World give 120 species from 15 genera. Austin (1961) and Fisher & Peterson (1964) give 119 species with 14 and 15 genera respectively. Delacour (1943) as well as Mayr & Amadon (1951) list 109 species from 13 genera. Considering only the African species we find that Delacour recognises 10 genera while Sclater (1930) recognises 24. In southern Africa where nine species occur the extreme in splitting was reached by Roberts who recognised seven genera whereas Sclater (1930) only recognised four genera for the same number of species. Delacour suggests that the genus *Chlorocichla* is the least specialised of all the family and is therefore ancestral.

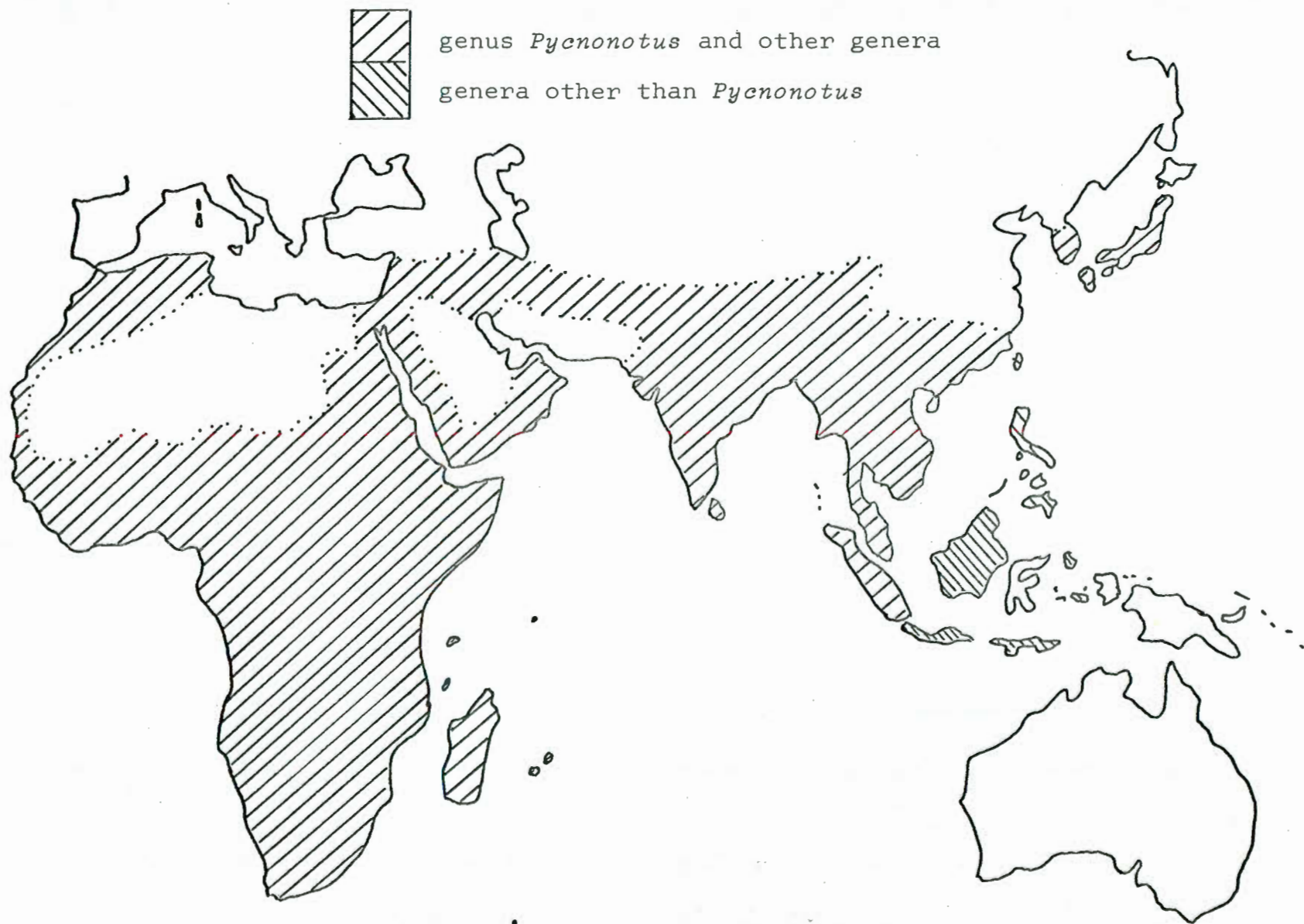


FIGURE 2. World distribution of the *Pycnonotidae*. The genus *Pycnonotus* is found over most of the families' range except on eastern islands.

A family tree is then suggested with increasing specialisation and this is diagrammatically illustrated in Figure 3. There is one point of difference with Meinertzhagen (1954) in that the latter believed the origin of the genus *Pycnonotus* was in Asia and not Africa but the arguments put forward by Meinertzhagen are not convincing.

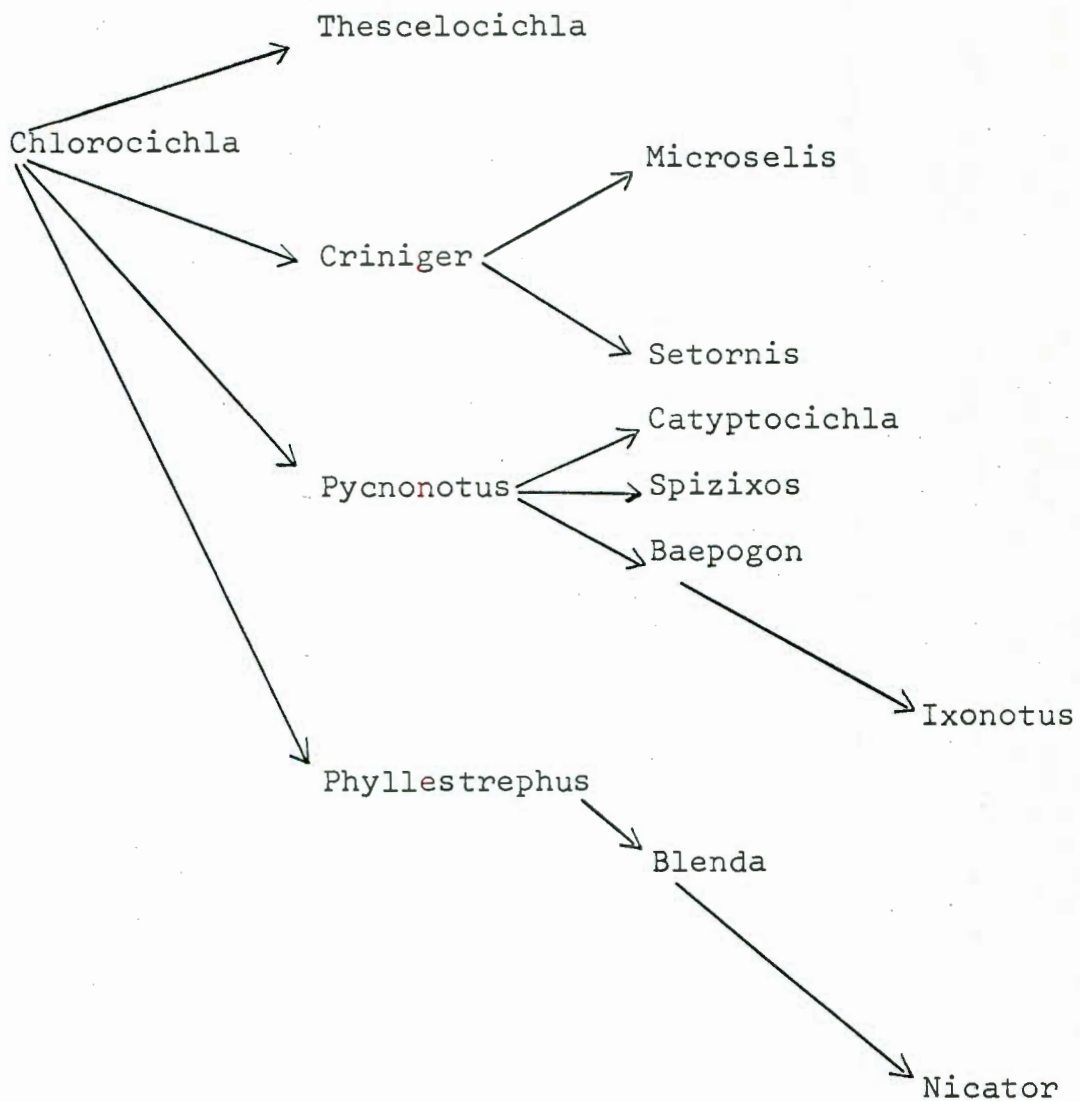


FIGURE 3. The suggested evolutionary tree of the genera of the Pycnonotidae.

#### 4. THE GENUS PYCNONOTUS

The genus *Pycnonotus* of modern taxonomists contains 47 species. Such a large genus is perhaps more a result of the desire to eliminate monotypic genera than it is an objective appraisal of the characters of the birds. Thus we find Delacour discusses the genus under sub-genera and his sub-genera are identical to the older generic grouping of Sclater (1930). He states that in defining his genera, characters of real importance are used such as general pattern of plumage; shape of bill and nostril; length of tarsus and toes. Other characters considered of value (by Delacour) are life habits, voice, behaviour, nesting and eggs. Surely at least some of these characters are the result of adaptive evolution. Shape of bill for example and length of legs and toes would depend upon the habits and feeding adaptations. In any case Delacour is not consistent.

*Andropadus* which he submerges within the genus *Pycnonotus* differs in the following manner; colour pattern lacks the highly coloured vent; shape of bill contains a notch absent in conventional *Pycnonotus* types; has completely different type of voice, nest structure and shape of egg.

Although the official World Check List follows Delacour, standard works on birds in southern Africa do not accept this lumping. Thus Traylor (1963), Praed & Grant (1963), McLachlan & Liversidge (1957) and Clancey (1964) accept the genus *Andropadus*.

With such confusion existing on the parameters of the genus *Pycnonotus* the correct number of species in the genus is uncertain.

As already mentioned Meinertzhagen (1954) suggested that the origin of the genus *Pycnonotus* was in the Orient. He states that the genus is absent from Malagasy but the fact that the family occurs there would imply that the genus is of more recent origin. Since Malagasy was isolated from Africa before the evolution of the passeriformes the argument seems to fall away and it is only somewhat slender evidence of a negative nature that supports Meinertzhagen's ideas.

It is extremely interesting to consider another

associated species in relation to this problem of the origin of the genus *Pycnonotus*. The Cuckoo *Clamator jacobinus* which parasitises the *Pycnonotus* group has two races; one breeding in southern Africa and migrating to central Africa in the non-breeding period; the other breeding in northern India and migrating in the non-breeding period to central Africa. Friedmann (1964) places the origin of the genus *Clamator* in Africa and states that the southern African stock of *C. jacobinus* is the oldest, most primitive of existing *Clamator* stock. There is no specific reason why *Pycnonotus* should show the same pattern of evolution as *Clamator*, however, I feel that it does indicate support for Delacour's belief that the genus originated in Africa.

##### 5. THE SPECIES PYCNONOTUS CAPENSIS

Meinertzhagen (loc.cit.) comments that no two authors have agreed upon the classification of the African (*Pycnonotus*) bulbuls. This is a fair statement. The African species have been variously lumped into one species, three species and in various combinations thereafter up to eight species. It should be evident from this confusion that the different populations of the genus *Pycnonotus* (stricto sensu) are very similar and obviously related.

In southern Africa there are three quite distinct sibling groups of this genus. The three groups are obviously related, being similar in size, colour, call notes, courtship, nest, eggs and feeding habits. The three groups are readily distinguishable from each other by the eye-wattle, its prominence and colour, and the colouring of the underparts. The *capensis* group has a conspicuous white eye-wattle and the brown belly extends down to the legs. In the other two groups the chest and belly are light; the *nigricans* group has a conspicuous red eye-wattle whilst the *barbatus* group has an inconspicuous brown eye-wattle much reduced in fleshiness compared to the other two species. Within the *nigricans* and *barbatus* groups there is geographical variation in the detail of colour and size giving rise to a variable number of sub-species.

Whether the three groups mentioned above should be

recognised as three distinct species or be lumped together is a problem that goes beyond normal taxonomy. Both Meinertzhagen and Lawson maintain that because hybridisation has occurred between two of the three groups they cannot be considered as different species. Such importance attached to hybridisation is quite unwarranted and as Mayr (1963 p.91) points out "cross fertility does not prove conspecificity". When one considers how few hybrids have been observed or collected in relation to the total number seen or collected, there can be no question but that we are dealing with three discreet populations. The real test of whether a species is a good one or not is not whether hybrids occur or can occur but rather whether the parental stock remains true in time and space although contact exists. Certainly the three groups of bulbuls in southern Africa have remained true for more than a century.

There are many examples in the *Pycnonotus* group of hybridisation having occurred both in nature and under artificial conditions. However, Lawson (1962) seems to exaggerate a good deal in stating that widespread integration has taken place. Of 80 specimens collected by the author within 20 kilometres of the Sundays River, eastern Cape within the zone of contact between *capensis* and *barbatus*, not one showed any sign of interbreeding. This in itself does not indicate that integration has not occurred. Sibley (1954) showed for two closely related red-eyed Towees, that along some parts of their range these closely related species showed the whole range of integration from one to the other species whilst along other portions of their range there was no hybridisation at all. Nevertheless, there is no known hybridisation in nature between *capensis* and *barbatus*. Since the Sundays River is the only zone of contact of these two groups Lawson's statement that the race *tenebrior* is somewhat unstable due to the influence of *capensis* cannot be accepted.

Hybrids of the genus *Pycnonotus* have been produced by aviculturists. The *capensis* x *barbatus* cross show in the F.1. generation large fleshy brown wattles with dark chest and belly. The *barbatus* x *nigricans* cross show either brown or orange wattles (Clancey 1960, Irwin 1958, Markus 1963a & b).

From these published sources there is no indication of any sexual differences in eye-wattle colour. From field observations with three breeding pairs of *barbatus* & *nigricans* I have noted that the males have large red wattles while the females have large brown wattles. This was recorded at Bedford in the zone of contact between *barbatus* and *nigricans*. Crosses between *capensis* and *nigricans* are unknown even though a special search was made for them in the field. Thus in what evidence we have from the abovementioned hybrids it is evident that the darker underparts dominate over the lighter underparts. In this respect it is interesting to note that the evidence shows that in the two lighter bellied forms the first plumage always shows darker below so that the darker underparts can be considered as the more primitive form. The large fleshy eye-wattle dominates over the small wattle and colour is apparently recessive.

In a paper entitled 'The genus *Pycnonotus* in southern Africa' Lawson (1962) discusses in some confusion the species of this genus. He concludes that all groups belong to one species *P. capensis*. He then discusses the three groups under the headings *capensis*, *nigricans*, and *barbatus* giving each racial status under the specific title of *capensis*. On page 168 Lawson (loc.cit.) says "populations formerly given sub-specific rank in *P. barbatus* can be regarded as linking populations with *P. nigricans*". This group of so called hybrids were collected near Pretoria by Markus who (personal communication) regards the specimens to be young first year birds (and therefore darker below) and not hybrids. On this evidence Lawson's conclusions cannot stand. Attention is also drawn to a glaring error in the photographic plates (1962 p.170) compared with those presented by Clancey (1955 p.205). The type specimens of the one race as illustrated in one plate shows a completely different pattern to the same species and race illustrated in the other plate.

In correspondence Markus has mentioned that there seems to be an indication that hybrids occur in the southern Rand area between *barbatus* and *nigricans* (see also Markus 1963b). This is an area much altered by man. The hybrids recorded in Botswana, however, are of natural incidence where only Bantu have altered the landscape. However, the author has observed

mixed winter flocks of *nigricans* and *barbatus* on several occasions feeding along the trees of the Limpopo and Thamalakane rivers in Botswana. This is also mentioned by Irwin (1958).

In India the *Pycnonotus* species hybridise (Sibley & Short 1959). Sibley (1959) states that hybridisation occurs because reproductive isolating mechanisms are not effective in preventing mating. Therefore when selection acts against the hybrid offspring of mixed matings, it is the (aberrant) parental genotype which is eliminated. Thus those individuals with faulty isolating mechanisms, have fewer offspring than those with effective ones and in each succeeding generation there are fewer of the former and more of the latter. This process is known as the decay of variability due to drift of genotypes in small populations - a process which was initially illustrated in *Drosophila*. A well documented case in birds of this process is the Siberian Azure Tit *Parus cyanus* which rapidly extended its range in the second half of the last century, eventually meeting up with the Blue Tit *Parus caeruleus*. Initially the two hybridised freely but the incidence of hybridisation declined rapidly and the invader withdrew (Vaurie 1957). Today the two species remain sympatric and only an occasional hybrid is found.

Summarising then we can say that the three groups of *Pycnonotus* above are three discreet populations. A few natural hybrids have been recorded where sympatry occurs and these only occurred in localities disturbed by man. It is presumed that the decay of variability will operate to reduce the incidence of hybridisation in these new zones as time progresses.

#### 4. DISTRIBUTION

## DISTRIBUTION

The Cape Bulbul, *Pycnonotus capensis*, is not a highly social species but it does have social tendencies especially in non-breeding times. Where the species occurs, it is usually common. Perhaps its association with humans and especially their gardens tends to emphasize the relative abundance of the species. The presence of the species as common about Port Elizabeth, only twenty miles from the limit of the species' distribution, however, illustrates the point that where the bird lives, it occurs in numbers. The extreme limits of its distribution are reached through areas of diminishing populations.

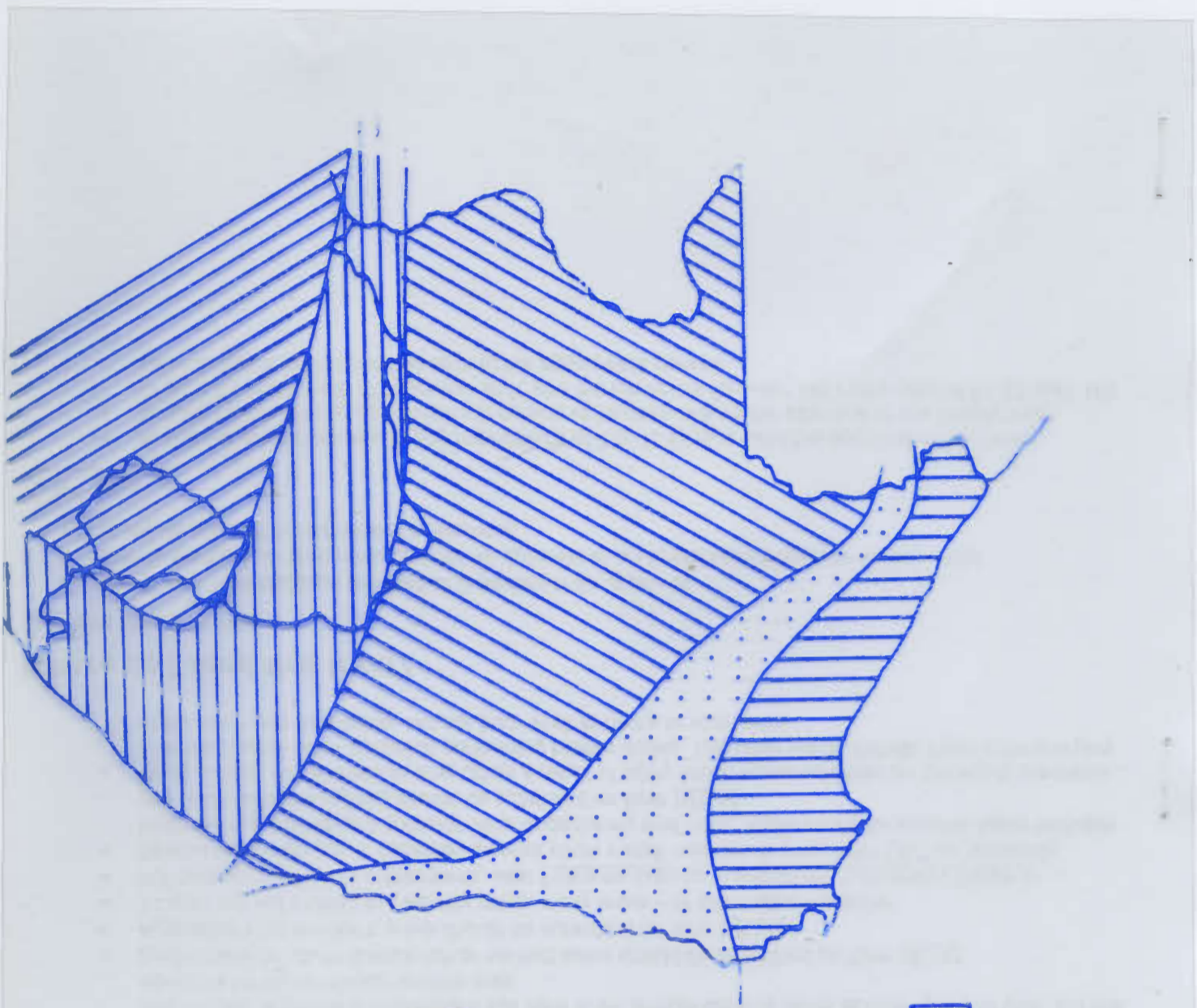
### Geographical distribution of the Species

Cape Bulbul specimens (333) in all South African Museums and the American Museum of Natural History have been inspected and their locality recorded. Information from the British and Berlin Museum collections and all references in the Ornithological journals have been tabulated. This information is illustrated in Figure 4. This distribution pattern fits what Lyons (1935) referred to as the Cape Triangle. The term is appropriate since the distribution does not fit the winter rainfall area (Figure 5) nor the Cape fynbos or Schlerophyll of Adamson (1938) - Figure 6.

According to Pole Evans (1936), Adamson (1938), Acocks (1953) and Levyns (1964), there is no typical vegetation type that occupies the Cape Triangle. The vegetation fits in with what Winterbottom (1968b) figures for winter rainfall region but he does not give his authority nor does he comment upon another such map, (Winterbottom 1968a), which agrees with Wellington (See Figure 5). The main point remains that vegetation distribution pattern is not the same as that for *Pycnonotus capensis*.

Most climatic factors mapped show little agreement with any feature correlated with the pattern of the Cape Triangle. Thus maps of mean surface temperature, average maximum and minimum temperatures, incidence of frost and mean rainfall show different patterns in the Cape.

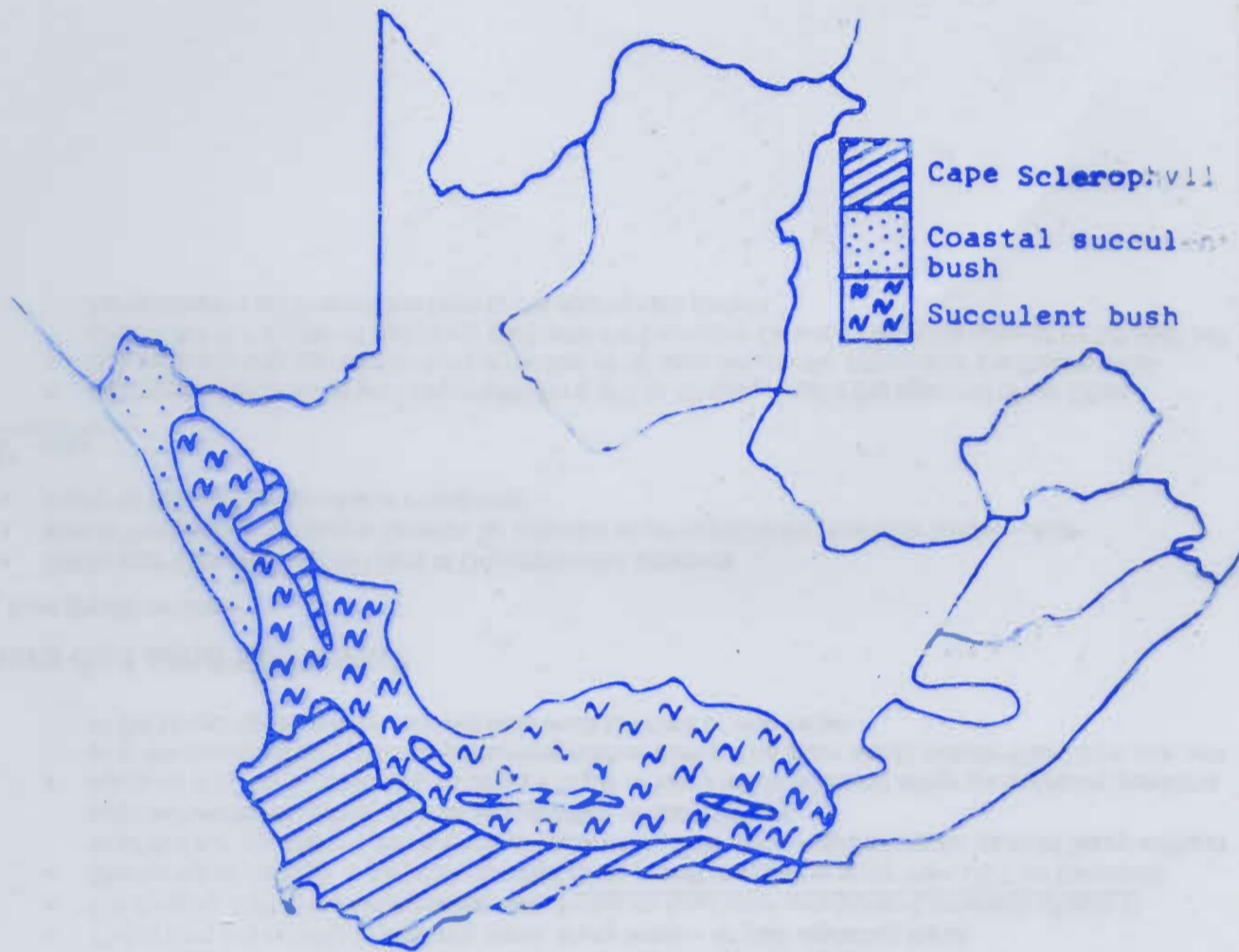
The map showing seasonal rainfall zones (Figure 5) does



Summer max. January  
 Summer max. Jan. - March  
 Summer max. March

All seasons  
 Winter

FIGURE 5. Rainfall zones. The rainfall zones (50% of annual rainfall) according to season (after Wellington 1958).



**FIGURE 6. Vegetation.** The distribution of the Cape Sclerophyll in the Cape Triangle - after Adamson 1938.

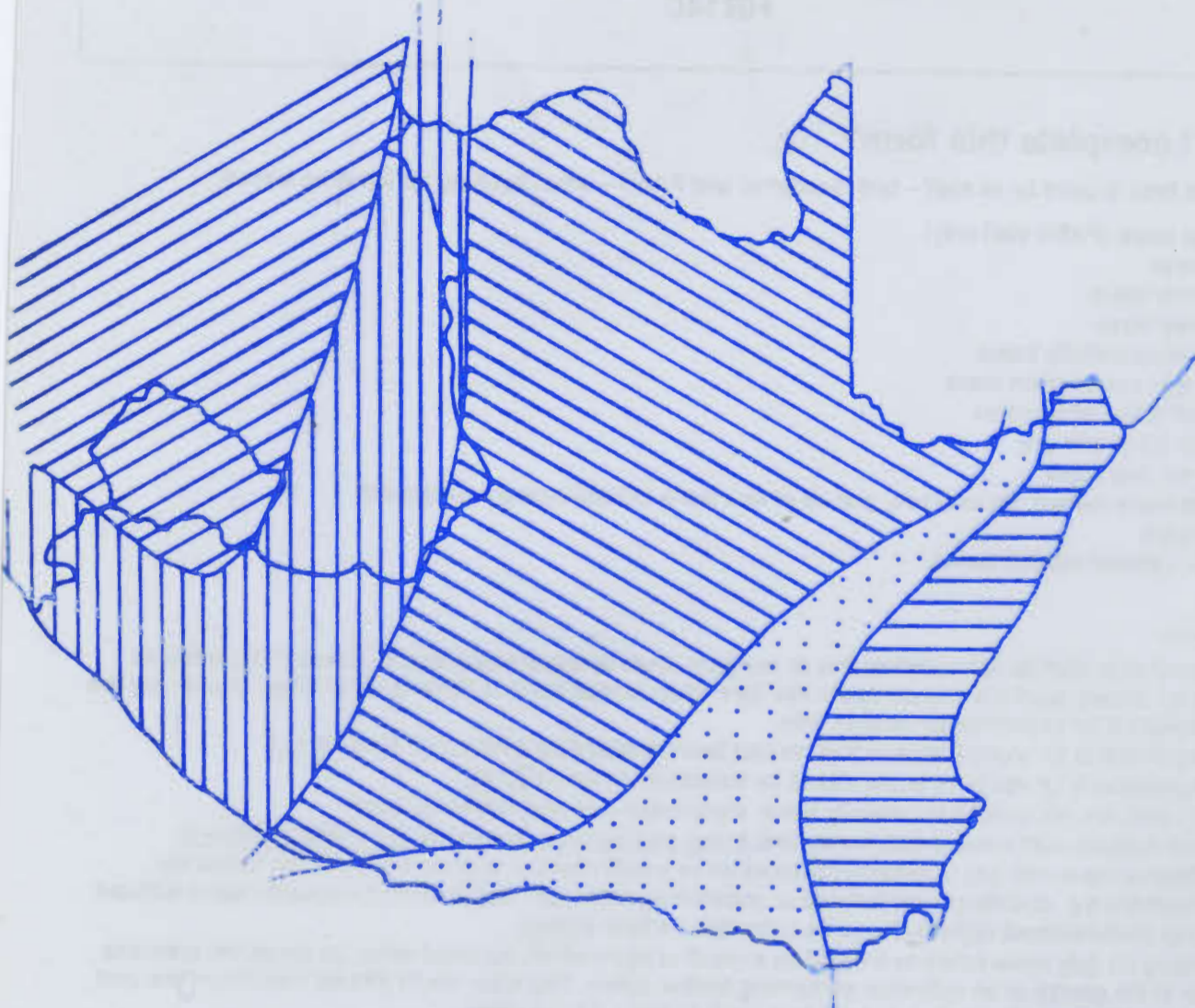


FIGURE 2. Rainfall zones in the rainfall zones (60% of annual rainfall) according to season (after Welting, 1958).



**FIGURE 7.** Altitude. The terrain higher than 500 metres above sea level is cross hatched.

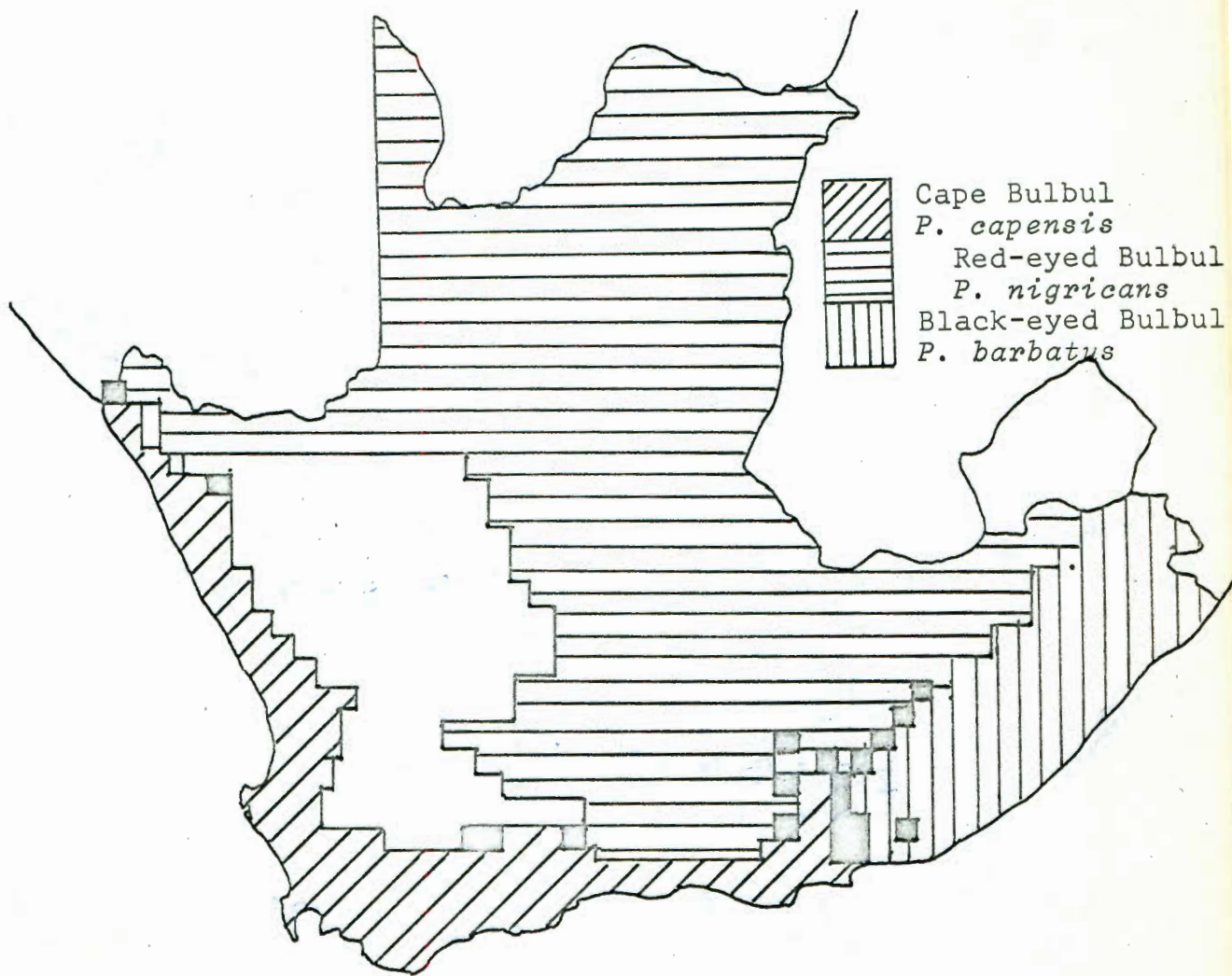


FIGURE 4. The distribution of the three bulbuls in the Cape Province. Mapped on quarter degree squares and where overlapping occurs the square is blacked-in.

show a region that might be covered by the term Cape Triangle. That is the 'winter rainfall' area along with the 'all season rainfall' area from the Orange River mouth around the coast to Port Elizabeth.

A physical feature which has a close similarity to the distribution of the Cape Bulbul is the occurrence of the species below an altitude of 500 metres - Figure 7. The species is more or less limited to the areas below 500 metres except in areas of human habitation and farming above this altitude. Along the coastal regions below 500 metres the bird does not extend north of the Orange River in the west or the Sundays River in the east and beyond both these boundaries the rainfall pattern changes.

Another factor of some interest is the close correlation of distribution with edaphic factors - compare Figure 8. It is clear that the distribution of *P. capensis* does not extend into the areas delimited by the desert soils except along the Sundays River valley system. In point of fact the area of Sundays River valley where the species does extend beyond the desert soils, as illustrated, there is an important difference in the soils that the map does not show. Namely that in the valley referred to, the soils are actually marine cretaceous based and therefore of coastal origin not desert origin.

It is not suggested that the bird's distribution is limited directly by soil. However, it seems likely that the winter rains on these soils probably have an indirect effect upon the vegetation - especially the fruit-bearing plants which provide food for the species.

Previously *Pycnonotus capensis* extended further north east than is the case now. There is a specimen in the American Museum of Natural History labelled from the Woodward collection "Port Natal". Clancey (1964) in "Birds of Natal and Zululand" has rejected the record, probably correctly since the Woodward brothers did not make mention of the species in their book "Birds of Natal" - 1899. There are, however, reliable records of the species occurring as far as Komgha, north of East London. Pym in 1909 recorded the species as not uncommon in King Williamstown and not as common as *Pycnonotus barbatus*. Haagner and Ivy (1907) record *Pycnonotus capensis* as not uncommon in lower Albany while

Hewitt (1931) records its presence in Grahamstown. There are specimens from early times in both towns mentioned. There is an unpublished record by Wood of the species breeding in East London as recently as 1931 (Original field notes supplied by Miss. M. Courtenay Latimer).

#### Distribution of the sibling species

*Pycnonotus capensis* comes into contact with the sibling species Red-eyed Bulbul, *Pycnonotus nigricans*, and Black-eyed Bulbul, *Pycnonotus barbatus*, at several places - See Figure 3. These places of meeting will be discussed in detail below but the most important observation common to all such records is that contact is established where man occurs. In other words, when the natural habitat has been altered and there has been a breakdown in the natural isolating mechanisms. This does not apply to places where *Pycnonotus nigricans* and *P. barbatus* meet. There they appear to occur together in non-breeding foraging flocks in certain undisturbed areas.

#### *Pycnonotus nigricans*

Essentially a bird of the drier regions, this species occurs to the north of *Pycnonotus capensis* in the Karoo and Bushmanland areas. Specimens occur from Oranjemund, Alexander Bay and Grootderm, all at the mouth of the Orange River. Here there are sight records only of *Pycnonotus capensis*. This is an area where normally *Pycnonotus nigricans* would occur but farms and the living quarters of two large mining concerns have created an unusually well-wooded and shrubby oasis for such surroundings. There is a specimen of *Pycnonotus capensis* from Klipfontein, near Steinkopf, and there are many specimens from Springbok. *Pycnonotus nigricans* has been seen at Klipfontein. This locality is on the edge of the escarpment and this may be a case of a natural incidence of the two species meeting. There are no records of specimens or sightings of any bulbul on the Namaqualand plateau.

In the southern and eastern Karoo, the bulbuls meet again. According to Winterbottom (1968b) there are sight records from Laingsburg for both species and there are

specimens for both from Prince Albert. *Pycnonotus capensis* occurs naturally along the southern foothills of the Swartberg range, whilst *Pycnonotus nigricans* occurs naturally along the arid northern slopes of the same mountain range. Both these records are from built up areas and evidently *Pycnonotus capensis* has wandered beyond its normal distribution and found suitable habitat in man-made areas.

In the south-eastern karoooid regions of distribution of *Pycnonotus nigricans* there are several areas where contact has been made, these are all in towns. In Graaff Reinett, Jansenville and Pearston, the two species have been visually recorded and both have been recorded within 20 miles of Steytlerville. Graaff Reinett is undoubtedly beyond the normal range of *Pycnonotus capensis*. It would appear from these records and others in this drier area that *Pycnonotus capensis* extends up the valleys of bigger rivers into areas normally occupied by the *Pycnonotus nigricans*.

In none of the areas of contact has there been any recorded interbreeding or competition between the two species.

#### *Pycnonotus barbatus* - Black-eyed Bulbul

The area of contact between this species and *Pycnonotus capensis* is over a smaller range. The area of contact in the eastern Cape has been well documented since the turn of the century and certain changes have occurred. Apart from the records for *Pycnonotus capensis*, we have specimens of the *Pycnonotus barbatus* from Uitenhage in 1886 and from Port Elizabeth at about the turn of the century.

The present position is that the lower Sundays River forms the barrier between the two species, *Pycnonotus capensis* crossing the river more inland in a few localities. There is a sight record of the *Pycnonotus barbatus* from Potberg, Bredasdorp district, several hundred miles from the species' normal distribution. This can only be considered an isolated abnormal incidence.

Though Figure 3 indicates several areas of overlap between *Pycnonotus capensis* and *Pycnonotus barbatus* there is no area where both occur together. The mapping is based upon a quarter degree grid and consequently where the two species

may be found near each other they are mapped as being together. At Colchester, a mere eight miles separated the species and about 15 miles separated records near the Zuurberg and Addo National Park.

Zones of overlap of *Pycnonotus nigricans* and *Pycnonotus barbatus*

Of some interest to the discussion is the natural incidence of *Pycnonotus nigricans* and *Pycnonotus barbatus* occurring together in some areas. The writer has studied mixed flocks feeding along riverine forest on the Limpopo River in the north-eastern Transvaal and at Maun on the edge of the Okavango Swamps. Both localities are on the edge of the normal distribution of the two species. The habitat was more typically that of *Pycnonotus barbatus* and in one flock of 20 birds only 4 were *Pycnonotus nigricans* and at least one of these was a youngish bird.

There has been the suggested incidence of interbreeding of *Pycnonotus nigricans* and *Pycnonotus barbatus* at Nata, Botswana, though this was not proven. This area has been heavily affected by human habitation and alteration of the natural landscape has occurred. If interbreeding did occur here it is possible because of this breakdown of natural isolating mechanisms.

The opportunity was provided of briefly studying the hybridisation of these two species at Bedford, C.P. Here a male *Pycnonotus nigricans* and a hybrid *Pycnonotus barbatus/nigricans* (with a larger, but brown, wattle than is normal for the species *Pycnonotus barbatus*) produced young successfully. The habitat had changed over the years with the encroachment of *Acacia karoo* as a dominant indicator of progressively drier conditions. This factor coupled with a prolonged drought brought *Pycnonotus nigricans* in as a common species where as previously *Pycnonotus barbatus* had occasionally occurred. Evidently a breakdown in isolating breeding mechanisms had taken place in the progress of the change.

Further reports of interbreeding are recorded from the well populated areas of the southern Transvaal (Markus 1963a). In some areas of dense human habitation it would appear that the interbreeding has been taking place for a decade or

more - probably due to the breakdown of natural isolating mechanisms in this case evidently the habitat.

### Habitat and Distribution

*Pycnonotus capensis* occurs predominantly in scrub (as defined by Yapp 1955). It is a bird that likes horizontal branches with a certain amount of shade from an outer leafy canopy. Generally speaking, succulent or spiny growth is avoided though the thorn tree *Acacia karoo* is used frequently. Yapp (1962) states - "If two species are derived from a common ancestor, their divergence in habits, as in structure, will be gradual, and the more recent that divergence and the greater their similarity in structure, the greater will be their similarity in feeding and other habits". By and large the three species of bulbul occur in similar situations and they are predominantly fruit eaters. Because of their close relationship (the three bulbul species) and as Yapp states the greater their similarity in feeding and other habits, no attempt was made to determine the morphology of the three different bulbuls' habitat. Emlin (1956) and MacArthur (MacArthur et al 1962) describe methods of measuring the habitat. Because the habitat did not appear of paramount importance to distribution this matter was not pursued. The reason that habitat did not appear so important was because the study area was in effect a southern extension of the warmer coastal forest and scrub, and if habitat was important *P. barbatus* should have extended at least to Port Elizabeth. While it should also be pointed out that many habitat features of the Cape Bulbul's distribution do extend further northwards than does the bird itself.

The present-day distribution of the three species of bulbul in the eastern Cape is shown in Figure 9. Lines of separation are drawn in to indicate more clearly the areas occupied by each species. Comparing these distributions with:-

- a) Vegetation: Shows no real correlation with the map of vegetation as indicated by Acocks Figure 10. There are fundamental shortcomings in detail of Acocks' map for this region which directly concerns the Cape Bulbul. There is no indication in the map of the extent of

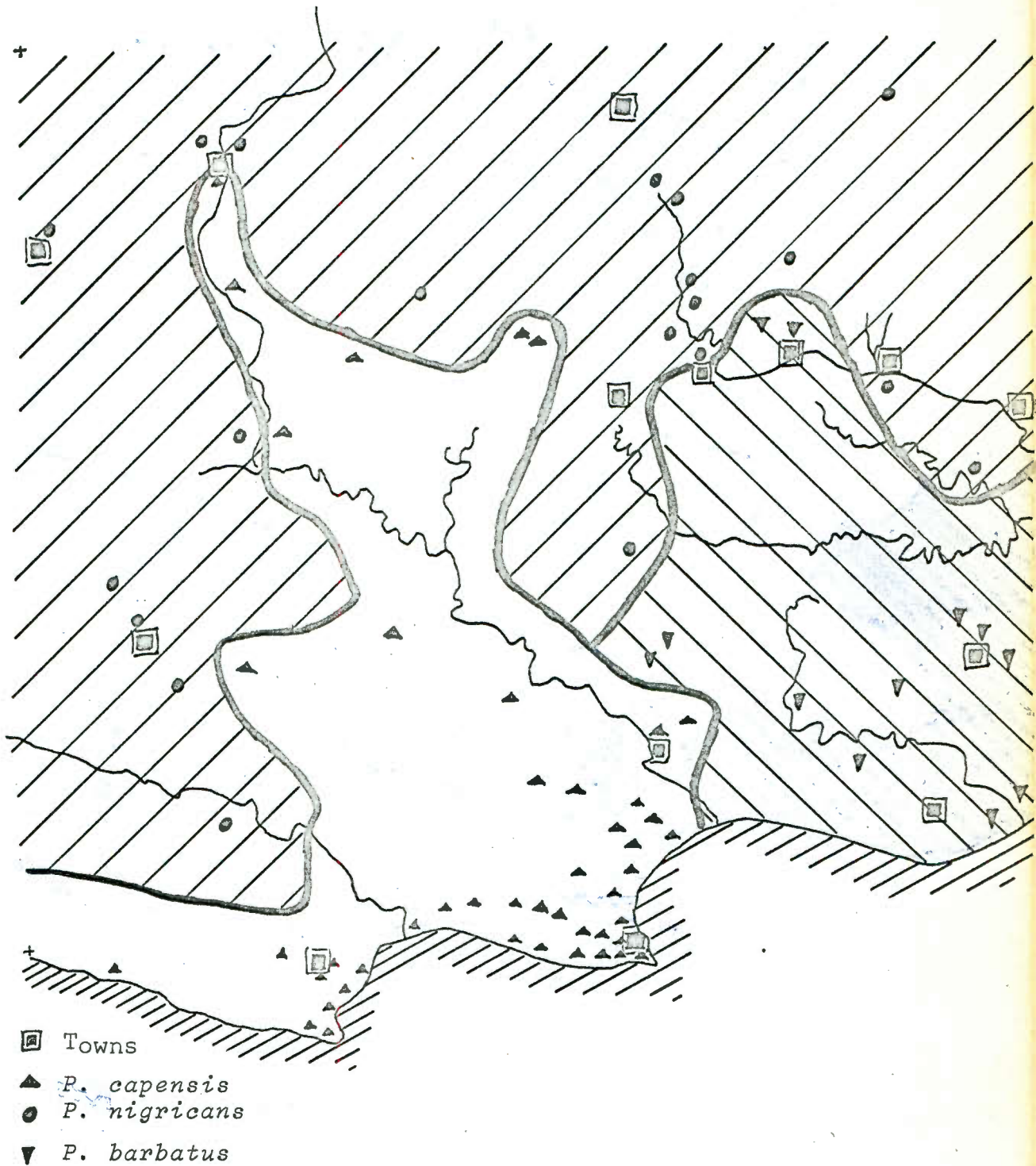


FIGURE 9. Distribution. Details of records of the three species of *Pycnonotus* occurring in the Eastern Cape.

intrusion of the dominant exotic *Acacia cyclops* which has a major effect upon the presence of the *Pycnonotus capensis*, in an area which would otherwise not support the species in such numbers as occur - (See section - Food).

The Wattle *Acacia cyclops* occurs commonly along the coastal region around Cape Recife and within Algoa Bay as far as Sundays River mouth. This is marked in Figure 10. Beyond this, only a few solitary individuals of the bush occur until Bushmans River, where a small patch of an acre or so exists. There is little doubt that the coastal distribution of the Cape Bulbul is influenced by the presence or absence of this food plant. The area where wattle occurs is mostly along the coastal heath and bush area which provides other suitable food for the species as well.

The valley of the Sundays River's mouth is dominated by 'Sundays River scrub' which is specially mentioned by Acocks (1953) from the 'wide flat lower Sundays River valley'. The vegetation is dryer and harsher than that normally inhabited by bulbuls. In the figures given by Acocks (1953 p.82-83) for one morgen (0.86 hectares) there were 307 species of plants totalling 87,395 individual plants. Of those species listed only two were known to be utilised for food by the Cape Bulbul. There were 882 individual food plants which provided the required food for the bird.

This indicates clearly that there is little food available for Cape Bulbul in the lower Sundays River valley. This is confirmed by the relative absence of the species in the natural vegetation of the area. Indeed the Cape Bulbul only occurs where wattle occurs or in association with human dwellings. Even here the intensive irrigation farming of Sundays River from Kirkwood to Addo does not attract the species as a resident. There are records from Addo and from Addo National Park but these are considered to be wandering birds since repeated visits (29 in 28 months) to the areas mentioned did not reveal further records (Liversidge 1965).

The occurrence of *Pycnonotus capensis* up the higher

reaches of the Sundays River is also within similar vegetation types. It is assumed that riverine bush and the increased human population along the river and its tributaries, provides a corridor of occupation beyond the normal range.

The distribution of the other two species is equally unrelated in detail to the vegetation types of Acocks (1953). There is one notable exception and that is the occurrence of *Pycnonotus nigriceps* in a relatively isolated area (as indicated on the map) where a patch of drier karoooid vegetation (No. 38 of Acocks False Central Lower Karoo) occurs as an island within less favourable vegetation to that species. There is also no vegetational correlation with the distribution of *Pycnonotus barbatus*.

- b) Altitude: Except for records from two localities, the Cape Bulbul occurs below the 500 metre contour (Figure 11). These exceptions at Bruintjies Hoogte and the farm Ebenezer to the south are puzzling as the vegetation is unfavourable too (see below).

It must be noted that the birds do not extend at low levels up the coast beyond the Sundays River.

- c) Rainfall: Detail of the rainfall from 189 stations recorded by the Weather Bureau (Publication 19; 1954 - Rainfall statistics) are illustrated in Figure 12. From this map, it can be seen that *Pycnonotus capensis* occurs primarily in winter rainfall areas or where the rain is evenly spread throughout the year.

The bird can occur in areas of summer or summer and autumn rainfall. The records for Bruintjies Hoogte is in an area of comparatively high rainfall compared to the rainfall of the low-lying surrounding it to the south. This could possibly explain the species presence also as rainfall influences some specific species of plant which attract the species.

### Conclusion

The distribution of *Pycnonotus capensis* is confined to the Cape Triangle. The drier regions with sparser vegetation on desert soils form a barrier to the north and west - this

last habitat being occupied by *Pycnonotus nigricans*. In the east the species extends as far as the summer rainfall area, beyond which *Pycnonotus barbatus* normally occurs.

Changes that have occurred since historic times are possibly due to the so-called encroaching karoo and desert conditions discussed by Acocks. The Cape Bulbul has been forced back from its earlier occurrence at East London to the present area of Port Elizabeth. This has co-incided with increased human occupation and the encroachment of *Acacia karoo* in the Border and Eastern Province areas. The unusually abundant numbers near Port Elizabeth are attributed to the birds' adaptation to the alien vegetation - *Acacia cyclops* in particular.

This bulbul is evidently a bird with a preference for moist conditions and its extension beyond what might be termed its normal habitat is confined either to riverine areas, higher rainfall areas or human habitations.

## 5. VARIATION IN POPULATION

## VARIATION IN POPULATION

In dealing with the population of a single species, one tries to determine the numbers present and factors influencing changes in these numbers in time and space. For practical reasons the field work was restricted to a local area and the method of determining the population was governed by local problems. These are discussed first and then the factors regulating the population are discussed.

### SIZE OF STUDY AREA

The size of sample block required to determine a species' total population will depend upon the area required by each species and the habitat required. Kendeigh (1944) specifies that sample areas should be large enough to include all the activities of the species involved except possibly the larger predators. This is not sufficient on its own since it must also be qualified by a minimum number of individuals to make due allowance for individual variations in territory. A qualification in the case of the Cape Bulbul covered by Kendeigh's definition is the need to cover the feeding range of the species which extends beyond the normal breeding area. This becomes serious when due consideration of the practical aspects of covering the area are borne in mind. Thus a bulbul may fly half a kilometre for food for its young or to feed itself. If one presumes such a flight may be taken in any direction from the nest, nearly a square kilometre is included in the area occupied by each breeding pair. Any study of the breeding population should cover at least several pairs.

The figure of 100 acres (40 hectares) is according to Campbell (1953) the accepted area and most desirable for such a study. Such a figure presupposes one is able to cover such an area. From the sheer mechanics of being able to move about in the coastal shrub such an area was impossible to cover in the study area. In fact, with coverage of only 20 hectares, with virtually unlimited time available, four broods in the four years of study were reared in undiscovered nests out of 29 broods in all; in other words, there was already a 14% error in attempting only half the area recommended.

Campbell loc.cit. does emphasize that 100 acres is desirable but whatever unit is chosen it must be neither so small as to be overweighted by freak factors or so large as to be beyond the compass of a single worker.

There is another important influencing factor in regard to size of study area and this concerns the habitat. It is desirable to cover one plant community type and if possible, to avoid habitat edge. The area of study is only a minute fraction of the whole surroundings of coastal dune vegetation which covers several square kilometres. Thus habitat edge which may alter population density, is limited to the actual seashore on the one side and golf course boundary on the other. The effect of the golf course as a boundary is rather to draw species typical of rank grass and open areas into the area. The habitat for the Cape Bulbul is however not affected.

The vegetation varied in height from a few centimetres to six metres in height and the topography was traversed with 10 metre high dunes. So the visibility was limited for the most part to under 100 metres. Hence for practical reasons it was not possible for one person to cover adequately the desired 40 hectares. The study area was divided by a road and further subdivisions were provided by a series of numbered telephone poles at 15.2 metres intervals along the length of the road. It was practical to work through the bush and record on a grid system the whereabouts of all birds observed.

In this way a study area of 20 hectares or 50 acres was intensively studied and kept under observation. It is of some interest to compare the fact that Kendeigh & Baldwin (1937) in their study of the yearly abundance of *Troglodytes aedon* covered approximately 15 acres which had an average number of adults 19.7; both figures being less in area and numbers than in this study.

#### THE METHOD OF DETERMINING THE BULBUL POPULATION

The problem of calculating bird population densities has been adequately covered for the northern hemisphere cool temperate conditions by a number of writers. A recent and comprehensive work, a methodological study by A. Enemar (1959)

gives a final unexpected comment (p.100) "the present investigation has been to show, . . . , the unavoidable error which is made in every single passerine bird survey". Workers from northern temperate regions base virtually all population studies on the recording of the song of the male bird. This has two serious drawbacks under African conditions. Firstly, it presupposes territory is universal and rigid in birds; a factor which, as will be shown, does not have the biological significance in the Cape Bulbul that it is supposed to have in European passerines. Secondly, it does not allow for mimicry in bird song. This last item is discussed by Yapp (1962) who points out the possibility of confusion even in British birds. Included in the song of the resident Bully Seedeater (*Crithagra sulphurata*) is the typical communication note "tiet-my-jol" of the bulbul and very often at a distance this is all that is heard. Such a mimic utters a medley of softer notes and comes out clearly with a particular favourite phrase. The "piet-my-jol" is locally common in the song of the Bully Seedeater and it caused confusion in the initial stages of the field work before consideration of mimicry was taken into account. Heard at a distance one was never sure what species was calling.

The determination of the population density of *Pycnonotus capensis* in the study area was not possible through the conventional count of the number of singing males. The song perches of males could certainly be established. However, it was found that visiting bulbuls to the area frequently used the same prominent perch from which to call. Until the individual birds were known by their song, the standard method of determining numbers of singing males was not considered reliable and was therefore discarded. Mimicry also contributed to confusion. The area was worked through repeatedly and careful notes were taken of all birds present and where seen and of any nesting activities. The figures of the population are based upon pairs of bulbuls and their nesting attempts - therefore a breeding population.

The problem of non-breeding individuals in the area is not overlooked. With the social feeding behaviour of the species, it was not possible to establish quantitatively the presence of such a group of birds. They were known to exist

because of the presence of one albinistic bird, unattached, during its first year of visits. This was the only recognisable vagrant in the area. However, no solitary males established territories or occupied even a regular song perch in the study area. The social feeding habits of the species make it easy for a group of unattached males and females to exist without interfering with the territoriality of the resident pairs. I would agree with Mrs. Rowan (1966) that because Lack observed no landless Robins this does not mean that they do not exist. The mere fact that lost adult birds may be replaced during the breeding season indicates that there is a supply of unattached birds available somewhere. Unfortunately it was not possible to determine how many were in the general area for reasons given above.

#### POPULATION DENSITY OF BREEDING PAIRS

The 1958 breeding season was used to learn about the area and become familiar with the species. It is possible that some nests were missed, but because it was at the end of a drought period there were probably fewer pairs than normal. Only nine breeding pairs were recorded, giving 2.2 hectares per bird. It should be noted that in 1958 nesting took place primarily in two areas of the 20 hectares, probably representing less than half the area. Because in 1958 there was no success in breeding (the observer was watched by Vervet Monkeys which learned to associate regular visits to an area with the presence of nests) this year (1958) has not been included in most of the tables of analysis. But for the purpose of population of breeding birds, the figures given above are acceptable.

The figures of known breeding pairs which occurred within the study area are given in Table 1. This does not include birds which collected nesting material or food within the area and took this to sites beyond the boundaries. Only birds which attempted to build nests within the area were included.

TABLE 1. Number of recorded breeding Cape Bulbuls in 20 hectares for each year.

	<u>1958</u>	<u>1959</u>	<u>1960</u>	<u>1961</u>	<u>1962</u>
No. of pairs	9	13	19	13	15
Average area occupied (hectares)	2.22	1.54	2.05	1.54	1.33

The density of *Pycnonotus capensis* in the area is low compared with similar-sized passerines from holarctic temperate regions as given by Welty (1964). The only figure available for frugivorous birds' territory is that given by Snow (1962) for *Manacus manacus* in Trinidad where 500 adult birds occurred in 450 acres in a population which was considered to be considerably higher than the species range on its continental range. Little information is available on territorial size in passerines in southern Africa. Comparing the density of breeding species within the 20 hectares studied (Table 2) - 30 species were recorded breeding and none was as numerous as *Pycnonotus capensis*. The next commonest breeding bird was *Prinia maculosa* with 12 pairs nesting each year. The other bulbul *Andropadus importunis* had six, three and five pairs breeding in the same area. Another frugivorous breeding species *Colius indicus* numbered two, four and six breeding pairs in the same 20 hectares.

The variation in the Cape Bulbul's breeding population varied substantially between years. The average population was 13.8 pairs for 20 hectare with standard deviation of 3.25 (n=5). This gives an average territory per pair Cape Bulbuls of 1.64 hectares with standard deviation of .3 hectare for the study area.

It is difficult to discuss the significance of territory size required by each pair of Cape Bulbuls. This is simply because there is considerable variation in size of territory occupied by passerines - thus the Song Thrush *Turdus ericetorum* varies from 1.5 to 6 hectares or the Marsh Tit *Parus palustris* from 0.4 to 6.5 hectares. There are no other records of the Bulbul's territory requirement. This subject

TABLE 2. Number of breeding pairs of each species recorded in the 20 hectares study area. The terrestrial birds have been omitted from this table.

<u>Species</u>	Number of breeding pairs for the years		
	<u>1960</u>	<u>1961</u>	<u>1962</u>
<i>Streptopelia capicola</i>	2	1	3
<i>Clamator jacobinus</i>	2	2	1
<i>Colius striatus</i>	2	4	6
<i>Pycnonotus capensis</i>	19	13	15
<i>Andropadus importunis</i>	6	3	5
<i>Turdus olivaceus</i>	0	0	4
<i>Cossypha caffra</i>	6	5	12
<i>Erythropygia coryphaeus</i>	1	2	2
<i>Sphenoeacus afer</i>	2	2	2
<i>Sylvietta rufescens</i>	1	1	0
<i>Apalis thoracica</i>	6	9	9
<i>Cisticola fulvicapilla</i>	0	1	1
<i>Prinia maculosa</i>	12	12	12
<i>Sigelus silens</i>	0	1	2
<i>Motacilla capensis</i>	5	7	8
<i>Lanius collaris</i>	1	1	1
<i>Lanius ferrugineus</i>	1	2	2
<i>Tchagra tchagra</i>	1	4	4
<i>Telephorus zeylonus</i>	0	2	2
<i>Zosterops pallidus</i>	0	1	3
<i>Passer melanurus</i>	0	0	1
<i>Hyphanturgus ocularius</i>	2	2	1
<i>Coliuspasser capensis</i>	0	0	3
<i>Serinus suphurata</i>	3	4	5
<i>Serinus flaviventris</i>	0	1	2
<i>Poliospiza gularis</i>	2	5	3
TOTAL	<u>74</u>	<u>85</u>	<u>109</u>

is dealt with later under Breeding Requirements. It is important to note that the species is the most abundant breeding species in the study area.

#### DENSITY OF NON-BREEDING POPULATIONS

Whilst annual variation has been shown in the breeding population, the picture is not so clear as to what happens out of the breeding season. Of a number of birds with coloured rings, one pair at least remained resident throughout the year whilst in two other pairs, the birds disappeared for six months after breeding. One of these last two was recorded during such an absence, 1.5 kilometres from the breeding area in a flock of some 30 loosely associated birds feeding in one patch of vegetation. In the non-breeding season, flocks of from ten to forty have been recorded gathered to feed on ripe berries. Normally winter parties of from five to nine birds fly about in search of food and such parties were often recorded in the study area. These flocks usually moved at speed and characteristically are noisy on such social occasions.

Bulbuls in pairs or singly, occurred in the area all the year round but whilst in the winter about a third to a half the breeding population might be present one day, not a single bird could be traced the next day. Foraging parties up to 4 kilometres from the study area were regularly checked but only the one ringed pair was seen. It was established that winter roosting could occur near the food source and this would explain why the birds did not always return to the breeding area to roost in the non-breeding period. One of the ringed pairs feeding 1.5 kilometres from its breeding area roosted near the food in company with the other birds that roosted near the food supply.

Only on 3 occasions in February, April and June were no bulbuls at all seen in the study area. The week after the February observation, birds had returned and started nest building.

For lack of further records, it is assumed that the non-breeding birds remain locally in the area. They are based at their breeding grounds but become partially social

when a crop of berries ripens and join in wherever the feeding is to be had, and also roost where the food supply is.

The presence of non-breeding individuals in the study area during the non-breeding season was evident and revealed usually by their more vociferous behaviour. A semi-albinistic bird was recorded in two non-breeding periods although during the second period it did appear to have a companion and was much quieter. Appearing first in late March, it was seen at irregular intervals through the winter. It seemed always to be chased by apparently resident birds. This bird was only seen twice during the breeding season when its presence caused no excitement though it did attempt to solicit one resident bird. The next time this bird appeared was in March a year later, when it was accompanied by a second bird. It is nevertheless interesting that the bird was seen two successive post-breeding periods in the same area. A similarly marked bird was seen 2 kilometres away in summer, and a year later another similarly marked bird was seen five kilometres away. Since these are the only albinistic birds I have seen, it seems likely that they might have been the same bird. If they were the same bird, it would indicate that the individual birds have the same non-breeding foraging routine returning to the same areas for at least a year.

#### REGULATION OF POPULATION

The theory of regulation of animal populations is going through a highly stimulating period of discussion, as shown by the number of books recently published on bird populations alone. In England there are two schools of thought. One led by Lack stresses that the balance is wrought at the level of the individual whereas Wynne-Edwards says that the problem is of group selection. The overall picture is certainly one of a balanced population which shows reproduction rate equal to mortality rate. This is not a simple equation as Wynne-Edwards illustrates.

Replacement = Loss

Reproduction + immigration = Loss from within  
& emigration

There is in fact a constant change in all four units and these changes vary from year to year in a given habitat and amongst resident species from season to season.

Wynne-Edwards (1966) unfortunately introduces a fifth variable "Social mortality" which includes stress diseases, cannibalism, etc. In the opinion of the writer, this is no more than another form of "loss from within" and its separation by Wynne-Edwards is unnecessary and confusing.

Viewing this equation by Wynne-Edwards, one must consider each item separately within the problem at hand - namely changes in populations that take place. It is first of all erroneous or perhaps abnormal to consider a population as a fixed thing - it is a dynamic concept and as has been stated it varies from month to month as well as from year to year. So that replacement equals loss is not a fixed figure.

First those factors likely to reduce the population -

#### MORTALITY

Adult mortality may be calculated from a knowledge gained from ringed birds and there are available complex formulae based on ringing recoveries of nestlings or adults. The adult mortality rate may be calculated from a small sample of colour banded adult breeding birds in the area of study and the subsequent history of these birds, provided that the observations extend beyond twelve months.

In the study area an attempt to ring all adult Cape Bulbuls was unsuccessful.

In all 19 adults were ringed and the highest population was 19 pairs so this represents at very best only 50% coverage. Only 18 birds are taken into consideration because it is necessary to have a record or potential record of more than twelve months so that the single bird ringed the last year of study is ignored. The albinistic bird was assumed to be the same individual and another bird with a light yellow spot on chest was recorded two seasons breeding in exactly the same locality each year so this is taken as the same individual, bringing known individuals up to 20.

Thus 5 out of 20 known records succumbed within one year, which gives a 25% annual adult mortality. In view of the fact that this can be considered a low annual mortality (see below)

one might be induced to reconsider the inclusion of the two naturally identifiable specimens in view of the fact that several birds which were naturally identifiable for short periods were not included. However this would give a loss of five in 18 and this is only 28% per annum.

TABLE 3. The number of individually ringed birds and their history in relation to subsequent breeding seasons

Consecutive breeding seasons (years) seen	No. of individual Bulbuls from each period
3+	3
2+	6 + 2 (unringed)
1+	4
-1	5

The annual mortality for an adult song bird as given by Lack is between 40 and 60%. Thus 28% for the Cape Bulbul can be considered as low. With 8 adult ringed Orange-breasted Sunbirds, Broekhuysen (1963) found a similarly low mortality rate of 35%.

There are thirteen recorded individuals more than one year after ringing as an adult. Using formula  $\frac{2-m}{2m}$  where  $m = \%$  annual mortality (Lack 1954) for the average expectancy of further life, we get for the adult Cape Bulbul 3.07 years. The assumption made to reach this figure is that the seven birds not subsequently seen after one year, represents mortality and not a movement away from the area. Since several breeding birds from immediately outside the study area were known and none had rings it can reasonably be concluded that none, or very few of these 7 birds settled anywhere nearby. From Lack's (1966) comments "if figures for a small population can be trusted" it would appear that there is reason to doubt the formula for small populations. The figure obtained for the Cape Bulbul is nearly twice the life expectancy for the average passerine as given by Lack loc.cit. but it is considerably less than the figure for the Manakin

in Trinidad as derived from Snow's (1962) figures.

#### COMPETITION

It is sometimes believed that competition for food influences size of territory and indeed there are some very clear observations which prove this. Wynne-Edwards (1962) in discussing this point quotes the case of pomarine jaegers *Stercorarius pomarnus*, where 4 pairs per square mile bred with moderate food supply and 18 pairs per square mile with a high food supply in different years. This was in Alaska and should give emphasis to Altum's statement (Wynne-Edwards loc.cit. p.147) "All the species of birds which have specialised diet .... need a territory of a definite size, which varies according to the productivity of any given locality". Thus in areas where competition is more vigorous, such as is common in cool temperate conditions, competition for a limited supply of food plays an important part. As Wynne-Edwards points out, this aspect of territory has overshadowed other aspects. As will be shown (under Reproduction requirements and Food) territory and competition for food does not exist as a limiting factor in populations of the Cape Bulbul.

In the section dealing with "food", it is shown that there is more food for the population of Cape Bulbuls in the study area than is required. Interspecific competition does not, therefore, concern the present problem. Furthermore, it is shown that there are no other fruit eating birds or animals that offer intraspecific competition worthy of the concept (see later). Competition for nest sites does not exist.

#### PREDATORS AND DISEASE

This subject is discussed at length in a section of its own. Suffice it to repeat here that no predators on adult birds or diseases would appear to seriously affect the population. Nest predation, however, is considerable and seriously affects the reproductive rate and is largely responsible for the low fledgling figure.

## EMIGRATION

As will be seen from Table 4 below, there are increases and decreases in breeding population which can only be explained by inward and outward movements by adult birds. Table 5 shows that in the year 1961 there was a total loss to the area of 18 birds (six grown young of the year before and 12 breeding birds) and 26 birds remained - this represents 69% of the population. There is no obvious reason for this phenomenal loss in the area of study. It would appear more likely that good conditions elsewhere must have attracted the birds away from the study area since there was no special or noticeable change that would account locally for this reduction in number.

## REPRODUCTION

Under normal circumstances, animal numbers are recruited by reproduction. Table 4 represents the figures available and the average fledgling rate of 27% is appreciably lower than the 45% average for nidicolous breeders (Lack loc.cit.).

TABLE 4. Breeding success of Cape Bulbul in study area

Year	No. of pairs	No. of eggs laid	No. of fledglings	% fledged
1959	13	53	15	28%
1960	19	93	32	34%
1961	13	29	4	14%
1962	15	58	12	21%
		233	63	27%

If the data in Table 4 is plotted out in relation to the numbers of breeding adult birds - Table 5 - it can be seen quite plainly that reproduction output within the study area shows no correlation with the breeding population.

Table 5 shows that theoretically three locally reared adult surviving birds were produced for 1960 whereas 12 appeared. In 1960 six adults were theoretically produced for

1961 when in fact the local population was reduced by 12. This same year only one young theoretically reached adulthood for 1962 whereas four more adults bred in the area. This shows that there was no correlation between rate of reproduction and density of subsequent breeding populations in the Cape Bulbuls in the area studied.

Discussion on the methods of calculating breeding success described by Mayfield (1961) will be discussed later.

TABLE 5. Breeding population changes from year to year compared with the number of young fledged the previous year and theoretical survival to the following year.

Year	No. of breeding birds	Young fledged	Theoretical survival - young to adult (80% 1st year mortality)	Change from previous year
1959	26	15	3 $+26-29$	
1960	38	32	6 $+38-40$	+12
1961	26	4	1 $+26-27$	-12
1962	30	12	2 $+30-32$	+ 4

#### IMMIGRATION

From Table 5 it is apparent that at least in some years immigration occurred. In 1960 six birds came in from outside showing an increase of 24% due to immigration. In 1962 there was a 10% increase of population due to immigration. There are no obvious reasons for this immigration.

#### DISCUSSION

In discussing population dynamics of the present species it is clear that the study area of 20 hectares is inadequate to provide the full story. However, there is sufficient information to indicate the factors controlling bird population in the study area.

According to what has been said above in regard to competition it is apparent that the predominantly frugivorous

Cape Bulbul cannot be considered to be a specialised feeder. Indeed the wide selection of different berries is evidence enough to support this theme.

It is also evident that reproduction has no direct bearing on the local population for a limited area. Over a wider area (and how much wider is unknown) reproduction is obviously the source of increased numbers or replacement numbers. We are dealing here with a species almost on the limits of its distribution. To quote Wynne-Edwards (loc.cit. p.11) "Towards the fringe of its range, the existence and population density of any particular species of animal is often overwhelmingly dictated by the physical conditions of the environment .... and by such biotic factors as the presence of better adapted competitors or absence of requisite vegetational cover...." He goes on further to suggest that the fringe distribution is not in fact normal. Whilst this might apply to many species, the case is surely different for allopatric sibling species. The density of bulbuls at Receife is considered quite normal for coastal regions and the habitat is basically similar towards the west. Within Algoa Bay, the vegetation and, within limits, the climate differs and it is in the 32 kilometres from Port Elizabeth itself to Sundays River that the population differs, diminishes and disappears, - to be superseded to the east of Sundays River by Black-eyed Bulbul.

It is evident that the Receife area population increases in good times greater than the reproduction potential allows; thus other areas supply the excess - in this instance this can only come from the west. There is also an assumption made that on the fringe of distribution, there is a greater need for replacement. Presumably because it is the fringe of distribution that there is some factor which plays a role in preventing an increase in local population which would give rise to an expansion of distribution. There is in fact no reason to believe that mortality rate need be higher than usual in such areas. The fact that physical conditions or better adapted competitors are present does not mean greater danger for the bird - unless it is weakened physically by such things. The population density of bulbuls of both sibling species is lower in the Sundays River valley area than on either side of the valley. Some idea of the low density is

obtained by comparing the fact that no birds were recorded in two and a half hours walk in the valley whilst ten minutes walking in the study area was usually sufficient time to obtain a sighting in fairly unfavourable conditions. As shown in the previous chapter, the absence of suitable naturally occurring fruit bearing plants keeps the numbers reduced in the wide lower Sundays River valley. Whatever the cause, we must presume the population is fairly static albeit lower than normal. Such a low density would obviously be little drain on neighbouring populations in times of need. When a fairly dense population can increase 46% over a previous year's breeding population at Receife quite obviously a change in a poorly populated area can also be managed. The population in the Sundays River valley seems less than one tenth of normal.

It is suggested that though the study area is near the limits of the species' distribution, there is no reason that this may be a mitigating factor in reducing the local population.

Density-dependent factors which may influence the population are not apparent at this stage of limited knowledge. It was thought at one stage that the Jacobin Cuckoo which parasitises the species might have had some influence since the Cuckoo population itself fluctuated. This is discussed in detail later but since 20 hectares only covers a small portion of the cuckoo's area of operation, nothing can be proven.

The two schools of thought on control of bird numbers (Lack and Wynne-Edwards) are so biased towards European conditions, where competition, especially for food, is paramount in influencing numbers, that not enough attention has been given to the broader issues or indeed to any other alternatives. Where density independent factors influence populations much of the detail of the arguments (clutch size, social dispersal, etc.) is not relevant. It is shown here that food supply is not a major factor nor is social behaviour especially as territoriality in these frugivorous birds is not pronounced.

Elton (1927) states that the chief cause of fluctuations in animal numbers is instability of the environment. This

statement is most important and relevant to African conditions and especially so to southern Africa. In a 35 year period no region south of the Limpopo River escaped drought conditions and in 38% of the Republic, one year in three is drought stricken (Wellington 1955). Drought is considered as a period defective in rainfall when natural vegetation suffers and usually successful farming practices become impossible. When one considers that most of our natural vegetation is xerophytic, the severity of the changes can be appreciated.

Bearing in mind the instability of the conditions one can expect fluctuations in animal numbers. In the eastern Cape, however, coastal conditions are the most equitable in the Republic and rainfall is fairly evenly and well distributed on the average throughout the year. The standard deviation of annual rainfall as a percentage of the average annual rainfall is below 20%. During the years 1958 to 1962 the annual rainfall was 539, 691, 621, 610 and 537 mm. Despite this apparently stable situation there is strong evidence that the major cause of increases or decreases in the studied Cape Bulbul populations was climatic, primarily rainfall. This was simply because rainfall had such an influence on local conditions that birds were attracted to wherever rainfall had created favourable conditions. It is well known how local the rainfall can be. The best example is provided by Port Elizabeth itself that suffered a 330 mm cloudburst in 24 hours while in areas not 8 kilometres away less than 50 mm of rain fell. This is perhaps an abnormal exaggeration of what happens but it is quite common for 25 or 50 mm to fall in one area whilst a few kilometres away no rain will fall. Thus insect life as well as plant life will improve appreciably in an area and draw many different species of birds and animals.

The changes that have been given for the breeding population of the Cape Bulbul are primarily due to immigration and emigration and the opinion is expressed here that these changes are not dependent upon the density of the breeding population. If this is acceptable then it is reasonable to use the phrase 'density-independence' for the changes that have occurred. However, neither Lack nor Wynne-Edwards define density-independence. Andrewartha & Birch (1954) not

only define the phrase but go so far as to state that density-independent factors do not exist. This is because a factor such as climate will influence mortality of a population according to the size of the population but this is a fallacious argument, for the reason that while mortality due to climate may be proportional to the size of the population, it is an external factor that influences the mortality and not one generated by the population itself. Indeed even the definition given by Mayr (1963) is not satisfactory for he states "Any factor, the effect of which becomes more severe as the density of the population increases is called a density-dependent factor". It would be more satisfactory if the qualifying phrase was altered thus 'Any factor generated within the breeding population itself ...'. Whether this is adequate is not certain for Kluver (1966) in his final summary regards emigration as density-dependent but this is because emigration occurs to reduce a large population not as is the present case where emigration occurs to occupy more favourable local conditions. The one is being forced out by internal factors the other is being drawn out by external factors.

Further comment will be made under section 12 'Discussion'. Nesting success in birds has been the subject of mathematical calculations based on a few observations by Mayfield (1961). These formulae are used to predict likely breeding success from little or fragments of information. It is felt with information available in the present study there is sufficient data not to require the estimate of probability. All nests were regularly visited and thus there is no point in applying a formulae which is intended for application to incomplete data. The information obtained in this study concerns observed facts and any bias in their collection is not likely to be greater than bias introduced by certain assumptions to predict what probably will happen. It therefore seems unnecessary to apply a theoretical prediction to adequate facts already obtained.

## 6. SEASONAL RHYTHMS

## SEASONAL RHYTHMS

The birds' year involves a number of regular events such as breeding and moulting. These changes may be regulated by internal physiological rhythms or by external factors. Some of these changes require considerable energy expenditure. Some involve behavioural changes which are controlled by internal and external stimuli. In this section the various changes will be presented separately with discussion and at the end the inter-relationship of the various changes will be indicated.

Whilst much of the matters to be discussed may be subject to experimental investigation, it has been clearly indicated by Marshall (1961b) that what can happen in an experiment does not necessarily happen in nature. It is therefore necessary to establish the natural course of events before interpreting results.

### MOULT

The sequence and timing of moult was established mainly from the information derived from 98 specimens collected in the general area of study. At the same time, field observations recorded whenever moult was observed.

The sequence of moult is not regular though in general it agrees with Stresemann (1966) and Moreau et al (1947). For example, Moreau suggests that the tail starts only after the first two primaries have started moulting. In the records for 25 Cape Bulbuls, there are four incidents where the tail was completely moulted while the primaries started to moult and there are five with advanced primary moult and no tail moult. Moreau was discussing the tropical race of the Black-eyed Bulbul. The moult sequence shown by the southern forms of this species agree with the Cape Bulbul in not being so regular. In one of the Cape Bulbuls there was a large difference between moult of right and left wing, but normally moult is symmetrical and occurs evenly on both sides of the bird.

Numbering the primaries from the carpal joint outwards, the first two primaries are usually completely replaced

before other moult is to be seen. Then follows the moult of the first secondary - numbering from the carpal joint inwards. The last secondary moults simultaneously with the second secondary. Further secondary moult proceeds from both ends inwards. Usually the gap in the wings during the moult period does not exceed more than one feather. The two centre tail feathers are usually lost first about the time of the fourth or fifth primary being replaced. The outer tail feathers are lost in quick succession and when they regrow the tail often appears gradated with shorter outer tail feathers.

Body moult starts after the primaries are replaced and is usually completed before the tail has been completely renewed. The head feathers, starting on the nape, are the first to show replacement though the moult here must be slow because the last body feathers in moult are in the same area. Next the back and chest show signs of moult. This is followed by the undertail coverts which are rapidly replaced followed by the rump and belly as the next areas to have completed the moult.

The timing of moult is illustrated in Figure 13 with details given in Table 6. The results are given as the percentage of birds in moult, of the number collected for the month. More convincing figures are given for the newly completed moult which is also expressed as a percentage of completely moulted birds of the number collected for each month.

For comparative reasons and to complete the picture for the species over its whole range, the museum collections from all South African Museums of all the bulbuls of the genus *Pycnonotus* were assembled and inspected. The results of the recording of the moult for all these specimens are also incorporated in Table 6. The moult period of the Cape Bulbul seems less restricted and to continue over a long time compared to the other two species of bulbul.

Only one field observation of moult did not conform to the collected material from the study area. This was the observation of moult in September in the study area while in fact moulting was recorded from museum material. Observation allowed inspection of far more individuals than in the case of the collected material so there was no reason to query the

TABLE 6. - MOULT. The moult pattern for the three species *Pycnonotus capensis*, *nigricans* and *barbatus* as indicated from Museum skins and *Pycnonotus capensis* collected near study area. The figure indicates the percentage of specimens showing moult for each month.

Month	<i>Pycnonotus capensis</i>					<i>Pycnonotus nigricans</i>		<i>Pycnonotus barbatus</i>	
	Receive area			Whole dis- tribution		Whole distribution		Whole distribution	
	No. of Specimens	% in Mould	% in fresh complete	Number	% in Mould	No. of Specimens	% in Mould	No. of Specimens	% in Mould
January	7	100+	0	9	88	3	66	8	75
February	12	100+	16	-	-	3	0	8	50
March	11	100+	80	5	80	7	86	5	80
April	5	100+	100	7	86	1	100	5	100
May	10	100++	60	13	15	16	100	5	100
June	12	33++	33	1	100	18	44	12	40
July	12	33++	0	3	33	4	25	10	30
August	6	0	0	2	0	6	31	10	20
September	4	0+	0	9	22	22	15	3	0
October	8	24+	0	7	14	18	0	12	0
November	6	17+	0	8	25	6	0	3	33
December	5	100+	0	6	33	1	100	-	-
Total	98			70		130		91	

++ Mould only recorded in 1963

+ Mould observed in the field in study area

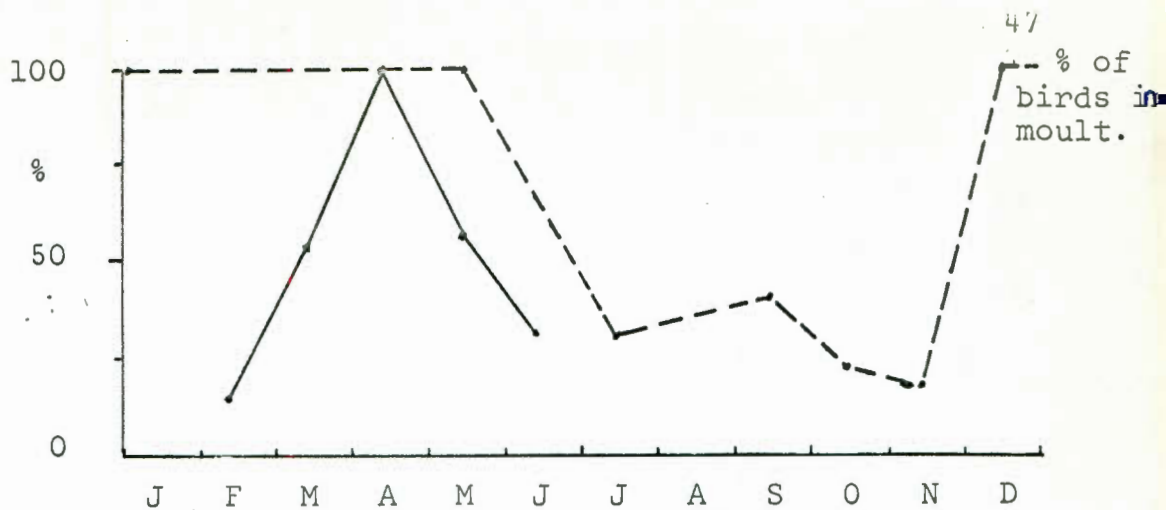


FIGURE 13. Moult. The percentage of specimens collected each month of the year near the study area showing moult on some part of the body - indicated by dashed line. The solid line shows the percentage of these specimens showing completed fresh plumage.

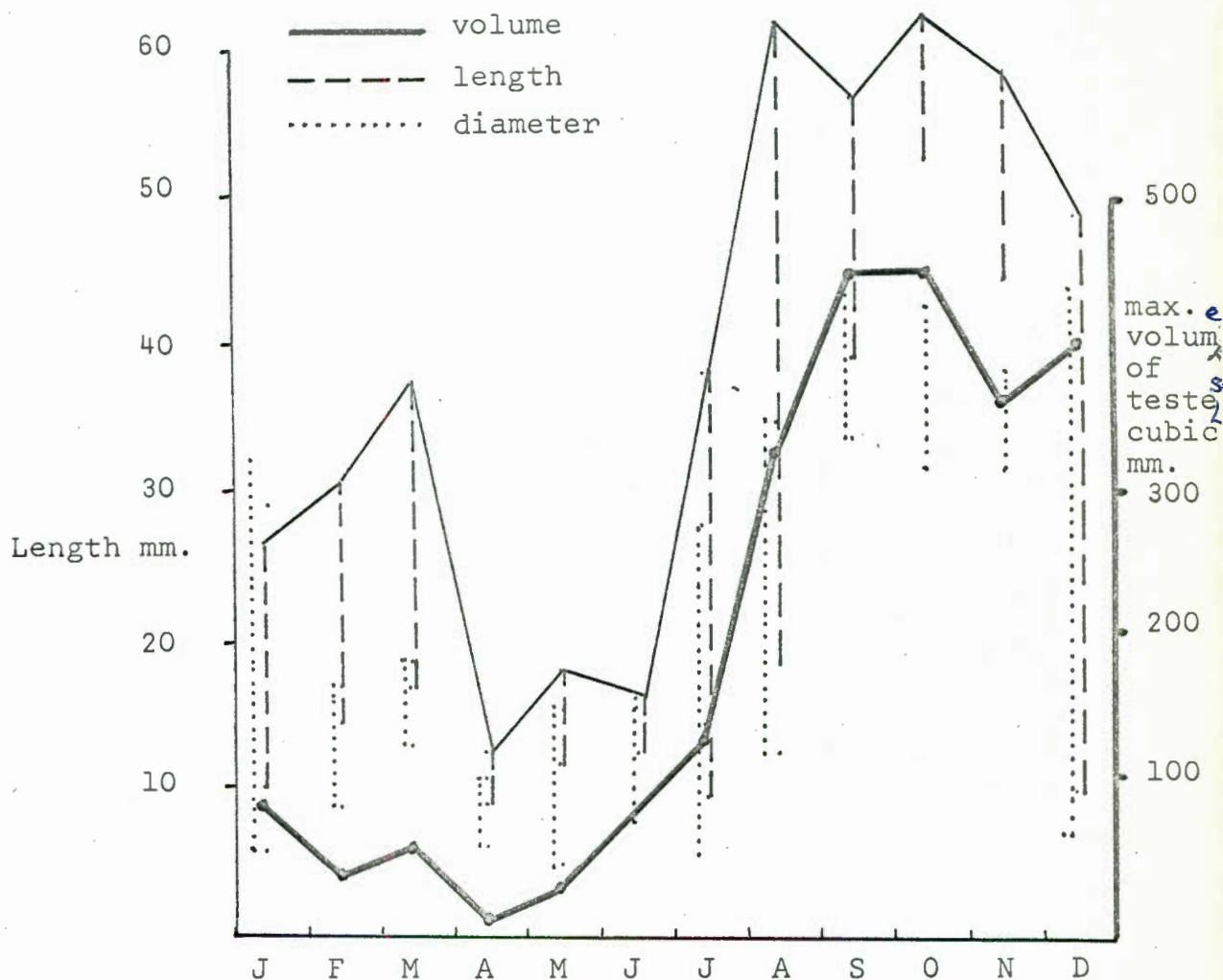


FIGURE 14. Testes. Showing relative changes throughout the year for the Cape Bulbul in study area. Solid line volume of testes - maximum is mm<sup>3</sup>. Line of dashes = variation in length of testes for each month. Dotted line is variation in diameter of testes for each month.

field observation.

A complete moult has been recorded to occur within two months in caged passerines - Stresemann E & V. (1966). Figure 13 shows that moult occurs over a period of six months. This long period is doubtless due to individual variation. It indicates that not all Cape Bulbul moult simultaneously. It is interesting that only in 1953 was moult recorded in May, June and July. Thus for 1963 the moult took place later than in the previous years. Moreau et al (1947) states that some Black-eyed Bulbuls moult fully four months after others. Snow (1962) also found individual variation from year to year in timing of moult. This confirms from other species the findings here of the Cape Bulbul that moult can vary from individual to individual, that this is not an internal rhythm but something influenced by some external factor. This is remarkable as Höhn (in Marshall 1961 p.100) states "in the majority of northern hemisphere birds at least, there is a main annual postnuptial moult. This fact alone suggests that the control mechanism, itself undoubtedly complex, is in the main hormonal and related to cyclic fluctuations in gonadal hormone production". The relationship of the timing of moult to breeding in *P. capensis* will be discussed below. The fact that moult does not occur regularly at a set time each year in the Cape Bulbul indicates that for this species no rigid internal physiological rhythm is controlling this phenomenon. There must be some variable factor, either internal or external, that triggers off the moulting process.

#### GONADIAL ACTIVITY

To establish the rhythm of gonadial activity a total of 79 specimens were collected along the coastal scrub a few miles from the study area so that this collecting would not effect the study population. Three or four birds were collected each month of the year, in all 61 male birds were collected, some for each month of the year and 18 females for only nine months of the year. The results are tabulated in Tables 7, 8 and 9. Fortuitously the testes provide the more satisfactory histological evidence of annual rhythm. The ovaries show no great increase in size except immediately prior to egg laying though from Table 9 there is a slight indication

TABLE 7. - TESTES. Details of testes for each month of the year for the Cape Bulbul obtained from near the study area.

		Volume mm <sup>3</sup>	Thickness of Tunica albuginea	Cell width of interstices	Melanoblasts	Resting	Spermatocytes	Meiosis	Sperm concentration	Free Sperm
Jan.	63	15	Medium	1	a	o	o			a
	62	1	"	2-4	o	o	o			a
Feb.	62	6	"	1	o		o	o	o	few
	62	14	"	1	a			o	o	few
March	62	14	Thick	1	o		o			
	62	57	Thin	1	o			o	o	few
April	62	4	Thick	4-6	o	o				
May	62	5	"	4-6	a	o				
	63	30	"	4-6	o	o	o			
	63	4	"	4-6	a	o				
June	62	5	"	4-6	a	o				
	62	5	"	4-6	o	o				
	62	3	"	2-4	o	o	o			
	63	5	"	2-4	a	o				
July	62	1	Thin	2-4	a	o	o			
	62	4	Medium	4-6	o	o				
	62	1	"	4-6	a	o				
Aug.	62	14	"	2-4	a	o				
	62	11	Thin	1	a	o	o			o
	62	138	"	1	a	o	o	o	o	o
Sept.	62	139	"	1-2	a			o	o	few++
	62	295	"	1	o		o			
	62	139	"	1	a			o	o	o
	62	426	"	1	a			o	o	o++
Oct.	62	428	"	1	o			o	o	++
	62	236	"	1	a			o	o	
Nov.	62	234	"	1	a			o	o	
Dec.	62	87	Medium	1	o			o	o	o

++ with unusually large venous blood vessels between tubules

a absent

o observed

that the largest ova are slightly bigger during the breeding period. Hinde (1967) also rejected weight of ovary as evidence of breeding state in the female canary. For these reasons not much attention was given the female reproductive cycle.

The avian testes is known to increase at least 360 fold in volume through the year - Marshall (1961a). Moreau et al (1947) mention the various ways of presenting the result regarding size of testes. They give for an ellipsoid, two formulae  $\frac{4}{3} \pi l d^2$  and  $\frac{4}{3} \pi \left( \frac{l}{2} \times \frac{d}{2} \right)^2$  both of which are incorrect. The more corrected form used here is  $\frac{4}{3} \pi l \left( \frac{d^2}{2} \right)$

where  $l$ =length and  $d$ =diameter. Using this formula it can be seen that the volume of the testes in the Cape Bulbul increases up to 428 times the minimum volume (Table 8). This is ten times more than the volume of increase observed in the Black-eyed Bulbul by Moreau et al (loc.cit.). These last authors indicate that the volume of testes in some passerines may increase some 2000 fold but in view of the fact that Marshall does not quote these figures they must have been rejected. It is perhaps of some interest that Moreau et al illustrate the change in size of testes in their paper by a figure plotting the diameter of the testes. Here I have plotted in Figure 14 the volume, length and diameter of the testes for each month of the year and it can be seen that the length shows more satisfactorily than the other parameters, the greater changes the organ undergoes during the year.

Marshall (1961a) has summarised the internal rhythm of gonadal development very clearly giving three phases - a) regeneration, b) acceleration and c) culmination. In the first phase which is a period of sexual quiescence the tubules are reduced and contain undeveloped primary germ cells distributed evenly in the tissue; the interstitium is enlarged and the outer tunica albuginea is rebuilt and consists of a much thicker layer of cells. The acceleration phase is accompanied by growth of the tubules with spermatogonia, spermatocytes arranged around the periphery of the tubules; the interstitium and the tunica albuginea are spread and with the growth of the organ the layers of cells are much

TABLE 8. Volume of testes in mm<sup>3</sup> from specimens of Cape Bulbul collected near the study area.

Month	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Volumes recorded	1	6	14	4	6	5	6	139	295	318	363	195
mm <sup>3</sup>	6	38	57	6	2	5	1	11	426	338	234	2
	5	7			31	4	2	14	139	428	378	415
	87	14			5	5	5	159	401	338	254	
	16				4	5	4	35	418	236	231	
					4	6	3	339	338			
					8	3	141		248			
						4						
No. of specimens	5	4	2	2	7	8	7	6	7	5	5	3
Mean volume	23	16.3	35.5	5	8.6	4.5	23.1	113.2	323.6	331.6	292	204

reduced. In the culmination phase meiotic division of the spermatids into spermatozoa occur. The spermatozoa are initially concentrated about the Sertoli cells before entering freely into the lumina of the vacuoles. These phases are illustrated in Figures 15 to 18.

From Table 7 it can be deduced that the period of regeneration of the Cape Bulbul extends from May to June with a slight acceleration commencing in July. It is important to note that there are signs of quiescence from January to April. However, one preparation of the testes collected in February showed more than half of one testes in an inactive stage with primary spermatocytes whilst on one side the tubules had enlarged and even had sperm in the lumina. There was some individual testes variation. In one specimen the two testes were of a different size: 59x50; 40x28 mm. The larger one had sperm and an enlarged lumina. The smaller one only showed sperm in concentrations in four sections of the tubules, the greater portion of the slide indicating the presence of primary spermatocytes only.

The variation in size of the testes is shown in Figure 14 and Tables 7 & 8. There is a striking increase for the months August through to December. Less spectacular are the changes in length and width of testes showing a secondary autumn peak in February and March. The small size of gonads in April, May and June coincides with the period of regeneration mentioned above. Information derived from these tables and figure indicates potential breeding on the part of the male for the eight months August through to March. There is an indication of a period of quiescence in January and possibly in February.

This will be discussed later under the moult and timing of breeding.

Though the information on the female is not very complete (Table 9) it is interesting to note that the ova was slightly larger from September and again in March. The oviduct was very much reduced from April to June. Fat was present in the body during the colder months March to September. The thyroid gland was noticeably larger from June through to September. Inspection of stained sections of the thyroid in an enlarged and reduced state showed insufficient morphological



FIGURE 15. Testes. Photomicrograph of testes of Cape Bulbul collected in May. Note thick tunica albuginea small tubules with melanoblasts deposited in the wide interstices (80x:H&E)

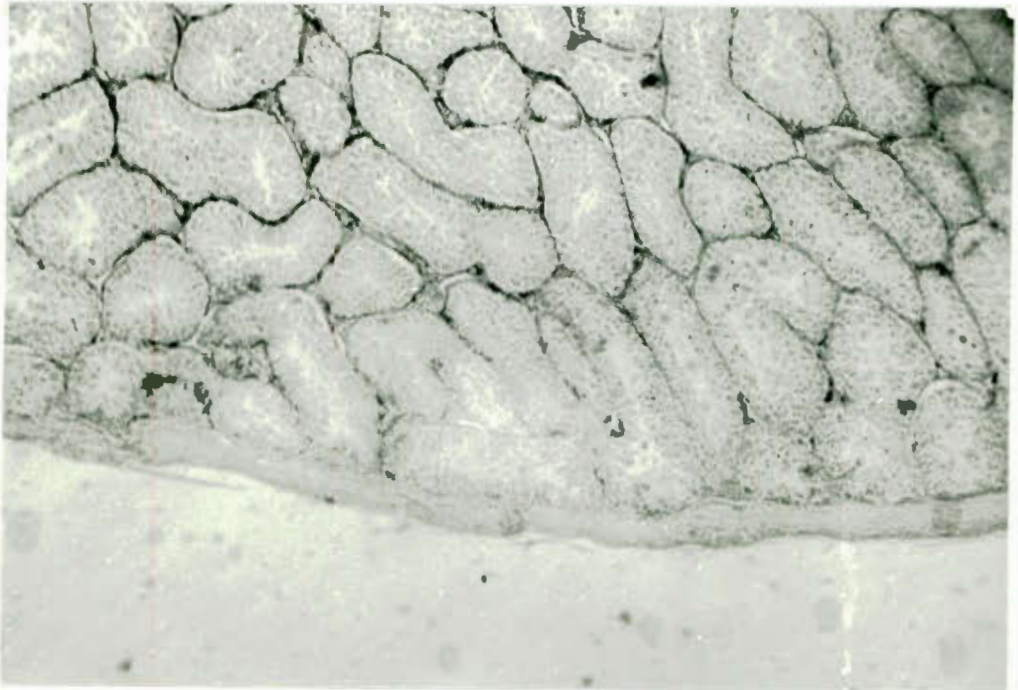


FIGURE 16. Testes. Photomicrograph of testes of Cape Bulbul collected in March. Showing similar features to Figure 15 but with narrow interstices (80x:H&E)

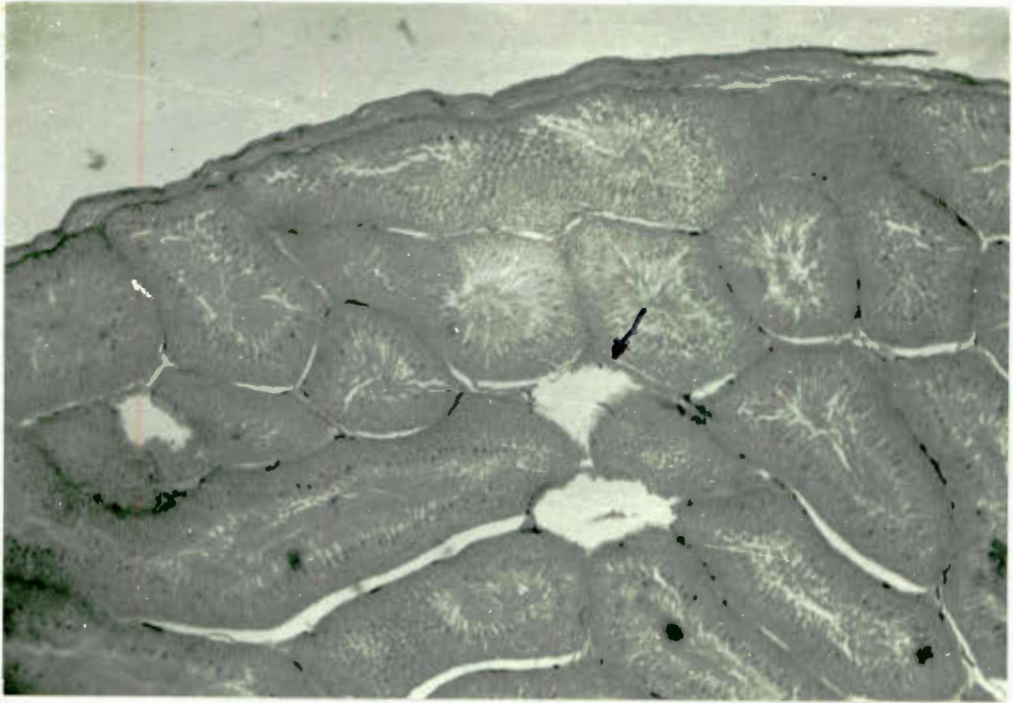


FIGURE 17. Testes. Photomicrograph of testes of Cape Bulbul collected in October. Note enlarged tubules with the unusual feature of enlarged vein - arrow (80x:H&E)

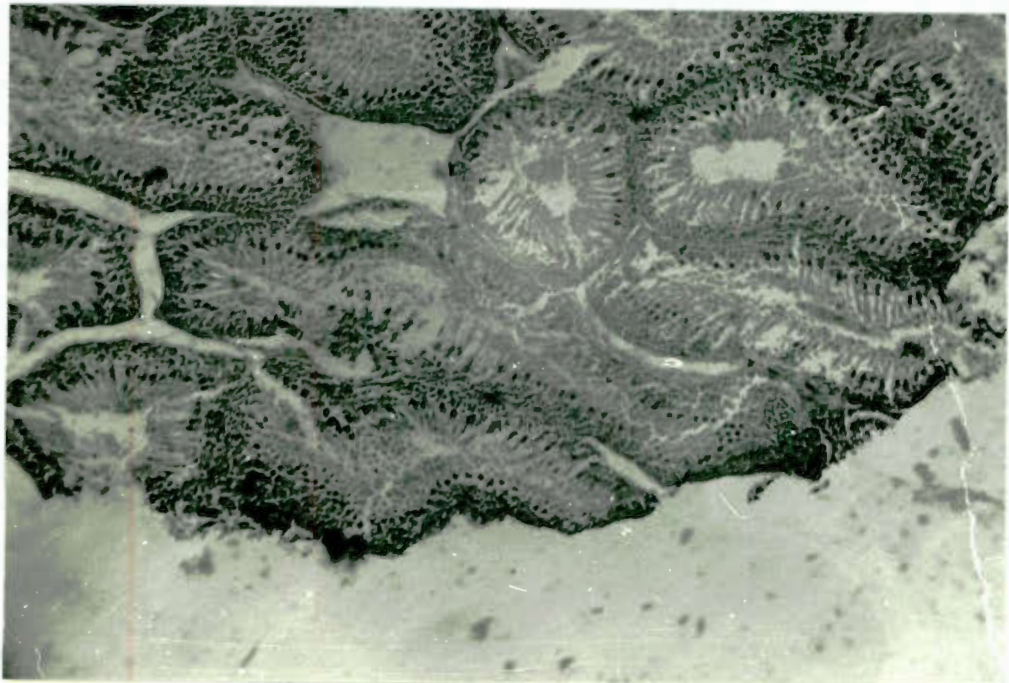


FIGURE 18. Testes. Photomicrograph of testes of Cape Bulbul collected in December. Note advanced spermatogenesis and sperm in lacuna (80x:H&E)

TABLE 9. Details from female Cape Bulbuls collected near the study area

Month	No. of Specimens	Size of largest ova mm.	Oviduct		Fat		Thyroid gland
			Width mm.	used	Present	Colour	
January	0	X	X	X	X	X	X
February	1	1	2.3	X	0	X	X
March	2	1.5 - 2.5	2.0	X	Fair	X	X
April	3	0.3 - 0.5	1	X	0	X	X
May	2	1	1	X	Little	Orange	X
June	2	1	1	X	0	X	Large
July	4	0.8 - 2	1-3		Heavy	Orange	Large
August	0	X	X	X	X	X	X
September	2	2.5 - 3.2	3+	X	Heavy	X	Large
October	1	11.6	X	X	0	X	X
November	1	X	X	X	0	X	X
December	0	X	X	X	X	X	X
TOTAL	18						

X not recorded or specially noted.

difference to distinguish the state of the activity of this gland, reliably. There was no change of shape from cuboidal to columnal interstitial cells as is the case in the human histology.

#### SEASONAL CHANGE IN WEIGHT

The weights of birds collected near the study area are plotted in Figure 19. The information for the male weight shows a drop in weight in autumn - with a low in April. The highest average weights of the male are from July through to September and January though the number of examples are inadequate to draw definite conclusions on this matter. Kluyver (1952) mentions for the Great Tit *Parus major* an increase in weight before breeding.

The drop in both maximum and minimum weights recorded for March and April will be discussed below.

#### TIMING OF BREEDING

It is usual to express the timing of breeding by nesting activity - involving the egg laying period as the most important time. Because in the present study severe predation frequently prevented the completion of the clutch, and on a few occasions it was suspected that the first egg was taken before being observed, the nest building activity was considered a more convenient measure of breeding and a more reliable indicator than the egg stage. The record of pair 18 for 1960 was nine nests, eggs lost in four and in 1961 the same pair (ringed) had three nests two of which were lost with eggs. In nest construction there were twelve attempts for this pair whilst if one recorded eggs only, there would have been seven records. It is felt that the more correct indication of the nesting urge or nesting activity is reflected by the nest building rather than the laying stage. It is interesting that Hinde (1967) finds "The coincidence between increased ovarian activity and nest building was established directly for canaries (*Serinus canarius*)". This would tend to support from experimental evidence my suggestion that the state of nesting activity can be indicated by nest building attempts.

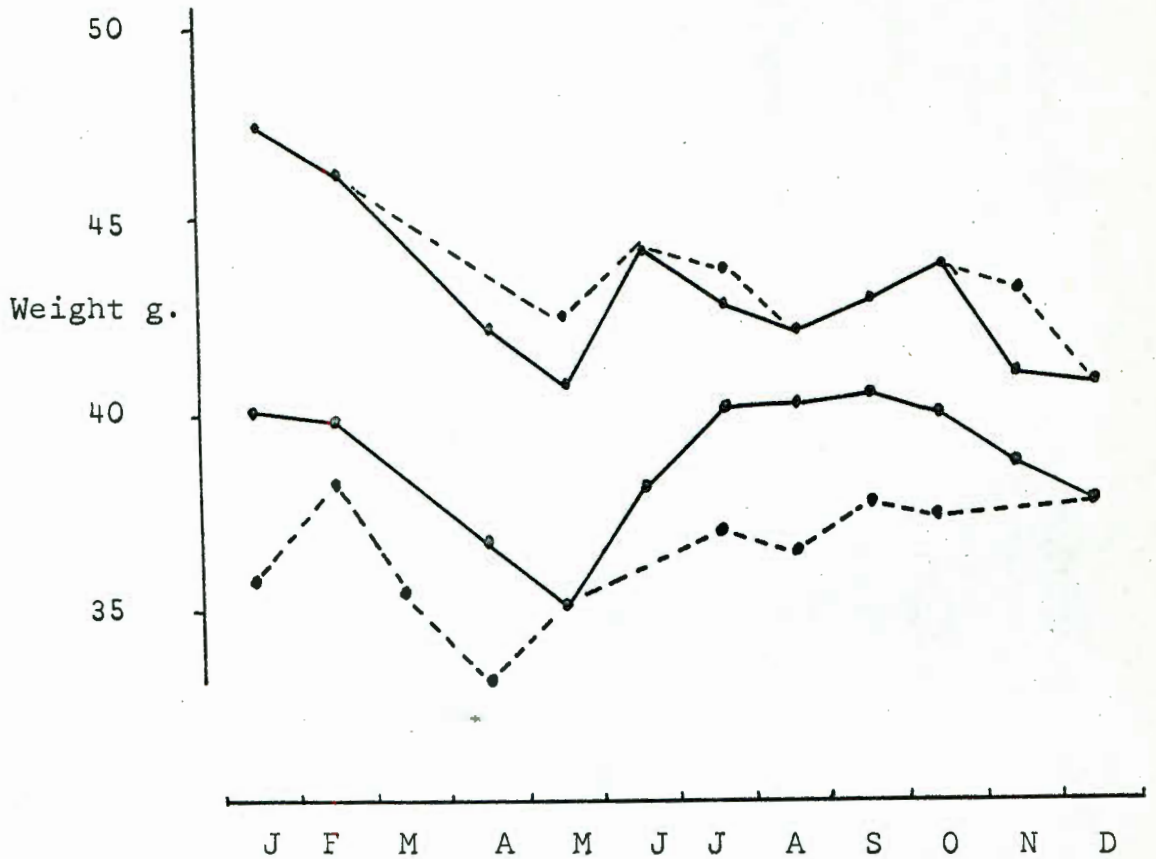


FIGURE 19. Weight. The monthly variation in weight of the Cape Bulbul near study area. Showing variation in male between solid lines, dotted line includes maximum and minimum weights (unsexed) recorded for each month (some from ringed birds).

The nesting activity as determined by the nest building urge is given in Table 10 for the four years 1959 to 1962. The month is divided into half so that roughly fortnightly evidence is presented. Where a nest was found with eggs the data was worked back to approximate with the timing of the first egg. From the table it is obvious that no two years are the same. In none of the four years did breeding commence in the same half of a month though all ceased nest building activity in the first half of December. In three of the four years autumn breeding was observed and especially in one of these years it was pronounced. Of considerable interest is the work of Snow (1962) with *M. manacus* which commenced breeding at different times of the year but stopped breeding at the same time every year. This will be discussed further below.

The nesting activity is illustrated in Figure 20 and compared with various climatic factors as recorded by the meteorological station two miles from the study area. These factors are discussed below:

(a) Light

Though not illustrated in Figure 20, photoperiodicity can be an important factor influencing internal rhythms in birds. There is experimental evidence to show that sexual cycles can be accelerated by increasing day length - Marshall (1955). The change of day from the winter solstice to 21st August at Port Elizabeth is 32 minutes. This is well within the limits of perception for passerine birds.

It is, however, significant that in no two years of the four recorded, did breeding activity start at the same time of year. If photoperiodicity alone was the dominant influencing factor for the beginning of breeding, a gap of approximately eight weeks between the beginning of two different breeding seasons would not have occurred.

There are indications that after the shortest day of the year the second phase of development of the gonads starts to take place. The influence of other factors is, however, not ruled out.

TABLE 10. - NESTING. Nest building activity of the Cape Bulbul in the study area of 20 hectares.

Month Dates	August		September		October		November		December		Jan.	Feb.	Mar.	Total
	1-15	16-31	1-15	16-30	1-15	16-30	1-15	16-31	1-15	16-31				
59	0	0	0	2	11	1	6	9	1	0	0	0	0	30
60	0	0	3	1	9	2	17	4	3	0	0	5	3	47
61	0	0	0	0	0	5	16	3	1	0	0	1	0	26
62	0	1	10	9	8	4	6	2	1	0	0	0	1	42
Total	0	1	13	12	28	12	45	18	6	0	0	6	4	146

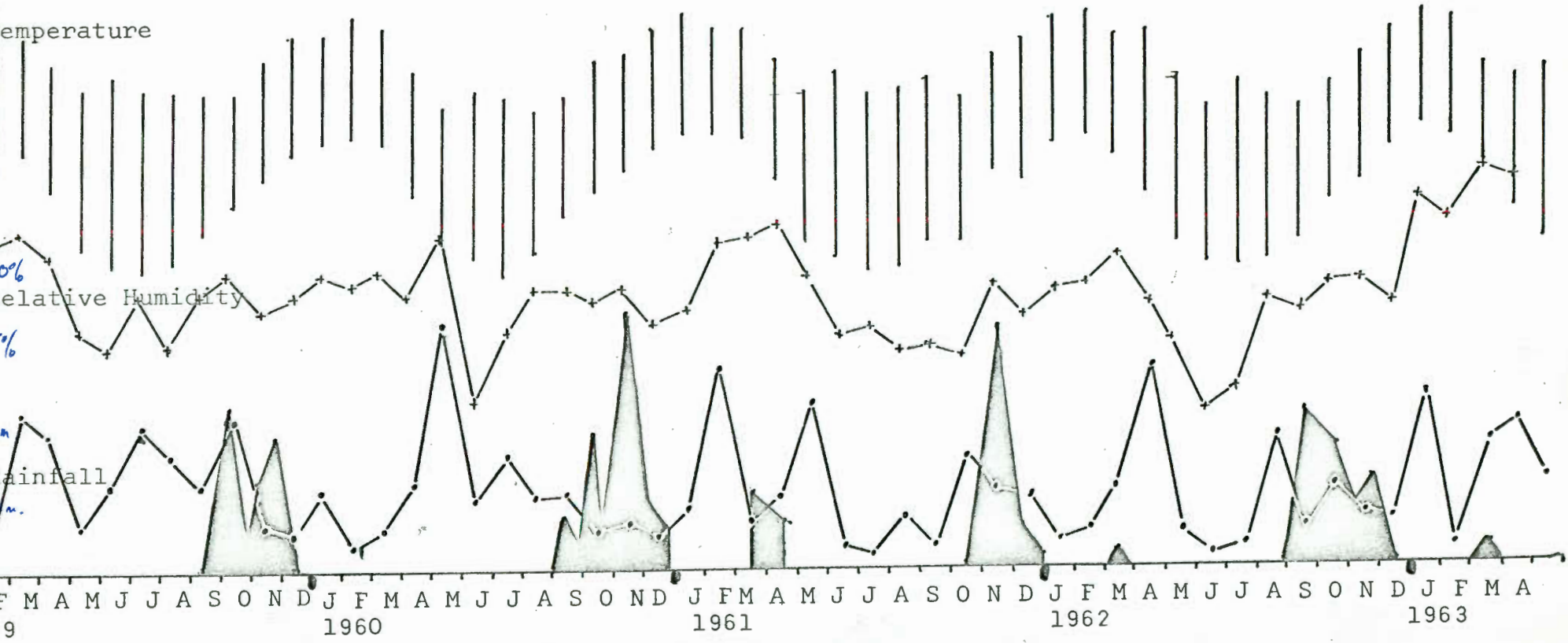


FIGURE 20. Breeding & Climate. Nesting activity of the Cape Bulbul in study area shown in consecutive months along with climatic conditions recorded at a weather station four kilometres away. Breeding activity shown in black according to number of nests each month.

(b) Temperature

The evidence available is not consistent. Each year breeding started whilst the temperature was increasing. The lowest temperature each year was recorded in July. The breeding started in each year with the exception of 1963, after the temperature had risen to above 60°F (28.4°C). In 1963 the first breeding occurred at a temperature of 59°F. There is little evidence from the information available that temperature played an important role locally.

According to Marshall (1961b) every species is physiologically adjusted to a temperature range. It seems that the temperature conditions in the study area remained well within the extremes that the species has to endure in other parts of its range.

(c) Rainfall and humidity

According to Marshall (1961b) rainfall or its effects forms a powerful regulator of reproduction. In the present study no consistent pattern was detectable that indicated the breeding started as a result of rainfall. In the spring of 1959, 1961 and 1962 good rainfall peaks were followed by good breeding but this was not the case in 1960. Also the second peak of spring breeding followed rainfall peaks in 1959 and 1962 but this was not the case for 1960. A check on field notes in 1960 indicates that there were many days of light drizzle and this possibly explains the lack of actual rainfall recorded for November that year.

The impression was gained in the field that good rain in spring usually brought a burst of singing and activity to the local Cape Bulbul population. There are unfortunately no figures to confirm this impression.

What does appear more significant is that on each occasion, autumn breeding occurred, it occurred in response to a noticeable increase in relative humidity but not actual rain. Good rains fell in January 1961 but no breeding occurred and the Relative Humidity did not noticeably increase then. But although no good rains fell after December 1962, the Relative Humidity increased steadily and breeding took place at the height of the Relative Humidity.

## SOCIAL CHANGES AND LOCAL MOVEMENT

From ringing evidence it is clear that some Cape Bulbuls remain paired for life and each year return to the same nesting area. During the non-breeding period the Cape Bulbul congregates in numbers to feed. These flocks range from 10 to more than 20 in loose association and they are much more vociferous than usual. These winter flocks occur also in the other two species of *Pycnonotus* and flocks of over 50 individuals have been seen together.

There was one record of a ringed pair seen in such loose winter feeding flocks and the pair were together. They in fact remained close together and mutual preening was noted under these conditions.

The number of observations of single, paired and flocks of 10 or more birds are given in Figure 21. These observations are random observations on birds outside the study area, but still in the same general area. From this it can be seen that social flocking occurs from January to March and May to August. The increase in number of single birds seen from September to November coincides with the breeding period. But the increase in single birds in May and June must be caused by another factor and it is suggested that these are young of the previous year breaking away from the flocks.

## CHANGES IN FEEDING HABITS

From Table 11 based on 321 field observations taken from throughout the year it is clear that there is a noticeable increase of insect food intake by adult birds in November and December. It was only in January and from April to June that no observations were made of insect food being taken. Thus the only month when insect food was taken and breeding did not occur was in July the month before the first breeding was recorded.

During the whole year fruits were eaten according to the supply available.

## DISCUSSION

It is inevitable that the seasonal rhythms mentioned above have some effect upon each other. They have been

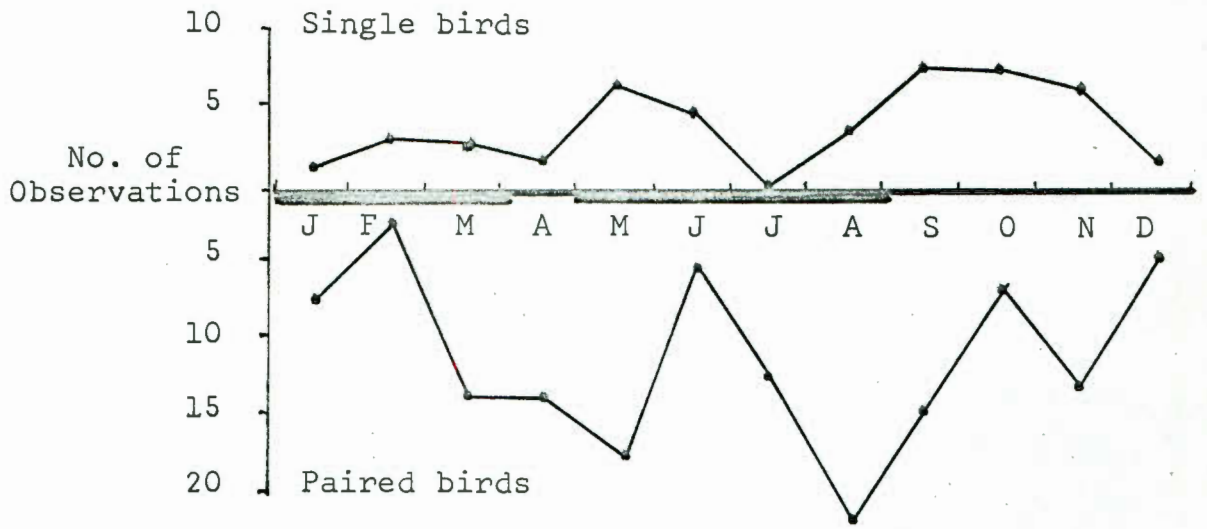


FIGURE 21. Social Behaviour. Giving the number of observations of Cape Bulbul single, in pairs or in flocks for different months of the year. Observations of single birds above line. Frequency of pairs below the line. Double line for months when flocks greater than 10 birds together were recorded.

discussed separately, but we shall now consider their inter-relationship.

The most important event in the annual cycle as far as energy requirements are concerned appears to be that of the moult. Perek & Sulman (1945) (as quoted by Sturke 1954) found in the domestic fowl an increase of about 45% in the standard metabolic rate during autumn moult, as compared with values for the summer and winter laying periods. Because of the known high energy requirements needed for breeding activities and moult and the fact that northern temperate birds moult after breeding, the phenomena is usually referred to as a "postnuptial" moult. The phrase "postnuptial moult" is persistently used throughout Marshall's (1961) classic 'Biology and Comparative Physiology' (c.f. Höhn, King, Farmer and Marshall).

Moreau et al (1947), however, showed that in the Pycnonotidae moult coincided with well-developed testes. This was the first such observation. Since then records have become available from Australia where desert breeding birds have been brought into a breeding condition by unseasonable rain despite the fact that they were in moult (Keast 1960 and Immelmann 1963). In South Africa, I have observed after late unseasonable rain near Port Elizabeth successful breeding to occur in both Cape Weaver *Ploceus capensis* and Red Bishop *Euplectes oryx* that were in partial breeding plumage at a time when they should have been in non-breeding plumage.

The information available on the Cape Bulbul shows conclusively that moult did occur whilst breeding was still going on in December. Furthermore the autumn breeding took place despite the fact that the birds were then in the middle of heavy moult. Two birds actively breeding in March - both females - showed heavy wing moult so that the same individuals that breed are actually moulting. Free sperm occurred in the lumina of the tubules in the testes during three of the six months that all birds collected showed moult.

The information of Moreau et al (1947) for period of moult and testes development for the Black-eyed Bulbul and my observations for the Cape Bulbul differ somewhat. The

tropical birds show a shorter and more regular moult pattern than the southern species. This difference could be due to specific differences; but because the southern Black-eyed Bulbuls have a similar pattern to the Cape Bulbul it seems that some climatic factor is the cause of the difference.

The testes in the tropical Bulbuls, as recorded by Moreau et al., have a five-month regeneration period which is longer than that for the Cape Bulbul, but the time of the year is similar. There is in addition in the Cape Bulbul a short quiescent period indicated for January and early February.

The differences in developmental stages of testes may also be specific but there is no other information available on such periodicity in Southern Africa.

In view of the differences between moult and testes development shown above between the tropical and temperate bulbuls it would appear that breeding and moult are two independent physiological processes. In the Cape Bulbul the moult takes longer whereas the period of regeneration is shorter than in the tropical Black-eyed Bulbul. The requirements for both processes to occur simultaneously can be met by the species. Of particular interest here is the fact that the only time insect food was seen being taken by the Cape Bulbul was during breeding times and in July. Whether this form of diet provided some essential food matter for the breeding condition or merely supplied additional energy required during times of high need could not be ascertained. Probably the latter was the case, as the greatest number of insects was taken (and eaten) in November-December when the feeding of young requires so much energy on the part of the parents.

It is interesting that in the House Sparrow *Passer domesticus*, according to Davis (1955), only a mean increase of 7.6% in daily energy is required for moult. The additional food requirement is small, and should not present any difficulties to the Cape Bulbul in an area where food is more than adequate.

Marshall (1961), referring to the testes development in the acceleration phase (p.315), states that "In most birds the postnuptial moult ends early in this phase". The

Cape Bulbul does not fit into this pattern at all, since the moult occurs prior to the regeneration phase. The moult, in fact, occurs between the culmination phase and the regeneration phase, the former state often recurring during moult. Marshall also states earlier (p.312) that "post-nuptial moult begins and proceeds strongly" during the regeneration phase. As indicated, this is not the case in the Cape Bulbul nor is it in the species studied by Moreau's et al (1947).

Reverting back to moult and the fact that the Cape Bulbul and the Black and White Manakin (Snow 1962) both have a uniform period when breeding ceases, we have a curious coincidence. For in both species this cessation is followed by moult. But we have already seen that it is feasible that the bird can cope with the additional energy requirement of moult comparatively easily. In the Cape Bulbul breeding may also be started during the moult and before the testes are in the complete regeneration phase. There appears no obvious reason why moult occurs when it does. The fact that in 1963 the Cape Bulbul moulted later than normal cannot be correlated with any obvious external factor. Snow (1962) suggests that the moult in the Manakin coincides with the onset of the wet season, but this correlation cannot occur under the climatic conditions in the study area because there is no real wet or dry season. It has been suggested by Marshall (1961b p.315) that the continuous abundance of food and the absence or relative absence of inhibitors permits the abandonment of the more or less precise annual cycle.

Having seen that moult and breeding can occur independently of each other, the next obvious question is: what controls these two phenomena. From the literature it is evident that there is some basic internal rhythm (Marshall et al 1961); but from the observations reported here it would seem that some proximal factors, possible external, trigger off the timing of these two stages in the bird's annual cycle. The day-length variation is sufficient for the bird to be stimulated by this factor, but because there is difference from year to year in the start of both breeding and moult it seems unlikely that this is a dominant factor. Temperature extremes are not met with under the field con-

ditions pertaining to the studied population. Rainfall alone is not the important trigger mechanism that was expected; but of some importance is the fact that relative humidity, at least in autumn, influenced breeding in some way. In this respect one is tempted to draw attention to Bargmann (1960), who mentions that water loss in rats can inhibit breeding through changes in the pituitary. Possibly there could be a similar situation in birds. The social behaviour patterns are not the same for cool-temperate regions in that the various phases of social activity and return to territory do not coincide with the state of testes as given for cool temperate species. This is especially so during the second autumnal breeding period.

Other interesting aspects of the Cape Bulbul are, first, that the female only was observed with an accumulation of fat. Snow (1962) points out that all birds which undergo annual periods of food shortage lay down in advance, reserves of fat. Unfortunately the evidence in the Cape Bulbul is rather limited and conclusions cannot be drawn from these facts. The indication is that in the Cape Bulbul there is no known shortage of food yet storage of fat does occur. Also in this regard the thyroid should have received more attention for the activity of that organ appears to be in early breeding period and not immediately prior to moult (Höhn 1961). Indeed the timing of the enlargement of the thyroid is opposite to that given by Höhn for the rhythm of temperate species.

The seasonal rhythms of birds are complex and inter-related. Opinions are mainly based on cold-temperate species in Europe and America. These opinions do not necessarily apply to warm temperate species that have been studied and there is some evidence that differences do occur. The evidence of the Cape Bulbul is:-

- a) Gonadal rhythm occurs with a slightly longer regeneration period than is the case under cool-temperate conditions.
- b) Moult occurs independently of breeding.

- c) Moults occurs independently of the gonadial developmental stages, in contrast with birds from cool temperate conditions.
- d) Moults is not necessarily a twelve-monthly cycle but may vary by several months from one year to the next.
- e) Social behaviour is not necessarily restricted by the phases of gonadial activity.

The results of Moreau's work on a Tropical species (Moreau et al (1947) agree with a) and b). Snow (1962) finds the same condition in the Manakin as mentioned under d). From these results it is evident that a lot more work is required for birds outside the northern temperate conditions, and that some rethinking will be required on the strict annual cycles discussed here.

## 7. FOOD

## FOOD

The primary concern of all animals is finding of the right kind of food and enough of it (Elton 1927).

An attempt has been made to establish what food the individual Cape Bulbul takes and the availability of this food throughout the year. Wynne-Edwards (1962) points out that a species will not use up its entire food resources; but we frequently find during the course of the year that the supply will become very limited. Lack (1954) postulates that food is a limiting factor for bird populations. However well this theory might fit the picture in cool temperate conditions, it does not appear to do so under conditions applicable to southern Africa. We have no severe cold winter when food supply might be drastically reduced.

It is one thing to obtain a subjective opinion derived from field experience, it is another to put down the facts to prove the point. With fruit-eating birds there had been no field work and there had been no phenological botanical work on flowering seasons let alone fruit production of indigenous plants. The first problem was to establish the food eaten by the local population in the study area. This was done in two ways: a) observations of food eaten and its identification and b) analysis of stomachs of collected birds. The second problem was to determine the availability of the food required. Thirdly, quantities required by individuals as well as the population as a whole had to be established. Finally, it was determined what other use was made of the same food source.

### FOOD SELECTION BY THE CAPE BULBUL

The rather tedious and exacting process of direct observation was used to determine what the local birds ate. Positive identification was made of 321 items eaten by adult birds and 155 items fed to the young nestlings. The results are tabulated in Table 11. The content of the stomachs of birds collected are given in Table 12. The results show that 84% of the diet was vegetable, the bulk of which constituted berries. Insects accounted for 14% of the observed diet whilst 2% was derived from debris discarded by

TABLE 11. Observed food items seen to be swallowed in the field by the Cape Bulbul in the study area. Results given for numbers each month and totals and percentages of each - below.

Species	J	F	M	A	M	J	J	A	S	O		N		D		Total		
										a	j	a	j	a	j	a	j	
<i>Viscum capensis</i>									1								1	
<i>Colpoon compressum</i>									2	2				1			5	
<i>Acacia cyclops</i>	21	6	2		2		4	1		5	1	17	16				58	17
<i>Carpobrotus edulis</i>								2		1							3	
<i>Agathosma apiculata</i>										1							1	
<i>Coleonema pulchrum</i>																		
<i>Mundia spinosa</i>									5			29	23	2			36	23
<i>Rhus crenatus</i>		1							2	5	1	20	13	2			30	14
<i>Rhus glauca</i>		4							1								5	
<i>Maytenus procumbens</i>				1	7				1			1					10	
<i>Cassine maritima</i>								1										
<i>Cassine tetragona</i>																		
<i>Rhoicissus digitata</i>								2	2					1			5	
<i>Passerina rigida</i>												3					3	
<i>Rapanea gilliana</i>					9	1	34	2	4			4					54	
<i>Chironia decumbens</i>						1											1	
<i>Salvia africana-lutea</i>									1								1	
<i>Solanum quadrivirgata</i>							13	1		2	2						16	2
<i>Chrysanthemoides monilifera</i>	2	7	5	4	4	5		2	3	1		8	1	3			80	1
<i>Cucumacea</i>				1	1													
<i>Gladiolus sp.</i>		1		1	1			1	1			1					6	
<i>Phytolacca americana</i>				1				1									2	
<i>Scutia indica</i>								1									1	
Unidentified fruit											1		42					43
Debris							2	3	1			2	2				8	2
Termites							1	4	1			2		3			8	5
Other insects		4	2				1	4	2	5	1	64	44	18	6		110	51
Total No. observation Plants	23	19	7	8	65	2	58	11	23	17	4	83	55	9	6		321	155
Total No. observations	23	23	9	8	65	2	58	22	27	22	6	151	143	30	6		592	
% Plant matter taken	100	83	78	100	100	100	93	50	85	77	67	55	38	30	0			

a = adult

j = juvenile

TABLE 12. Analysis from Cape Bulbul stomachs collected within 24 kilometres of the study area. Plant species and insects counted tabulated for each month.

Food identified	Months of the year												Total No. of each species
	J	F	M	A	M	J	J	A	S	O	N	D	
<i>Nauphaea cyclops</i>	31	8	18		13	18	3		1		8	6	106
<i>Phyllanthus crenata</i>						3			2	12	158	2	177
<i>Phytolacca procumbens</i>							3						3
<i>Passiflora sp.</i>							4						4
<i>Phytolacca digitata</i>							15						15
<i>Phytolacca racemosa</i>						9	7		2		4		22
<i>Phytolacca quadrivirgata</i>							2					14	16
<i>Phytolacca monilifera</i>						24	22						46
<i>Phytolacca sp.</i>						1	1	4	2				8
Unidentified seed	3		7			10		10	5	2			37
													434
Insects		1	1		2	1		1	3	2			11
No. of stomachs investigated	4	3	4		3	4	8	2	2	3	4	3	40

humans in the study area. In food fed to the young in the nest the insectivorous portion increased to 42%. The analysis of 40 stomachs collected within the same area and type of vegetation indicated that 97% of the identifiable items were vegetable.

The discrepancy between the two sources of information can in part be explained as a bias of observation. By the very action of catching insects the bird is more conspicuous than normal. An observer will pick up the sight of such activity more rapidly than the action of picking off a berry from a bush. Hawking of termites only accounted for 4% of the observations but other insects were often taken on the wing or taken from a flower.

Allowing for bias of observation, a fair generalisation would be that 90% of the diet of the Cape Bulbul population in the study area was vegetable matter, the bulk of which constituted fruits. The remaining 10% was predominantly insect life.

Where stomachs were investigated, ten had only one species of berry present; only four of the remaining 17 stomachs had more than two species of berries. This indicates that though a wide range of berries may be eaten, individual birds normally consume one type of berry at a time. This is also indicated by comparing Tables 11 & 14. In January only two types of berries were seen to be eaten (23 observations) by Cape Bultuls although ten species of plants bearing fruits eaten by the bulbul were available in that month.

This recorded selective preference was not a chance observation. Selection was even more sophisticated as certain individual bushes were attracting berry-eating birds whilst the same species of bush nearby, apparently in a similar state of ripeness of berry, did not attract these birds. This was shown on one occasion when more than four pairs of Cape Bultuls fed freely on one bush all day for several days, even though one of the four pairs had a nest 8 metres from the feeding bush.

Some observations on the preference shown by caged birds, given the choice of several types of berry for several days together with their normal cage diet, are given in Table 20. *Rhoicissus* berries were all taken in the first day. It is

of interest that under natural conditions there were 80 observations of *Chrysanthemoides* fruits being eaten to five of *Rhoicissus*.

TABLE 13. The order of preference for berries eaten provided to caged Cape Bulbuls.

Species of berries	No.	No. remaining	
	Supplied	after 1st day	after 2nd day
<i>Rhoicissus digitata</i>	75	0	0
<i>Euclea racemosa</i>	35	9	0
<i>Chironia decumbens</i>	20	19	5
<i>Chrysanthemoides monilifera</i>	40	29	10

#### AVAILABILITY OF FOOD

The availability of berries is not an easy matter to determine quantitatively. There is no standard method for determining quantity and quality of fruit available, and so by trial and error a crude method was evolved. By walking along a path of known length at monthly intervals and counting the number of fruits within a 1.8 metre wide strip, some comparative figures of availability of fruits were obtained. Three paths were used, to cover as wide a variety of botanical plants and conditions as possible in the area. This monthly record continued over three years, and the results are summarised in Tables 14 and 15 (see Liversidge - in press). These tables indicate the numbers of berries available over the chosen route. The area covered in the counts was estimated to be one/379 of the total study area. This estimate was derived in the following manner. An aerial photograph was enlarged and a grid drawn on the photograph on the scale with sides representing 7.5 metres. The number

of squares or fractions of a square that covered bush, heath, sand and roads were then added together. From this the surface area occupied by bush in the 20 hectares of the study area was estimated - see Table 16. With the total area and the berries available over a small portion of this area the total count for the area was derived by simple multiplication. The dry weight equivalent of these berries was then worked out and the results are added to the bottom of Table 14.

From this information it can be seen that there is considerable variation in quantity of fruit available each month of the year. In no single month were there less than eight different bush species flowering or fruiting in the study area. Over an area stretching for some 20 kilometres along the coast the variation of fruit available must have been very much greater. Another interesting and unexpected finding is that the lowest figure of fruit available was for the month of February. The reason that this was unexpected was because *Acacia cyclops* (one of the important food sources) is normally most abundant during the months December, January and February. Indeed, a look at the figures will show that the figure for March is reasonably high and a normal curve should have given February a higher yield. A similarly unexpected situation arises with another dominant food plant, *Chrysanthemoides*. However, even though there are some anomalies, the information for all plants should give a fair idea of the overall position.

The total number of plant species bearing fruits in the study area was not known. Twentyfour were observed in the counts. Martin & Noel (1960) list another four that commonly occur in such coastal woodland as was studied. In addition, there were eight different unidentified seeds in the stomachs analysed from the collected birds. We know, therefore, that at least thirtysix plants were providing food for the Cape Bulbul in the area.

The seasonal variation in available insects was determined by use of a 'black light' nocturnal insect trap. It is appreciated that only certain insects were attracted by this form of trap. However, it is considered that seasonal variations shown by such insects reflected the general

14. The number of berries counted, averaged for each month of the year along the same path in the study  
 The equivalent dry weight is given with each observation and the totals are shown below.

Plant Species	Month of Year												
	J	F	M	A	M	J	J	A	S	O	N	D	
<i>m capense</i>	No		550	100	120	51	50	60	20	53			
	wt/g		44.00	8	9.60	4.07	4.00	4.80	1.60	4.24			
<i>on compressum</i>	No	6	2	39	16	?	71	3	7	28	2	6	
	wt/g	0.48	0.16	3.12	1.28		5.68	0.24	0.56	0.56	2.24	0.16	0.42
<i>a cyclops</i>	No	485	?	100	30		20			275	40	3	
	wt/g	6.15		1.27	0.42		0.38			3.49	0.51	0.03	
<i>a spinosa</i>	No			500	?	48			887	262	5	?	
	wt/g			25.00		2.40			44.30	13.20	0.25		
<i>crenatus</i>	No	8500	?	1230	1205	1260	200	580	1228	3943	100	340	
	wt/g	56.00		8.20	7.94	8.30	1.32	3.82	8.08	26.00	0.66	2.24	
<i>glauca</i>	No						14		250	10			
	wt/g						0.08		1.65	0.06			
<i>nus procumbens</i>	No			3120	4900	1445	993	10	?	3			
	wt/g			261.50	410.10	121.00	83.40	0.83		0.25			
<i>ne maritima</i>	No			600	20	?	?	65					
	wt/g			28.00	0.93			3.98					
<i>ne tetragona</i>	No	260	65	1	20		80			6			
	wt/g	12.22	3.27	0.05	0.93		3.73			0.28			
<i>issus digitata</i>	No	9	?	62	58	28	31	35	16	19	27	43	54
	wt/g	0.72		4.95	4.64	2.24	2.48	2.80	1.28	1.54	2.16	3.44	4.32
<i>ea gilliana</i>	No	10		280	43	102	170	?	37	50	42	60	95
	wt/g	0.59		16.42	0.25	5.89	10.00		0.22	2.95	0.25	0.35	5.50
<i>oxylon inerme</i>	No	?	?	32	4	49		50	200	173	9	5	85
	wt/g			0.42	0.05	0.64		0.65	2.60	2.25	0.12	0.07	1.11
<i>a racemosa</i>	No	85	9	179	450	220	265		1		136	6	
	wt/g	2.20	0.23	4.64	12.65	5.69	6.85		0.03		3.52	0.16	
<i>exasperata</i>	No	3		440	28		3						40
	wt/g	0.21		35.40	2.25		0.41						3.22
<i>nia decumbens</i>	No			627	65	30	81			23			
	wt/g			43.90	4.55	2.10	5.67			1.61			
<i>anthemoides</i>	No	83	6	54	788		373	?	1	8	200		
	wt/g	7.47	0.54	4.85	72.00		33.55		0.09	0.72	18.00		
dry wt per count/month		86.07	4.20	246.72	523.23	161.01	157.21	16.56	9.58	65.69	73.28	7.85	16.90
dry wt in study area		32,460	1,591	93,613	198,217	61,019	59,494	6,291	3,631	24,899	27,691	2,966	6,405

TABLE 15. The weight of fruits recorded at different times and the dry weights (oven dried 102°C for 48 hours).

Species	Date	Weight of 100 fruits g.	Dry weight 100 fruits g.
<i>Viscum capense</i>	9. 3.64	12.5	(8.00)
<i>Acacia cyclops</i>	6.12.69	17.3	14.69
<i>Acacia cyclops</i> aril only	6.12.69	8.9	5.12
<i>Mundia spinosa</i>	30.11.62	57.3	-
	6.12.69	49.5	11.36
<i>Rhus crenata</i>	31. 7.61	1.37	0.66
	30.10.62	2.10	-
<i>Maytenus procumbens</i>	27. 3.61	13.4	8.29
	3. 5.63	39.4	-
<i>Cassine maritima</i>	31. 7.61	18.2	4.67
<i>Rhiocissus digitata</i>	30. 3.62	28.7	(8.00)
<i>Rapanea gilliana</i>	31. 7.61	43.6	5.87
	3. 5.63	72.2	
	3. 6.63	76.2	
<i>Sideroxylon inerme</i>	27. 3.61	7.6	(1.30)
<i>Euclea racemosa</i>	30. 1.63	9.6	2.59
	30. 3.62	13.1	
	9. 3.64	14.0	
	27. 3.61	17.1	2.59
	26. 4.63	22.0	
	3. 6.63	28.8	
<i>Olea exasperata</i>	27. 3.61	22.0	
	3. 6.63	28.8	
<i>Chironia decumbens</i>	27. 3.61	10.3	(7.00)
	30. 3.62	13.4	
	9. 3.64	13.7	
<i>Chrysanthemoides monilifera</i>	30. 3.62	15.0	(9.00)
	26. 4.63	19.4	
<i>Solanum sp.</i>	6.12.69	61.9	8.37

TABLE 16. The proportions of bush, heath and other forms of cover derived by subdividing and aerial photograph into squares.

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Total area including beach	4430 $\frac{1}{2}$ squares = 51.029 acres	
		= 20.65 hectares
Amount of bush - coastal forest	1645 $\frac{3}{4}$ squares =	37% of total
Amount of heath- coastal forest	1753 $\frac{1}{2}$ squares =	40% of total
Amount of road	205 $\frac{1}{2}$ squares =	5% of total
Amount of sand dune	825 $\frac{3}{4}$ squares =	19% of total

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situation. Virtually all insects taken by the trap have been recorded as being eaten by birds, though moths are not so frequently taken as other insects. During the summer months rain often reduced the catch to zero. The results of these catches are presented in Table 17, and they indicate a paucity of insects for the winter period from the second half of May until the first half of August. For reasons beyond control the sampling of insects was not carried out for a full year.

#### DAILY FOOD REQUIREMENTS

The quantity of food required by the individual Cape Bulbul was not determined at the time of the investigation. It was anticipated that already published bioenergetic experiments on frugivorous birds would provide this information. However, the only information found in the literature was that Waxwings *Bombycilla garrulus* require three times their own weight of berries in the winter in England (Gibb 1951). The circumstances were so different to those of the study area that it was obvious that some experiments would have to be carried out under local conditions. Initial experiments were carried out with the related Red-eyed Bulbul using artificial food as used by aviculturists for feeding fruit-eating birds. Such food was known to keep the birds in good condition and it was reckoned that this would give some idea of the food requirements of the wild birds. The results of Experiment 1 are described below. The figure derived from this experiment was not entirely satisfactory. It was therefore decided to collect Cape Bulbul in the study area together with their natural food and repeat the experiment (Experiment 2 & 3). Experiment 2 was started with seven birds but three died after 13 days feeding. The experiment was temporarily discontinued while the surviving birds were nursed back to health. The experiment (No. 3) was then started again until the food had run out.

#### Experiment 1:

Five specimens of Red-eyed Bulbuls were kept in two cages (two birds and three birds). Twice a day each cage was provided with a dish of artificial food; for the first ten

TABLE 17. The availability of insects through the autumn, winter and spring as indicated by catches using 'black-light' trap. The figure given is the mean net weight in grammes for each half month.

	April	May	June	July	August	Sept.	Oct.	Nov.
Mean weight of insects caught at night in g.	10.6 2.7	4.5 1.7	1.1 0.8	0.7 0.8	0.2 -	- 6.2	7.9 10.7	7.0 5.7
Number of nights catching	7 9	12 15	13 11	13 15	2 -	- 7	5 13	13 11

TABLE 18.

Experiment 1. Feeding artificial food to five Red-eyed Bulbuls to determine amount consumed by each bird. See text for explanation.

Diet	Day of exp.	Weight of food lost g	Less Evapo- ration g	Wet weight food eaten g
Bread, Milk, Tomatoes	1	51.751	14.445	37.306
	2	55.414	22.966	32.448
	3	57.669	15.938	41.731
	4	38.500	10.372	28.128
	5	53.946	15.098	38.846
	6	50.129	15.030	35.097
	7	59.997	15.384	44.613
	8	52.901	17.472	35.429
	9	46.209	20.480	25.729
	10	49.888	19.852	30.036
Tomatoes, Apricots	11	60.752	15.782	45.470
	12	117.909	18.215	99.694
	13	90.913	14.993	75.920
	14	75.951	12.046	63.905
	15	85.725	13.836	71.289
	16	32.193	10.228	21.965
	17	50.568	11.850	38.718
	18	52.420	11.701	40.719
	19	57.670	16.075	41.595
	20	52.995	15.260	37.735

Mean wet weight of 1st diet per bird per day = 34.94 g.  
= 6.744 g dry wt.  
Mean wet weight of 2nd diet per bird per day = 53.70 g.  
= 6.713 g dry wt.  
Mean weight of live birds (40) = 31.22 g.  
% dry weight of food eaten of body weight of bird = 21.55%.

days the first type of food was tomatoes with bread and milk sop, and for the second ten days the second type of food was tomatoes and apricots. Only freshly ripe fruit was given to the birds and more was given than was required with each feed. Because of the local very low Relative Humidity, usually about 15%, a third dish of food was prepared every day as a control for evaporation. The dishes of food were weighed before and after feeding to determine the quantity of food taken and a correction factor for the days evaporation of the quantity of food eaten was derived from the control dish of food. The dry weight of the two types of food was determined with three samples of food each.

The results of Experiment 1 are presented in Table 18. The results show that for the first type of food mentioned 6.744 g dry weight per bird per day was eaten. The second type of food required 6.713 g dry weight per bird per day. Adding the two types of food together the overall average requirement for the 20 days was 6.73 g dry weight per bird per day, which was 21.55% of the bird's own weight.

The average weight of 42 Red-eyed Bulbuls caught from the same area as the experimental birds was 31.22 g. One bird weighed at the end of the experiment prior to release was 23.26 g. This shows that at least for this bird there was a loss of weight and it was presumed that all birds in this experiment were losing weight.

#### Experiment 2:

The same procedure was followed for the Cape Bulbul, using natural food taken from the area where the birds were caught. The droppings of the birds indicated that they were only eating wattle *Acacia cyclops* at the time they were caught. However a patch of Duinbessie *Mundia spinosa* was found in fruit some three miles from where the birds were caught and sufficient of these were collected to supplement the wattle. This was a more satisfactory diet since it involved a dryish fruit as well as a moist berry. When the birds were caught they were in heavy moult and the loss of seven birds en route must be attributed to this as well as the fact that the first day of catching had been the hottest day of summer locally (indeed, two died the first night whilst still camped out catching the birds). The same precautions

with the feeding were taken as in Experiment 1, in that excess food was made out twice a day, and a control was kept to check evaporation. Three birds were in one cage and four in another. With natural food it was found that the birds were more particular about their food. They would move the berry around in their beak and finally accept or reject the item. If it was rejected it was tossed to one side. Each day the floor sheet of paper was removed and the discarded uneaten food retrieved and weighed so that the amount eaten could be accurately worked out.

On the fourth day of the experiment one of the birds was found dead, and from its weight it would appear that loss of condition and weight must have contributed to its weak state. On the seventh day a second bird died under similar circumstances though it had been seen taking food the day before. Both birds were in heavy moult of wing and tail feathers. Some of the survivors were also in moult so it was decided at this stage to give supplementary live food. Termite larvae and eggs were then fed for the following six days when, however, a third bird died. To prevent any further loss Experiment 2 was discontinued at this stage, and the survivors were given artificial food. The results of the experiment are tabulated in Table 19.

The weights of the birds were recorded before and after this experiment (see Table 21) and it can be seen that although several birds died, the majority of the survivors gained weight. The average weight showed an increase at the end of the experiment. The birds in this experiment took, on the average, 11.38 g dry weight per bird per day which worked out as 29.39% of their own body weight.

### Experiment 3:

After four days of feeding up the survivors, Experiment 3 was started. The only food supplied was *Acacia cyclops* and (refrigerated) *Mundia spinosa*. The experiment continued for nine days at which stage the supply of *Mundia* berries had run out. Details of this experiment are tabulated in Table 20.

From the weights of the birds after this experiment (Table 21) it can be seen that on the average there was a loss of weight. The daily requirement per bird was 7.268 g dry

TABLE 19.

Experiment 2. Feeding Cape Bulbul with their natural food - amounts eaten. See text for details.

Day of exp.	No. of birds	Wt. of food lost from dish. g	less for 3.11% evaporation	Less 10% for spillage g	Plus termites g	Wet weight of food eaten. g
1	7	129.554	4.031	12.956		112.567
2	7	122.092	3.797	12.210		106.090
3	7	276.707	8.606	27.671		240.430
4	6	216.949	6.747	21.695		188.507
5	6	120.299	3.742	12.030		104.527
6	6	136.497	4.245	13.650		118.602
7	5	144.042	4.479	14.404		125.159
8	5	159.597	4.915	15.960	22.740	161.412
9	5	102.308	3.182	10.231	19.100	107.995
10	5	109.366	3.402	10.937	17.896	112.823
11	5	133.374	4.151	13.337	12.349	128.225
12	5	135.730	4.220	13.573	5.876	123.813
13	4	85.785	2.669	8.579		74.517

Mean amount eaten by one bird 1st - 7th day 22.63 g wet S.D. 7.143

Mean amount eaten by one bird 8th -13th day 24.44 g wet S.D. 3.711

Mean amount eaten by one bird = 23.34 g wet weight  
equivalent to 11.38 g dry weight

Mean weight of birds at start = 32.623 g  
at end = 33.445 g

% dry food of body weight = 29.39%

TABLE 20.

Experiment 3. Feeding Cape Bulbul with natural food without "live food". See details in text.

Day of exp.	No. of birds	Weight of found lost g	Less 3.11% for evaporation g	Less 10% for spillage g	Wet weight of food eaten g
1	4	63.51	1.978	6.354	55.209
2	4	62.807	1.953	6.280	54.472
3	4	69.936	2.175	6.994	60.767
4	4	62.271	1.950	6.227	54.094
5	4	122.382	3.800	12.238	106.344
6	4	83.939	2.605	8.394	72.740
7	4	69.295	2.155	6.930	60.110
8	4	74.117	2.305	7.412	64.400
9	4	44.279	1.375	4.428	38.476

Mean amount eaten by one bird 14.91 g wet weight S.D. 4.201  
equivalent to 7.268 g dry weight per day

Mean weight of birds at end of exp. = 32.828 g  
at start = 33.445 g  
% dry food of body weight = 22.18 %

TABLE 21. Weights of Cape Bulbuls used in feeding experiments 2 and 3. Taken at the start of the feeding, between experiments, at the end of experiments and prior to releasing.

Date	28th Feb.	15th March	28th March	1st June	Death weight
	g.	g.	g.	g.	g.
1	31.363	36.035	29.332	35.671	
2	30.669	28.175	33.934		
3	33.149	34.478	34.350	42.339	
4	37.342	+			22.205 6th March
5	31.809	35.093	33.697	42.805	
6	33.622	+			22.855 9th March
7	30.406	+			22.449 15th March
average	32.623	33.445	32.828		

weight of natural food and this works out at 22.18% of the bird's own weight.

The results from these feeding experiments were surprisingly similar. Namely that in Experiments 1 and 3, when the birds lost weight the food required was 21.55 and 22.18% weight of the bird's own weight, even though the birds differed in weight, and more so, the wet weight of the food varied so much (from 44.32 g to 23.34 g to 11.91 g). It is assumed that since the birds in these two experiments were losing weight the figure given can be considered to be a minimum food requirement for the species, since quite obviously they could not continue to lose weight indefinitely. In Experiment 2 the average weight of the bird increased and the % of body weight of food required went up to 29%; this was remarkable in view of the fact that the birds at this stage were all in heavy moult. In fact the additional 7% increase in food consumption shows some agreement with the figure given by Davis (1955) for additional food requirement during moult. Although the comparison cannot be strictly made since moult was also taking place in Experiment 3, I believe it is reasonable to assume that the difference in food requirement between these two experiments gives some indication of the magnitude of the additional energy required for moult.

The three experiments gave reasonably agreeable results and therefore it may be assumed that the bulbuls require approximately 24% (24.4) of their own weight of food per day.

Daily food requirements of non-fruit-eating birds in relation to their own weight has been the subject of much research. This is expressed as a percentage of the bird's own weight. Figures given by Welty (1964 p.97) are from 3.4% in the domestic fowl to 30.0% in the insectivorous Blue Tit *Parus caericleus*. An interesting experiment on the Masked Weaver *Ploceus cuculatus* (Welty, loc.cit.) showed that the amount of food required varied with ambient temperature: thus, it was 20% at 18°C, 25% at 9°C and 28% at 7°C. There is no figure given for the dry weight of food required for a fruit-eating species. Gibb (1951), however, gives figures for the Waxwing (which weighs 57 g), and indicates that 170 g is required daily. The berries referred to were *Cotoneaster horizontalis*, also eaten by the Cape Bulbul. The

average dry weight of berries taken from Table 14 is about 26% of the wet weight. This would indicate that the Waxwings took about 61% by dry weight berries. This is high, but the conditions were extremely cold.

Before considering the gross food available it is necessary to have some idea of food competition from other bird species and rodents. The only other frugivorous species in the area were the Sombre Bulbul *Andropadus importunis* and the Speckled Mousebird *Colius striatus*. The highest number of pairs recorded for each species during the three years was six. Thus in effect we have to deal with another 24 frugivorous birds as potential residents. In actual fact the total number of resident frugivorous birds varied from 20 to 26 pairs.

In addition to the birds, the Striped Mouse *Rhodomys pumilio* was a heavy feeder on *Acacia cyclops*. It would climb the trees and feed on the 'wattle' direct from the pods but only when the seed pods had already burst open. Other rodents took *Acacia cyclops* seed from the ground. *Rhodomys pumilio* is more or less distributed in association with *Acacia cyclops* (Middlemiss 1961). It is difficult to estimate the population of this mouse, but the number present must have been in excess of the numbers of birds involved. However, competition only occurred in respect of *Acacia cyclops* so far as is known. This competition is limited to the period when *Acacia* is seeding, and it is difficult to estimate its effect upon the whole food supply. As a sheer guess it is suggested that the mouse was responsible for about the same quantity of *Acacia cyclops* as the competition provided by the total number of frugivorous birds other than the Bulbul.

#### THE SUPPLY AND DEMAND FOR FOOD

From the information already given the amount of fruit available for each month of the year has been estimated. Thus, from Table 14 it can be seen that the smallest quantity dry weight of fruit available was in February, and the figure given is 1591 g. It has already been suggested that this was abnormally low, and indeed, since it is between two very much higher figures (32,460 g and 93,613 g) we can regard this as abnormal. However, it is 54% of the next lowest figure, that for November (2966 g). As a test case, and to take the extreme

low recorded, we can take the February figure with the proviso that this may well be regarded as a minimum figure for any one month of food supply from the fruit.

The next problem is to interpret the figure of 1591 g dry weight of fruit available in February. This is the figure derived from counts made in one morning. For convenience and as a rough approximation the assumption is made that this is equivalent to one day's fruit supply. If the fruit was in such demand that all ripe fruit was eaten as soon as it ripened, it can be presumed that the fruit counted was in effect that day's crop. Quite obviously there is a constantly changing quantity and berries are ripening all the time as well as being consumed. It seems reasonable, then, to assume that the number counted can in effect be considered the quantity available on any one day.

With a maximum count of 19 breeding pairs for any one year, we may assume that there must be sufficient food for at least 38 birds. Whilst in the year there were 19 pairs, 35 fledglings left the nest, so that at least in the early summer the quantity of food had to be sufficient for at least 73 birds. If we take the weight of a Cape Bulbul to be 40 g (the average is slightly less), and take the requirement per bird as 25% dry weight of food (the experimental evidence shows slightly less), then about 10 g dry weight of fruit per day is required. This gives a total requirement of 380 g per day total dry weight of fruit for the adult Cape Bulebuls alone. At peak requirement - with both adult and young birds - the requirement could very likely have been 730 g dry weight fruit per day.

It has been suggested that other birds feeding on the fruit were at most 26 frugivorous birds. The one species, the Sombre Bulbul, normally selects the harder and dryer fruits. The competition from *Rhabdomys pumilio* can only be guessed at as roughly equivalent to the other frugivorous birds. Their competition is restricted to the plant *Acacia cyclops*. If the same figure of 10 g per head is used for these competitors, and we have 52 heads, the additional demands upon the fruit will be approximately 520 g.

In February we have at minimum a supply of 1591 g dry weight of fruit available per day. The demand so far as can

be estimated totals 1250 g dry weight fruit per day. Note should be made of the fact that it is unlikely that the demand for 73 bulbuls would occur at this time of year. At the second breeding period, young of the previous season would very likely be chased out, as indeed was the case in one observation. The estimated total demand can therefore be brought down considerably. Indeed, if only the 38 adult bulbul population is taken into account, the supply of food is more than double the demand.

These figures can only be an approximation but they do give some idea of the magnitude of the supply and demands. The most important matter is that they do indicate that the food is in excess of the demand. It is my personal opinion that one could safely assume the minimum supply to be 3000 g dry weight of fruit per day so that the safety margin is quite considerable. However, having seen the selective nature of the way the birds feed one cannot anticipate that all the food is eaten. This possibly accounts for the movements in and out of the area which occur all the year round. Not only do the resident birds feed in the area and go out as well, but others from outside come in. However, if hard pressed the birds would be able to take any of the food that has been counted so that under adverse conditions there is always more than enough food.

## 8. DISEASES, PARASITES AND PREDATORS

## DISEASES, PARASITES AND PREDATORS

Birds have many enemies. In this section, all these are discussed concerning the Cape Bulbul.

### DISEASE

No known diseases have been recorded for bulbuls. However, a single specimen was collected with an abnormality known to aviculturists as 'French Moulting'. This disease is apparent when birds do not produce feathers after moult and naked skin is exposed. This condition is known to coincide with iodine deficiency, but this is not the only cause of 'French Moulting'.

The specimen affected had no feathers along chest and belly, exposing a thickened grey-blue coloured skin. It was a female collected on a ridge between the Swartkops and Sundays River near the limit of distribution of the species. The area falls within a zone of iodine deficiency from which the medical reports indicate that there is a prevalence of goitre in the resident farming community.

In view of this coincidence of 'French Moulting' and iodine deficiency known in the area, the specimen was sent to the pathologist of the Zoological Society, London. No important details could be determined from the specimen.

Further searching in the area revealed no more specimens suffering from 'French Moulting'.

### INTERNAL PARASITES

Apart from specimens collected near the study area, many birds have been collected from other parts in the Eastern Cape (over 100 in the five years). Internal parasites were found in two specimens. These occurred in the intestine and were a form of *Dypilidium*. The specimens were sent to the British Museum but identification was not possible owing to the absence of the scolex.

It should be mentioned here that in working on captive Red-eyed Bulbuls an unidentified trematode worm was found in several birds that died all in the same cage. None was recorded in wild birds.

### EXTERNAL PARASITES

Of many specimens handled both in netting and shooting, only two hippoboscid flies were recorded. These were collected and identified as *Ornithoetona laticornis* (Macqs), a rare species. Dr. Zumpt (personal communication) reported that there is only one specimen of this species in the collection of the S.A. Institute for Medical Research and it is from the Congo.

Hippoboscid flies are known to carry avian malaria-like parasites (Rothschild & Clay 1952). Consequently blood smears of the specimens of Cape Bulbuls were made but no protozoan parasites were ever observed.

No ticks were taken from the Cape Bulbul.

### BREEDING PARASITES

The local population of Cape Bulbuls were, however, subject to the attention of the parasitic Cuckoo *Clamator jacobinus* - the Jacobin Cuckoo. The only bird parasitised by this cuckoo in the study area was the Cape Bulbul (Liversidge in press). The population of Jacobin Cuckoos varied inversely to that of the host.

The study area of 20 hectares was quite inadequate for the study of the Jacobin Cuckoo. Another problem was that it was very difficult to identify individual cuckoos. This was only possible through the identification of pattern on a freshly laid egg and hence only females were identified with certainty. From this information, it was established that three female cuckoos were operating in the 20 hectares in 1959 and in 1962 only one female was identified. There were probably two females only in 1960 and 1961. The number of cuckoo eggs laid in the 20 hectares is taken as an indication of the population of cuckoos present. This is in part supported by the fact that the number of eggs laid was not related to the number of nesting attempts by the host bulbul so at least host-nest availability did not limit cuckoo egg numbers. The number of cuckoo eggs laid are given in Table 22.

**TABLE 22.** Breeding data on the Jacobin Cuckoo and the host Cape Bulbul recorded over four years in 20 hectares.

Year	Jacobin Cuckoo						Cape Bulbul				
	No. eggs		No. of Young		Hosts nests	% of eggs laid to fledge	No. of breeding		No. eggs	No. of Young	% of eggs laid to fledge
	Laid	Lost	Hatched	Fledged	Parasitised		Pairs	Attempts	Laid	Fledged	
1959	20	12	8	3	16 (73%)	15	13	22	35	15	43
1960	17	7	10	6	13 (33%)	35	19	39	93	23	59
1961	9	7	2	1	8 (38%)	11	13	21	29	2	7
1962	4	1	3	0	4 (12%)	0	15	31	58	9	15

It can be seen from Table 22 that the number of eggs laid - thus presumably the cuckoo population - dropped from 1959 to 1962. This drop was not related to the number of host breeding pairs or the hosts nesting attempts.

The Jacobin Cuckoo parasitises the Cape Bulbul by laying eggs in the bulbuls nests. Parasitism may be a symbiotic or it may be at the expense of the host and the latter applies with cuckoo parasitism. Quite obviously intense parasitism would be detrimental to the parasite itself but with the cuckoos this stage is not reached. At first it was thought that the degree of parasitism on the Cape Bulbul population was such that it could be compared with the prey-predator type balance. This was because in 1958 there were many cuckoos and very few bulbuls and it was assumed that over parasitism had drastically reduced the host population. It will be recalled that in 1958 the breeding population of Cape Bulbul was down to 9 pairs. In that year it was believed that the Jacobin Cuckoo population was even higher than in 1959 but there are no facts to confirm these subjective observations. However it is doubted that the Jacobin Cuckoo population is influenced by the host availability especially as the host can vary.

Although the parasite's population may not be affected by the numerical abundance of the host, the converse does not apply. This can be realised from the figures of the percentage of hosts' nests to be parasitised - between 73 and 12.

Thus almost three quarters of the nests may be parasitised one year and quite obviously this is potentially a serious threat to the host. Especially as the clutch of the host is normally two sometimes three eggs, the number of host young to fledge in a year of heavy cuckoo parasitism could be small. The figures indicate that when there is heavy parasitism there is not necessarily a high degree of success as far as cuckoo fledging is concerned. Thus when 73% of the nests were parasitised there was a 15% success of cuckoo eggs to fledglings, when 33% of the hosts nest were parasitised there was 35% success from eggs to fledgling stage. There is no correlation between degree of parasitism and success of parasitism. The best years for cuckoo success for fledglings in the study area was when the hosts also had their best year. This results in a fine balance with the host better able to

withstand this parasitism without critical influence upon its own population.

It is interesting to note that the average incidence of parasitism as recorded in Table 22 is 39%. This is appreciably higher than the figure of 25% as given by Reed (1968) for the Diederik Cuckoo *Chrysococcyx caprius*.

It was found that on an average 39% of the Cape Bulbul nests were parasitised in the study area. Although this figure may appear high it must not be overlooked that some of these nests would have come to grief in any case for other reasons than by cuckoo parasitism. Thus although 41 host nests out of a total of 113 were parasitised, only eight cuckoos fledged so that 33 nests came to grief. There was no evidence that the presence of the cuckoo egg increased rate of nest predation over those nests without cuckoo eggs. Thus the effective loss to the host may be considered to be only eight clutches out of 113 which represents a figure of 7%. Of the 41 nests parasitised only one successfully reared both cuckoo and bulbul young from the same brood. This phenomenon has often been recorded in the literature (Friedmann 1964) but at least under local conditions this can be said to be uncommon.

As has been shown elsewhere the changes in local population are not density dependent and hence the importance of the effect of this breeding parasitism on the Cape Bulbul population was not as serious as it might otherwise have been. In fact the figure of 35% loss of potential breeding, activity due to cuckoo parasitism, if it had resulted in a 35% increase in number of young fledged bulbuls would not have altered the existing state as far as cause and effect of annual changes in the breeding population of bulbuls. One must also remember that the Jacobin Cuckoo parasitises another host not three miles away and as suggested (Liversidge loc.cit.) parasitises the commonest occurring potential host in an area. Thus as far as the Cape Bulbuls in a larger area of, say, 100 square kilometres along the coast to the west are concerned, the activities of the Jacobin Cuckoo would be patchy or local on the population as a whole. The effect would therefore be limited. Indeed this must be the case, otherwise the parasitic habit could not survive in the restricted Cape Bulbul/Jacobin Cuckoo relationship studied.

## PREDATORS

Predation was mainly recorded for eggs or young still in the nest but there is no doubt predation on adult or full-grown birds existed. This is indicated by the adult Cape Bulbul reaction to certain predators. No actual predation of adult birds was seen but there is evidence given below which would indicate some predators could only have taken adult birds (c.f. under Puffadder). Each known predator is recorded below and following this the effect of predators on the population is discussed.

### *Lamprophis inornatus* - Olive House Snake

The alarm of several birds including three Cape Bulbul drew attention to two Olive House Snakes at the base of a bush. The larger snake had already swallowed the head and neck of the smaller. The smaller snake had a swelling midbody and the remains were identified as *Mastomys* species.

This alarm shown by the Cape Bulbul was probably innate behaviour but the fact that the snakes had taken a mammal would indicate the probability that birds would also be taken.

### *Dasypeltis scabra* - Egg-eating Snake

This snake as its name indicates, is an active predator on bird eggs. A number of nests of various species of birds were attacked by this snake. Cape Bulbul was included in the contents of nests positively taken by this species. Characteristically the egg shell is regurgitated in a compressed pellet. The eggs, as is well known, are sawed longitudinally by the serrated throat bones and the contents taken into the stomach whilst the egg shell pellet is spat out. The pellet is thus usually made up of long narrow folded lengths of shell held together by the inner skin. In marked eggs the colour and markings were still visible. A feature of the snakes' activity in regard to the Cape Bulbul was that the regurgitated pellets were usually found within half a metre of the nest on the ground or in the vegetation below the nest. With some smaller eggs the pellet is often removed some distance from the nest - presumably because the snake can escape with the smaller egg and move off more easily

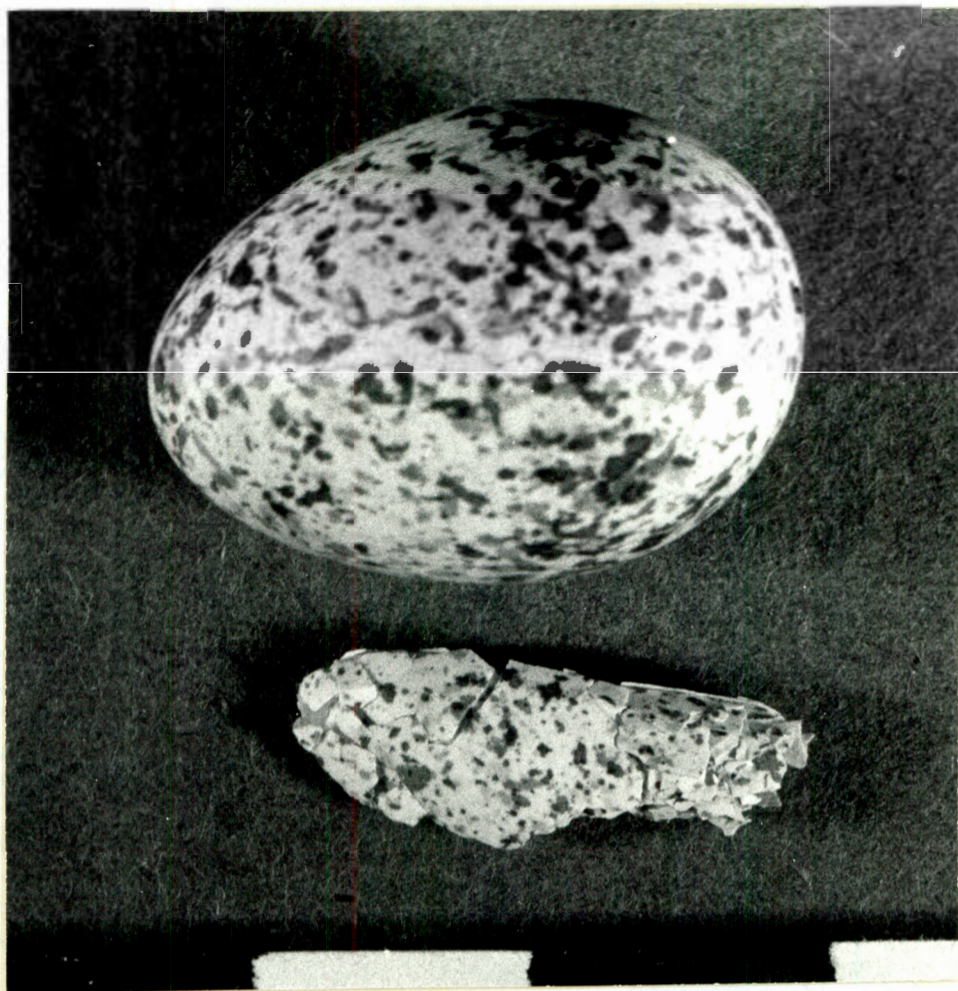


FIGURE 21b. Egg pellet ejected by Egg Eater Snake - found in Cape Bulbul's nest. Shown alongside the whole egg of a Cape Bulbul.

before 'processing' the egg (Figure 21b).

*Bitis arietans* - Puff Adder

There are two observations concerning this species. Circumstantial evidence indicated that one breeding bird was killed.

The first observation was when I had been sitting in a small hide observing from close quarters the feeding of young by nesting Cape Bulbuls. Observations started before first light. About three hours after sunrise when it was getting hot, I noticed that several birds of different species became excited over some object which slowly made its way towards the hide. This was a puff adder about 60 cm long. When several birds called alarm the snake wound itself into a circle beneath some vegetation until the noise had abated. The one parent Bulbul watched the snake within two metres of the nest. Fortunately the snake past the nesting area so that nothing happened in this event.

The second incident was less harmless. A clutch of three Cape Bulbul eggs was due to hatch within 48 hours. I visited the nest several times during the day. Pulling back a small leafy branch obscuring the view of the nest at mid day and releasing the branch something seemed wrong. Suddenly I saw a largish ( $\pm$  80 cm) Puff Adder draped over the branches just beneath the leaf canopy with its head and neck in a striking position. The snake was about 60 cm from the ground. I decided not to interfere. Both birds had noted my presence in silence. After retreating some distance one bird remained silent and close to the nest without actually returning while the second flew off presumably to feed. After two hours no change had occurred except that the mate had come and gone twice. Neither bird returned to the nest.

Next day there were several Cape Bulbul body feathers lying about the nest and bush. The eggs were in the nest and only one bird was seen but not near the nest. It was very likely that the female had eventually returned to the eggs and been struck and caught by the snake. There was no trace of the snake.

In another case but concerning another species of bird it looked as if a Puff Adder had taken the young nestlings. Probably attracted by the constant coming and going, the snake had climbed up 120 cm to investigate. On the neighbouring golf course there were regular records of Puff Adders sunning themselves up in the branches of trees and this may give some explanation from an otherwise terrestrial snake taking to the bushes.

*Circus ranivorus* - The Marsh Harrier

This bird of prey really created consternation with the Cape Bulbul. As soon as one could be discerned over the distant dunes, the alarm would go off and all birds would call alarm until the predator was out of sight. Initially the alarm would be a single note uttered from a prominent perch but when the hawk came nearer, the Cape Bulbul, would flutter excitedly, call alarm and generally remain within safe reach of a thick leafy canopy.

On one occasion a fledgling Cape Bulbul flew over an open area between bushes. The Marsh Harrier took a swerve down but the distance was too great and the prey too near cover to be caught. It did, however, indicate prey-predator relationship. It could be that the Marsh Harrier preys on juvenile Cape Bulbuls.

*Accipiter tachiro* - African Goshawk

In the study area this known predator on small birds was observed once only. The bulbuls took cover and called alarm when this bird appeared.

*Centropus superciliosus* - Burchell's Coucal

There was circumstantial evidence that this bird was responsible for the disappearance of the contents of a Speckled Mousebird's nest *Colius striatus*. The disappearance of the eggs of a Cape Bulbul's nest was also suspected to have been caused by this species. The Coucal is a known raider of birds' nests and its presence alarmed the Cape Bulbuls.

Laniarius ferrugineus - Boubou Shrike

This species was actually seen to take an egg out of the nest of the Cape Wagtail *Motacilla capensis* and fly off with the egg. On other occasions this shrike was chased off from nest bushes by several species of birds. One clutch of the Cape Bulbul was believed to have been taken by this shrike.

Dicrurus adsimilis - Fork-tailed Drongo

This was a potential predator of nestlings since it took young birds out of a nest of another species of bird in the study area.

Cercopithecus aethiops - Vervet Monkey

A troop of this monkey ranged within the study area though their main residential area was a kilometre to the east.

During the first year of study (1958) it was found that there was 100% loss of nests studied. Early in 1959 the reason for this was found to be that the monkeys had been watching the observer's early morning movements. This was clearly established when a pen had fallen out of my notebook at one Cape Bulbul's nest while I crawled on hands and knees below a thorny canopy to inspect the nest. Returning to find the pen ten minutes after the first inspection a monkey was found sitting on the nesting bush and the eggs were already destroyed. Subsequently I noted that the next morning a row of black faces was watching my movements from a particular patch of wattle. Once this was discovered precautions could be taken. The nearby water hole (erected by the S.P.C.A.) was tilted to prevent water staying in and later a trained monkey predator, the Crowned Eagle *Stephanoaetus coronatus* was flown to the glove in the area, and this chased the monkeys out of the study area.

The Vervet Monkey destroys the whole nest of the Cape Bulbul. The nest is plucked out of its site and systematically pulled to pieces. Occasionally a pad of fine nest lining remains together but it would appear that the monkey is looking within the nesting material for something

else that may be edible. Thus the complete disappearance of nests was attributed to this monkey. Usually portions of the nest lining could be found somewhere in the vicinity.

Both eggs and young nestling were taken by the monkey.

After the second year, little trouble was experienced. Occasionally a solitary monkey would work its way through the study area, visiting bushes here and there as though looking for nests. This was a random inspection and by its rareness it was evidently unproductive.

*Genetta felina* - Small spotted Genet

One bird was taken either by this species or a feral domestic cat. It must have been caught on its nest at night by some predator of this nature. There was certainly sign of the lair of one of these species just outside the study area.

*Felis domesticus* - Domestic cat

Several feral animals occurred in the area - see comment above.

*Myonax pulverulentus* - Cape Grey Mongoose

One of these animals resided near the study area for a few weeks during the nesting season. Since several nests were robbed in its area of residence, it must evidently be a potential predator on the nest of the Cape Bulbuls though it did not actually rob this species in the study area - so far as was known.

Several nests were robbed by larger predators that pulled the nests down or tilted them. It was presumed these 'bird predators' were either this or the following two animals.

*Cynictis penicillata* - Yellow Mongoose

Single specimens were observed ranging the area of study but there is no record of one having attacked a nest of the Cape Bulbul.

*Atilax paludinosus* - Water Mongoose

For the entire study period one of these animals patrolled through the study area. Though known to eat wild birds, there was no evidence that Cape Bulbul were taken here.

*Aonyx capensis* - Clawless Otter

Footprints - at first not recognised - were found near a destroyed brood of nestlings of Cape Bulbul in a nest situated only some 30 cm above the ground level. Subsequently a single animal was observed searching the area in a manner which can only be regarded as 'nesting'. Cape Wagtails *Motacilla capensis* nests were also taken by this animal. These animals are common along the shoreline here and from evidence of the droppings found inland they evidently range away from the water more than is generally realised.

*Otomys irroratus* - Bush Otomys

This rodent was identified as one of the predators through recognition of the droppings. In all cases the eggs' yolk and shell were completely eaten.

*Clavigulus murinus* - Forest Dormouse

This rodent would not only remove the eggs, shell and all but at least two made a nest in the Cape Bulbul's nest. Utilizing the lining available from the nest itself, the dormouse constructed a domed nest on the bulbul's nest base.

*Rhabdomys pumilio* - Cape Striped Mouse

One of the most important rodent predators on nests with eggs or small young. There are several records of this mouse eating Cape Bulbul eggs. This was established by identification of droppings. Characteristically this mouse could not make a clean job of eating the eggs and invariably there was broken shell and yolk to be found in the nest lining. Evidently the mouse had difficulty in breaking the eggs since there were always depressions in the lining of the nest and sometimes an egg unbroken would be found pushed into the lining at the edge of the nest cup.

DISCUSSION

The potential bird nest predators in the study area were three snakes, five birds and 10 mammals of which two snakes, three birds and five mammals were suspected of paying attention to the Cape Bulbul. Considering that this was all in 20 hectares this is quite a remarkable number of predators that the Cape Bulbul has to contend with. There are no other population studies which allow comparison and thus one does not know whether this can be considered a normal predation rate. Table 23 shows the facts as recorded.

TABLE 23. The details for each year of nest, egg and nestlings destroyed and what predator was responsible.

	<u>1959</u>	<u>1960</u>	<u>1961</u>	<u>1962</u>	<u>Total</u>
No. of pairs nesting	13	19	13	15	60
No. of nests built	30	49	25	34	138
No. of clutches or young destroyed	17	23	21	22	83
Percentage loss from clutches laid	57	47	84	65	60
Suspected predator					
Bird	3	1	2	2	8
Carnivores	2	5	2	1	10
Monkey	2	1	0	3	6
Rodent	5	4	7	3	19
Egg-eater snake	1	0	2	0	3
Puff Adder	0	1	0	0	1
Human agency	1	1	0	1	3
Unknown predator	3	10	8	12	33

From Table 23 it can be seen that Rodents seem to be the most important destroyers of nests followed closely by carnivores which are the larger mammals other than the monkeys in the area. The mammals apart from man accounted for 70% of the nests destroyed and birds destroyed 16% of the nests

where predators were identifiable. In all nearly 40% of the nests were lost to unknown causes.

The very high figure of 60% loss of the nests with eggs or young in the study area of 20 hectares over a three year period was due to predators. Figures for the northern Hemisphere concerning open nests of altricial birds averages between 45% (Lack 1954) and 49% (Nice 1957). However it is interesting to note that in the Tropics only 19% of the clutches produced young (Snow 1962) in the Black and White Manakin *Manacus manacus* - this was due mainly to predators, 86% of which were snakes.

There is no doubt that the poor rates of reproduction of the Cape Bulbul (which is discussed in detail elsewhere) are primarily due to the heavy predation on the eggs and young in the nest. Compared to birds recorded from cool temperate regions summarised by Nice in a table concerning 35 studies involving 7788 nests, there are only 5 records of success below 40%. So that compared to cool temperate conditions, the predation in the study area was comparatively high. With only the figure by Snow (1962) on the Black and White Manakin for the tropics it is insufficient to draw any comparisons with the low figure of success that he obtained.

## 9. REPRODUCTION REQUIREMENTS

## REPRODUCTION REQUIREMENTS

In some species of birds specialised reproductive requirements independent of the bird's own internal rhythms are essential for successful breeding. Absence of such requirements may inhibit reproduction. Some idea of the fine discrimination that does occur in breeding requirements can be imagined by considering the fact that the Black-eyed and Red-eyed Bulbuls interbreed in areas where man has altered the natural vegetation. Some barrier that had existed in the natural vegetation has gone and the two birds that were kept apart are no longer separated.

6 / Although this section is closely associated to Section 4 - the seasonal changes - the latter concerns mainly physiological problems whereas this section concerns more the habitat. There is some repetition of what has been said but this is inevitable, when considering the ecology of breeding requirements.

### BREEDING HABITAT

It is difficult to determine the limitation of habitat for breeding in the Cape Bulbul. Indeed, I rather expect that the limits are not placed on breeding requirements so much as food requirements as mentioned in Section 4 - Distribution. Where the bird occurs, even though in a sparsely distributed population, breeding appears successful as elsewhere. Several nests were found in the lower valley of the Sundays River - indeed with few pairs of Cape Bulbul, it is easier to find their nests.

In all 97 nest sites were recorded in detail in the study area, and are recorded below. From the point of view of general habitat, one can only say that all but one of these sites were situated in bushes or shrubs. Indeed no nests were found in the low xerophilous "Cape" vegetation of Restios, Struthio, etc. which covered quite a portion (40%) of the study area.

Elsewhere the Cape Bulbul has been found breeding in what might be termed unsuitable habitat. One nest I can recollect in the Bredasdorp district was situated in a lone

shrub some 100 metres from its nearest neighbour on an open hill without much suitable cover or feeding within 200 metres. The danger from predators (hawks and especially Marsh Harriers which were common) for the parents flying back and forth across the open heath was obvious. Here the only requirement was a bush suitable in size and cover.

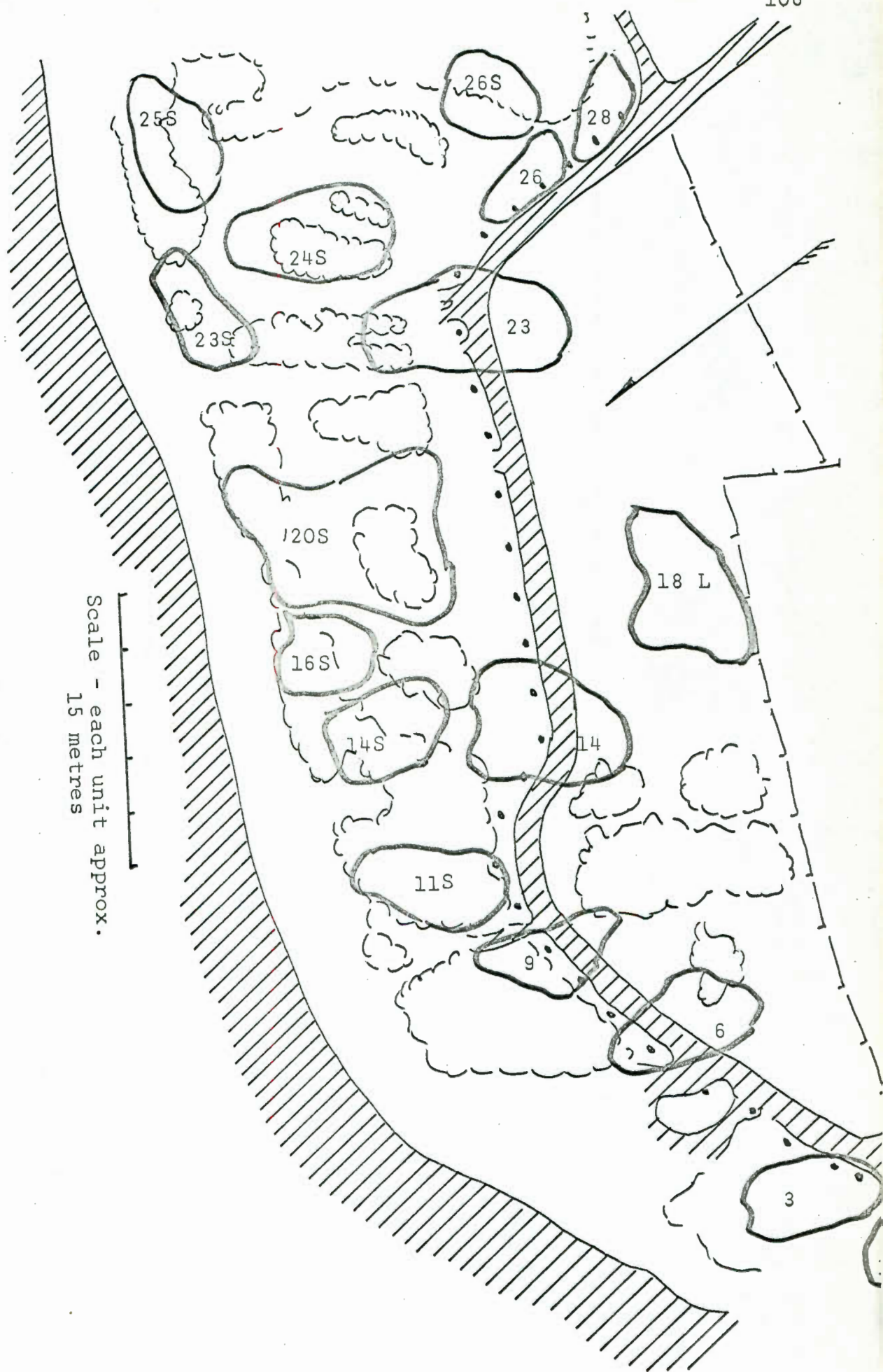
It seems then that the habitat for breeding is more likely to be restricted by the birds' food requirement than any special nesting need.

#### TERRITORY AND TERRITORIAL BEHAVIOUR

A definition of territory as given by Tinbergen in "A New Dictionary of Birds" (Landsborough-Thomson 1964) is "a defended area". Such a definition is a most inadequate one for the Cape Bulbul and if it is strictly applied, perhaps one should use the phrase "Home Range" as the heading for this section.

The breeding pair of Cape Bulebuls occupy a definite and regular area. Within this area the male bird will have one or two well-defined prominent song perches. Also within this area will be two or three smaller areas which are favoured for nest site. The extent of the Cape Bulbul's so-called territory is illustrated in Figure 22. From this it can be seen that the areas of occupation vary from 200 square metres to some 1000 square metres. For the most part these territories did not substantially change from year to year even when different pairs occupied the area from those birds of the previous year. There was only one record where a pair (16) increased its area of proclaimed activity during the breeding season.

The territory was occupied from July or August (depending upon 'the season' being early or not) through the main breeding period September to November, less strictly from December to mid-February when a definite return to territory occurs. By April the birds might have returned to the territory or they might range about for food over an area of several square kilometres. This continued through to July or August again. During the winter period, April to August



**FIGURE 22.** Sketch plan of study area indicating some of the territories occupied by Cape Bulbuls by the heavy circles. The numbers applied to each pair are also indicated.

the entire local breeding population might return or only the odd pair. During this period there was one observation of a resident pair which chased off a single intruder so there was some winter territorial behaviour.

Although there were definite song perches in each area, these were not defended as well as one would expect if the birds were defending the area. Thus there are two records where neighbouring males were caught perching on song perches by the resident male and challenged. In the one instance the resident bird was calling 20 metres away from his favourite perch; when it saw the intruder it flew up immediately and landed five metres from the perch. After a minute the stranger left, without pursuit by the resident male which returned to its perch 20 metres away. The second incident was where a strange bird flying through the study area settled incidentally on the song perch. The resident male flew to a perch near the strange bird, called the challenge note and partially fanned its tail in threat. The strange bird flew on without further delay and the resident did not pursue it. The telephone poles and wires through the study area also formed favourite call perches but there seemed less defence for these sites than the normal lower perches (there were no trees as tall as the telephone poles).

Inspection of the territories figured in Figure 22 will show some territories along the coastal sections and others inland. In collecting nest material or food for young, the bulbuls would fly some distance and inevitably cross occupied territories. Thus there are six records of pairs that regularly crossed their neighbouring territory. These flight paths were tolerated even when the foraging bird paused along the route. Only in one instance was there any indication of resident males' resistance. This was for a bird (14 L.) that constantly assumed a threat posture when the neighbour (12) flew across its nesting area (? displacement or real threat).

If pursuit did take place the resident male would chase the intruder a comparatively long way off - at least through a couple of other territories before abandoning the chase.

There was some defence of the nest bush itself. But the intensity of defence varied enormously between individuals

apparently unrelated to the stage of breeding. There is a record of a bulbul which was chased off when nine metres from the nest whilst another bird was tolerated on the nest bush without active pursuit, though in the latter case the nesting bird came up and sat calling at the intruder which immediately departed. There are 19 records (Table 24) of other species of birds being chased away from the nesting bush and four where no action was taken by the breeding pair. The Sombre Bulbul was tolerated on the nesting bush until it attempted to call from the bush, then the resident Cape Bulbul chased it off by threat.

The territory or better 'home range' of the Cape Bulbul is the one in which breeding takes place and not feeding. This is the major difference between the standard concept of territory as used by northern temperate workers (Tinbergen, Howard, Lack, etc.) and the territory as considered here for the Cape Bulbul. Feeding in the Cape Bulbul is a social activity and not confined within a limited territory from which other Cape Bulbul are kept out. What motivates the 'territorial' activity is not quite certain or what objectives it serves is not clear. It was found, for example, in pair 13 which had a nest and eggs near the sand dunes that the male which had song perches only in the coastal section, suddenly took to a song perch near the other (south) side of the study area. The new song perch was certainly out of earshot on a very windy day from the incubating female. The song perches are used particularly vociferously prior to nest building through to hatching of the eggs. They are used primarily for the song which is called loudest and longest during nest building operations and early incubation. Records of spells of singing lasting from 10 to 23 minutes from such perches were made during this period only. Though the birds could occupy a territory at any time of year, it was seldom proclaimed as such by the male from the song perch except during the nest building and incubation period. Indeed, until nesting commenced it would often take considerable searching to establish the presence of a pair out of season.

At this stage one can discuss briefly the form, purpose and function of territory in the Cape Bulbul leaving for

TABLE 24. Record of species chased from the nest bush by breeding Cape Bulbul in the study area.

Species		No. of times seen chased from nest
Jacobin Cuckoo	<i>Clamator jacobinus</i>	10
Burchell's Coucal	<i>Centropus superciliosus</i>	1
Speckled Mousebird	<i>Colius striatus</i>	1
Sombre Bulbul	<i>Andropadus importunus</i>	3
Fiscal Shrike	<i>Lanius collaris</i>	1
Boubou Shrike	<i>Laniarius ferrugineus</i>	2
Bully Seed-eater	<i>Crithagra sulphurata</i>	1

later discussion the more controversial issues. Reference is made to two important articles on territory; the first 'The Role of Territory' by M.M. Nice (1941) and the second 'The Biological significance of the Territories of Birds' by Hinde (1956) and both articles discuss objectively the various viewpoints on territory. Using the sub-headings of Hinde (loc.cit.) the Cape Bulbul possess the 'large breeding area not furnishing most food' and the behaviour can be classified in the group 'self-advertisement' but not within the territory since when the birds are building the male will accompany the female and sing where the female gathers nest material. The objects defended, as listed by Hinde but, in order or priority for the Cape Bulbul would appear to be mate, nest site and song-perch. The site attachment is without aggressiveness but the reasons given for this type of site attachment do not follow those given by Hinde. Under hostile activity there are several sub-headings and it is better to discuss each in turn in relation to the species studied than to attempt to put them in order of importance.

(a) Limiting density: In this case we are dealing with a habitat that is able to carry more Cape Bulbuls than normal through the fact that an exotic plant provides important food and nest sites. Perhaps, through the dispersal which territory brings about, this highly favourable habitat is not over populated but the picture is not as simple as this. Why should immigration and emigration occur if the habitat is so favourable? Why should territory function as a dispersal mechanism when not all territories are occupied? There is no obvious survival value of territory in Cape Bulbuls that requires it to function as a density limiting factor.

In this section 'limiting density' is regarded as quite distinct from dispersal per se. It is assumed that limiting density is referring to a population control by interaction between adult breeding pairs. Dispersal and its effect in reducing nest predation is discussed under section (f).

(b) Pair formation: It has been shown by Broekhuysen (1963) for the Orange-breasted Sunbird *Anthobaphes violacea* that territory functions in bringing the male and female back together to nest in the same territory - the advantages of

which are obvious. There is no indication that territory functions in this way with the Cape Bulbul in view of the fact that pairs remain together through the non-breeding season and return to the old territories. Even though in one case a pair returned to the old territory and then subsequently split up, the part played by the territory here was incidental (see later).

(c) Reduction of interference: This appears to be out of the question with the bulbul which is essentially a social bird and presumably does not require the seclusion that Nice's sparrows required.

(d) Nest site: The abundance of nest sites would eliminate any function of territorial activity to defend such a site.

(e) Food: As already mentioned the birds are social and food is not taken only in the nesting territory of the pair.

(f) Reduction of loss to predators: Without doubt this is the most important function of the territory for the Cape Bulbul. With the high nest predation the importance of reducing the predation can be appreciated. Quite obviously if the nesting was of a loosely social nature as is sometimes found in the *Timaliidae* Babblers any predators would make short work of whole colonies. The *Pycnonotidae* are somewhat similar in some respects to the *Timaliidae* since both are vociferous and conspicuous in their habits. The social feeding habit has possibly some value in this problem of nest predators too for with conspicuous habits there is an advantage in the fact that feeding is carried out some distance from the nest - which keeps attention away from the territory where the actual nest is. Nest predation is evidently one of the main problems limiting breeding success and quite obviously, if the nests are widely dispersed this has a survival value. The ineffective searching by the wandering monkeys through the study area illustrates how the most advanced and effective predators' influence can be dissipated by dispersion.

#### NEST SITE

Mention had already been made that nest site is dependent upon a tree or shrub. Nests are always situated

on branches five to 20 mm in diameter, usually these branches are between the horizontal and about 30 degrees above or below the horizontal. The nest is situated just within the outer canopy of leaves and not usually deep in the bush. The only nest not found in a bush was actually in a creeper hanging over a dead bush so that the nest was in a bush but the canopy of green leaves was provided by the creeper.

The nest position is evenly spread from ground level upwards - see Table 25. From nest records taken from elsewhere in the species' range, there were twice as many nests higher than 150 cm as the two next commonest heights of 60-90 and 90-120 cm. In the study areas there were no higher trees that supplied the requisite conditions. The taller trees had their branches pointing upwards at the higher levels and thus the angle of the stems were unfavourable for nesting for the Cape Bulbul.

The shrubs used for nesting in the study area were very variable. Some were small leaved, some large leaved, some with xerophilous leaves, others with soft coastal foliage. Most unexpected was the discovery that the most popular nesting tree was the exotic *Acacia cyclops* the Wattle or Rooikrantz with 24 nests recorded. Compared to 12 nests in *Chrysanthemoides monilifera*, 12 in *Rhus crenatus* and six in the Milkwood *Sideroxylon inerme* of a total of 63 identified bushes. Information from the S.A.O.S. nest record cards from elsewhere in the birds' range added to those of the study area gave 20 different species of bushes used for nesting. Included in the range elsewhere are the exotics Eucalyptus gum tree, Cyprus tree and Pittisporum. The fact that so many exotics play such an important part for nesting sites for the Cape Bulbul would show that the bush or tree supporting the nest is not a specialised factor that might inhibit breeding.

#### NEST MATERIAL

The nest is cup shaped constructed in four main sections, the foundation, the bulk of the structure, main lining and final inner lining (Figure 23).

The materials used are fairly variable even within the study area and there does not appear to be any specialised

TABLE 25. The height above the ground at which the Cape Bulbul's nest was situated.

Height above ground level cm.	30-60	60-90	90-120	120-150	150+
No. of nests recorded in the study area	5	5	5	5	5
No. of nests recorded in the Western Cape	2	18	19	11	37



FIGURE 23. The nest. Above one egg and two nestlings of the Cape Bulbul with a Jacobin Cuckoo egg. Below showing structure with normal Cape Bulbul clutch of two eggs and two Jacobin Cuckoo eggs.

requirement.

The base is made of coarse twigs. The bulk of the nest is made up of twigs, rootlets, grass-stems and dried twigs of vegetation still retaining small leaves - such as *Passerina* species. The main lining is highly variable with layers of paper, a few feathers, sheep's wool, cobwebs, bits of rag or any similar human rubbish including string, cotton-wool and tissues. The final lining is of some vegetable material usually fine pieces of *Restiostems* but fine roots are also used so that the requirements of *Restiostems* is not necessarily a limiting factor. A nest built rapidly and three-quarters completed in ten hours of building consisted of 125 items as follows: 55 small sticks, 52 bits of rootlets (longest measuring 60, 50, 35 and 30 cm), nine pieces of paper, five dried leaf stalks, two pieces of grass, one piece of creeper and one piece of string.

#### FOOD REQUIREMENTS FOR YOUNG

This matter has been touched upon in Section 7. The food of young is 30% insect food, 27% berries and 33% unidentified food. At the time of year that young are being fed, it has been shown there is an adequate food supply.

It is doubted that there is any limit or restriction on breeding on account of food for young.

#### OTHER FACTORS

The other external factors such as climatic, social and local movements have been discussed in relation to internal rhythms which in themselves will provide the most important reproduction requirements.

#### DISCUSSION

Reproductive requirements in the Cape Bulbul are not very great and can hardly be considered very specialised. It is, in fact, a bird of catholic habits and requirements.

Perhaps the most important finding was the absence of a true territory in the restricted defined sense of a 'defended' area. Constant mention has been made through this work of

## 10. BREEDING BEHAVIOUR

## BREEDING BEHAVIOUR

The general breeding behaviour is a most important and critical period in the life history of any bird.

The collected information has been tabulated wherever it was sufficient to indicate trends.

### CHANGES IN PARTNER

The life expectancy of an adult breeding bird according to the figure given earlier is about three years. It can be expected that there would be few records in the field of birds more than three years after ringing as adults, especially since the main period of study only extended four years. There were 19 adult birds ringed with colour rings amongst which there were six breeding pairs. Five birds were ringed in 1959, three in 1960, 10 in 1961 and one in 1962. One ringed pair remained together and bred in the same territory for three successive years. In the fourth season the same area was occupied by two unringed breeding birds. Another pair (white and red) bred together in 1959, in autumn 1960 they were seen together more than a kilometre from the nesting area and in mid-August 1960 they were seen together in their old nesting area. However, at the end of August, the male (white) had a new colour-banded mate (yellow) - which had been a neighbouring breeding bird the previous year. The female of this original pair (red) was mated with an unringed bird where the new female (yellow) had bred in 1959. There were five colour-marked birds that returned and bred in the same area in a second year. Two birds recognisable through a yellow spot and white patch were seen in two successive seasons in the same area.

The evidence is a little conflicting on whether the species retains its partner for life. However, despite the one case of a change of partners, I believe that the Cape Bulbul normally pairs for life. The fickleness of the red/white pair was from the first confusing because after these two had been caught, the red was seen to solicit and mutually preen with an unringed bird. The same day, the white male chased the red female. The next day these two birds were

together. There was ample evidence of single males and females separately returning to the same breeding territory in two successive years. This was not necessarily to join up with a partner of the previous year that might have been wintering apart from its mate. It was thought that several pairs returned to the same site including some where one partner was marked. Where the birds are unringed the evidence cannot be accepted. Dixit (1963) refers to *Pycnonotus cafer* as changing its partner but provides no evidence from marked birds.

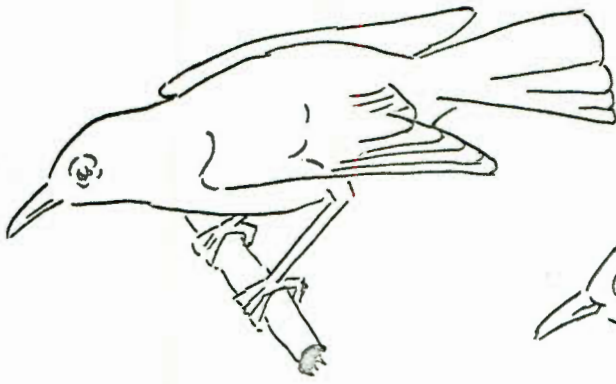
The period when partners are selected would appear to be about May and June. It is at this period that display is first noticed and groups of three and four seem involved in this display. This may concern only the young birds of the year since it has been shown above that older birds may change partners as late as late August, a time when breeding had already commenced in some years. However, since no ringed young birds were seen involved with courtship, there is no certainty when this may happen.

#### DISPLAY

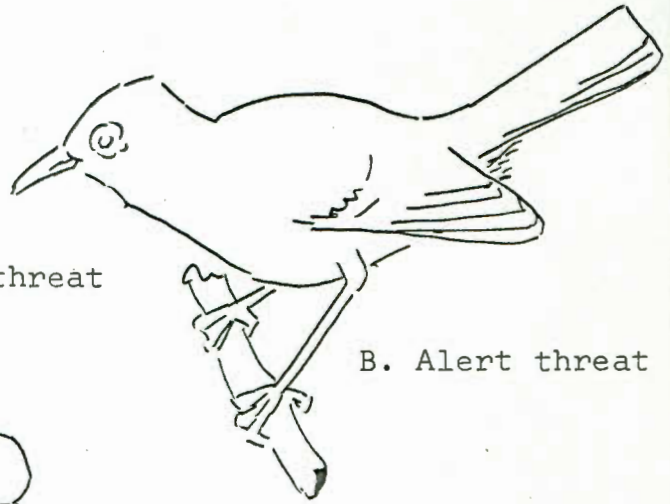
The behaviour of the Cape Bulbul has not been described. The following displays were noted.

##### (a) Threat

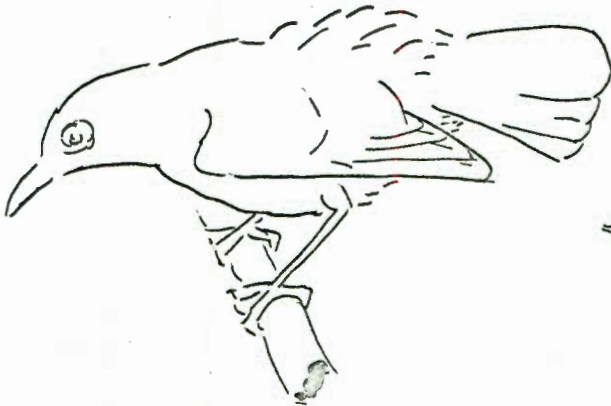
- i) Crest flattened: In low intensity threat the crest is flattened and the head is lowered so that the crown and back form a straight line. The wings are somewhat lifted out so that the carpal joints are prominent. In high intensity threat the tail is spread wide and turned down (Figure 24a).
- ii) Alert threat: When the bird is more active and excited, threat is shown by a slight lifting of the crest, the tail is lifted up and the wings are pressed close to the body. The under tail coverts are fluffed out (Figure 24b). Further provocation of a bird in this attitude makes it spread its tail widely.



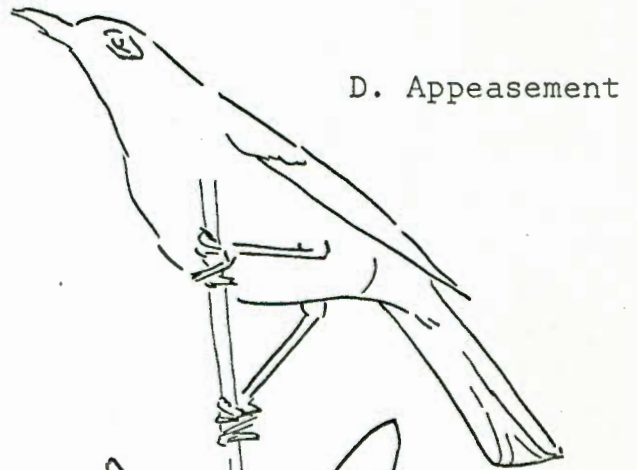
A. Threat - crest flattened threat



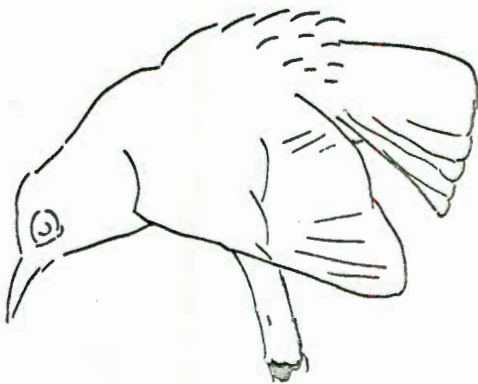
B. Alert threat



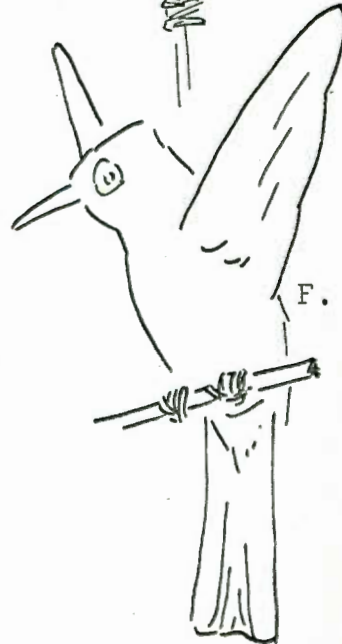
C. Fluffed threat



D. Appeasement



E. Arched-fan courtship



F. Wing flicking courtship

FIGURE 24. Sketches of behavioural stances in the Cape Bulbul.

- iii) Open beak threat: Similar to (i) but the bird keeps its bill wide open showing the red gape. This was seen to be performed by a ringed male bird.
- iv) Fluffed threat: This was used when another species of bird was threatened. Similar to (i) but the wings were spread out more and the back and rump feathers were fluffed up giving the appearance of a slightly larger than normal hunched bulbul (Figure 24c).

An interesting variation on the intra-specific threat was observed when a Boubou Shrike *Laniarius ferrugineus* came near a nest. Here the threat started by the bird fanning its tail and swaying it up and down. As the shrike came closer the Cape Bulbul hopped forward and lowered its head and crown so that they formed a straight line with the back.

(b) Submissive or appeasement postures

This is very similar to a.(i) above, but at all times the beak is lifted upwards. The crest is flattened and the neck is drawn in but the wings remain compressed to the side as at rest (Figure 1d).

In a caged bird being attacked by another, the bird being attacked constantly turned its head away from the attacker presenting the back of its head almost as though it was trying to shield its eyes from the attacker.

(c) Courtship

- i) The arched fan: The crest is flattened with head bent right forward and down and usually with back sloping forward. The primaries are spread out widely and the tail is spread so that the outer tail feathers are close to the primaries. The rump and lower back feathers are fluffed up. This form of display was usually performed with the male on a higher perch than the female and from below the yellow under tail-coverts showed up conspicuously against the darker flight and tail feathers (Figure 24e).

Variations and modifications of this form of display were the commonest forms of courtship. These displays and postures were seen from June through to December and again in February and March.

- ii) Fluttering flight: The first signs of courtship was usually in the form of an exaggerated fluttering flight, with tail well spread, around the female.
- iii) Wing flicking: Attention is drawn to this display by a loud chattering trill uttered by a bird in a very upright stance, with tail down. The wings which appear to remain folded are flicked quickly up to a vertical position over the head (arms up) and then snapped down to the side of the body. This action is repeated so quickly that it is not possible to see the details of movement. This behaviour was performed by a ringed female once and occurred only at the height of the nest building egg-laying stage.

Courtship displays were often performed with one partner sideways on to the other except for the wing flicking which was always performed facing the second bird. Sometimes the birds performing the arched fan display would sway from side to side and even swing right around and complete one or two revolutions on its perch in front of his mate.

Another display was commonly seen at the height of nest building and laying. It mainly consisted of an excited and loud chattering trill uttered by a bird in a very upright stance, with tail down and the wings which appeared to remain folded being flicked up and down in a vertical movement from over the head back to body side. The displaying bird always directly faced the other bird (Figure 24f). It is believed that this was performed by the female as on one occasion this was definitely established and on an other occasion it would explain the sequence of subsequent events.

On one occasion a displaying male, with head bent well down was approached by a strange female which sidled up towards the male. The mate, however, turned up on a nearby perch and the male displayed with greater frenzy to both females. After a while, the mate assumed a threat posture, and the strange female left.

Pre-copulation display was not spectacular. The crest was slightly raised, the tail slightly fanned and turned up above the horizontal. The female bent her head down with flattened crest but the body remained horizontal and the wings were rapidly but only slightly flicked in and out in a folded position.

Mutual preening was often seen in the Cape Bulbul at all times of the year and could occur between paired birds but was also recorded between parent and 54 day old fledgling. The birds could sidle up to each other until their bodies met. Preening might be beak to beak - usually only performed during courtship. Normally one bird would preen the other behind its head but sometimes both would preen each other.

It is interesting to compare the displays of the Cape Bulbul with other bulbuls as well as other birds in general. It might be noted that in threat very often a bird will make itself as large as possible and often crested birds will lift the crest. Here in the Cape Bulbul this behaviour is not seen except in one form of display. Also the difference between threat and appeasement is not very great here. Comparing the behaviour of *Pycnonotus cafer* and *P. leucogenys* as recorded by Short (1964) there are several differences in behaviour; some can be attributed to the colour pattern differences of the displaying bird. Since the study was from caged 'pairs' there may have been some difference due to the artificial conditions.

- i) Tail spreading: Accompanied by raising of crest and semi-fluffed body feathers. This compares with the 'alert threat' display mentioned for the Cape Bulbul.
- ii) Tail flicking: Tail movement is quick upwards, followed by slower dropping of the tail to normal position. Associated with a low intensity response

and lacking in encounters resulting in overt attack. This was never seen in the Cape Bulbul; where only the swaying (not flicking) up and down occurred and this was at a high intensity response seen only once when a nesting bird was moving in towards a Boubou Shrike near the nest.

- iii) Gaping: Seen only in *Pycnonotus leucogenys* and tentatively considered to be a threat display. Although rarely seen in the Cape Bulbul this gaping is definitely a part of the threat display since the carpal joints were always lifted away from the body during the performance.
- iv) Crest Raising: Considered the commonest threat display of *Pycnonotus cafer*. This is most certainly not the case in the Cape Bulbul where normally the flattening of the crown feathers is the most frequent and first evidence of threat.
- v) Undertail coverts spread: This was not seen in the Cape Bulbul but might in fact have occurred during the high intensity courtship display when the lower parts was not easily seen from anywhere except immediately below the displaying bird.
- vi) Bill up: No really similar posture was noted for the Cape Bulbul. The appeasement or submissive posture had bill upwards but not as vertical as the display described by Short (loc.cit.).
- vii) Crouch: This 'sleeking' of feathers and facing the opponent was rarely observed in the Cape Bulbul and was usually a flight intention attitude.
- viii) Pendulum display: Not noted at all in the Cape Bulbul.
- ix) Head Turning: This was observed once in the caged Cape Bulbul when a dominant bird was attacking an individual.
- x) Wing flicking: Similar to the same display mentioned that is performed by female Cape Bulbuls. Short regards this as a threat display, an attack followed this

display. Twice in the Cape Bulbul the display was followed by departure of a second bird, and on one occasion the chattering and display attracted two neighbouring species to the calling bird. However, in the Cape Bulbul a female coming off the nest during incubation greets its mate with this display.

### SONG

As explained above, song perches exist but these are not very vigorously defended. In the Cape Bulbul it was found that the male usually has two or three song perches and the nesting sites need not necessarily be near. Indeed there is no doubt that in one case already mentioned, a new song perch was taken up that was undoubtedly beyond earshot of the incubating mate on a windy day. The perches could also be varied during the breeding period.

Song as proclaimed in loud and noisy form was only heard when nesting activity was under way and during incubation. It rarely occurred except at times when strange bulbuls or predators caused some excitement to the male bird. The usual call was a loud melodious "piet-my-jol" or sometimes a "Piet, Piet-my-jol" with interspersed songs in short bursts paraphrased as "chup-wheet-churryup"; with a slightly more challenging tone "what-yer-rightaway" and a cheerful oft repeated "whetcha-willya".

The typical call note, is the "piet-my-jol" which is not particularly loud but it carries well. This may be heard throughout the year but usually not repeated frequently in quick succession unless provoked by some event.

The excited chatter described in "wing flicking" sounded as a sharp quick "chop-doodle-it" or "chop-chop-doodle-it" repeated at least half a dozen times in a quick excited manner.

When the male accompanied the female as she collected nesting material, his song sounded like:- "chip-chewip-chuddle-oo" or "chup-chip-chicheeoo".

The communication note, when one bird was calling for its mate can be described as a "chirrup" and when with slight anxiety "key-link" or more anxiously "chit-tee" or "chit-tee-tee" or "whit-whit" followed by the alarm note, a "churr" or "churrert" often repeated in a low tone.

The impression was gained that the normal and the loud form of the song could occur together during the same period. Knowing that the Cape Bulbul did not defend its territory very strongly, the need for a loud advertising song would not be so important in male birds. The mere fact that the male did sing loudly from a song perch may have acted as a form of threat anyway. However, it would be expected that the female would be stimulated by such song prior to the commencement of nesting.

#### DIVISION OF LABOUR

The selection of the nest site would appear to be the duty of the female. In one instance, it was seen that the male (white) sat calling while the female picked up a twig and flew into a bush - the process was repeated by the female but each time flying to another bush; until after ten minutes, it was noticed that she returned to the same site several times and continued in the new site subsequently. Dixit (1963) holds the opinion that the female *Pycnonotus cafer* also selects the nest site.

As in the case of *Pycnonotus cafer* (Dixit 1963), the Cape Bulbul female does all the nest building. Whenever the female flies off after nesting material, the male follows and keeps close to her. Usually he sings from nearby bushtops. On two different occasions, two different male birds, were seen carrying nesting material to the nest, so that it cannot be said the nest is built by the female only, but it is certainly rare for the male to assist. The only times that this was seen was during the early stages of rapid rebuilding.

Only the female incubated and on no occasion was the male bird seen on a nest containing eggs. The male was seen to brood the young when they were small but only on rare occasions. Details are given below.

The feeding of young was shared by both male and female, through the nestling stage and early fledgling period. If the female was occupied at a second nest, the male alone would feed the fledglings but by this stage the young were feeding themselves as well.

### NEST BUILDING

The female does virtually all the building of the nest. Of 52 observations where the sexes could be determined, the male was only seen to bring in nesting material twice.

No building activity was observed by any bird prior to 7 a.m. (sunrise on August 21st is 6.51 a.m.). Building was only observed irregularly between 7 a.m. and 11 a.m. with greater activity between 8 and 9 a.m. (8 minute intervals) and 10 - 11 a.m. (6 minute intervals) (Table 26). A total of only 530 minutes was spent watching nest building activities at the nest sites but if any building material was seen being carried elsewhere, a note was made of the observation. These casual observations of nest building activity all fell within the periods given above.

However there may be exceptions and records only extend through early building activities. For example, nest 24 on 12th November at 6.20 a.m. 1959, the nest base only was completed. Another inspection revealed at 5 p.m. 24's nest was virtually completed. On 13th November, 7 a.m. there was no change in the nest; by 11 a.m. the lining was much thicker than earlier and by 3 p.m. the final lining was almost completed. These observations showed that nest building activity took place only during the middle part of the day, - this particular nest was built in an unusually short time, and most probably was an exceptional case.

The time taken to complete the building of a nest varies according to the time within the breeding season. The longest recorded period was ten days' building and that was in August. The shortest period for completion of nest was two days recorded in October and November (Table 27). It is interesting to note that the length of time to complete a nest was slightly longer during the two peak nesting periods of September and November.

### EGG LAYING

There was a definite lapse of time between the completion of the nest and egg laying. The interval was recorded from 35 nests. The results were as follows:

TABLE 26. The timing of nest building activity as recorded for different periods of the day. The lack of records for afternoon was because detailed observations were only made whenever nest building was seen.

Time of day	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19	Total
Minutes of observation	0	0	65	240	77	58	28	5	35	0	0	22	0	0	530
No. of times building	0	0	5	31	6	10	0	0	1	0	0	0	0	0	53

TABLE 27. Observations on the time taken to complete the construction of the nest in different months of the breeding season.

Month	No. of Records	Average time to construct nest in days	Max. and Minimum construction time in days
August	1	10	
September	8	5.5	4-7
October	8	3.4	2-5
November	17	4.1	2-7
December	5	4.0	3-6

Interval of time between nest completion and laying of first egg -

less than	24 hrs.	-	7 occasions
between	24-48 hrs.	-	13 occasions
between	48-72 hrs.	-	9 occasions
between	72-96 hrs.	-	5 occasions
greater than	96 hrs.	-	1 in August

It is possible that some predators may have removed the first egg before an observation was made but this is unlikely to affect the above figures significantly.

The time at which egg-laying occurred was accurately determined by use of the continuous temperature recordings made to determine incubation periods. A thermistor was placed so that it protruded into the bottom of the nest cup and this was coupled to a portable recording potentiometer. The following times were recorded:

<u>Nest</u>	<u>1st egg</u>	<u>2nd egg</u>	<u>3rd egg</u>	<u>Date</u>
26	-	-	5.50 a.m.	11.11.59
24	5.20 a.m.	5.36 a.m.	-	27.11.59
3	5.48 a.m.	6.52 a.m.	-	6.12.60
4	5.35 a.m.	5.48 a.m.	6.03 a.m.	8.12.60

In the case of Nest 4, the female actually came onto the nest at 5.12 a.m. and was on and off at short intervals after this. It is assumed that she was disturbed at this period. According to Dixit (1963) *Pycnonotus cafer* lays her eggs much later. In all cases, except one, the second and third eggs were laid at 24 hour intervals. In the one exceptional case a 48 hour interval occurred between the two layings.

#### CLUTCH SIZE

The clutch size was two or three in the study area. Elsewhere clutches of four or five have also been recorded. Details have been given in Tables 28 and 29.

From the Tables 28 and 29 it can be seen that 61% of the full clutches from the Western Cape were more than two. It can be seen from Table 26 that the three egg clutches were

TABLE 28. Completed clutch size for each year with success of hatching in relation to clutch size. N.B. There is no statistical difference between the mean difference success of fledglings from 2 egg and those from 3 egg clutches.

	1959	1960	1961	1962	Total
No. completed clutches	13	31	10	20	74
No. 3-egg clutches	9	20	4	12	45 (61%)
No. 3-clutch-hatched-fledged	3	4	0	3	10
percentage success	33	20	0	25	22
No. 2-egg clutches	4	11	6	8	29 (39%)
No. 2-clutch-hatched-fledged	3	9	2	1	15
percentage success	75	82	33	12	52
No. 2-clutch 1 only hatched-fledged	0	2	0	1	3
No. young hatched	18	40	4	23	85
percentage of eggs	51	49	8	44	32 → 44
No. young fledged	15	32	4	12	63
percentage of hatched	83	80	100	52	74
percentage of eggs	43	39	8	24	32

TABLE 29. The distribution of successfully hatched clutches according to the different months in the study area and from the Western Province for clutch size.

	Clutch size	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total
Western Cape	2	1	10	1	1					14
Western Cape	3		4	6			2	1		14
Western Cape	4		1	1						2
Western Cape	5			1						1
Total for Western Cape		1	15	9	1		2	1		
1959 : Study area	2			2	1					3
1959 : Study area	3				3					3
1960 : Study area	2			4	5	1			1	11
	3			2	2					4
1961 : Study area	2				1	1				2
	3									
1962 : Study area	2		1		1					2
	3			1	1					2

more numerous than the two egg clutches for all the years except 1961. This will be discussed later. There is not sufficient evidence to indicate any advantage in either sized clutch (see below).

There are 19 records of identified females laying more than one clutch; fourteen females in one season and five from one year to the next. Nine of these records show no change in successive clutch size. Five of these records show an increase from a two-egg clutch to a three-egg clutch. What is of some interest is the fact that five of these records show that the second clutch from the same bird was actually smaller than the first clutch. These records are too few to be able to indicate reasons why there was a reduction in clutch size.

### INCUBATION

From the temperature recordings it appears that the female did not sit the day before egg-laying commenced. Observations showed that the female first came to the nest at intervals between 16 and 58 minutes before the egg was laid.

Incubation normally started with the laying of the last egg of the clutch. The figures for a complete period from one nest was recorded on only one occasion; even here the recording machine broke down on the 9th day but the record was otherwise complete. The information is summarised in Table 30, Figure 26. The chart reading for the 12th November is shown for the early morning in Figure 25. The clear drop in temperature when the bird first gets off the eggs and the rise when incubation recommences is clearly visible. Table 30 also shows the other relevant incubation information as documented by Broekhuysen (1959), Kendeigh (1952) and Nice (1937 and 1943).

From the information from this one nest it can be seen that there is a daily rhythm of less coverage in the first few hours and the last hour of daylight. This is particularly noticeable. The number of times the female gets on and off the eggs varies as incubation proceeds. During the first half of the incubation period she sits more patiently on the eggs. The mean attentive periods for the first eight days is 24 (S.D. 3:7) and for the tenth to fourteenth day the mean

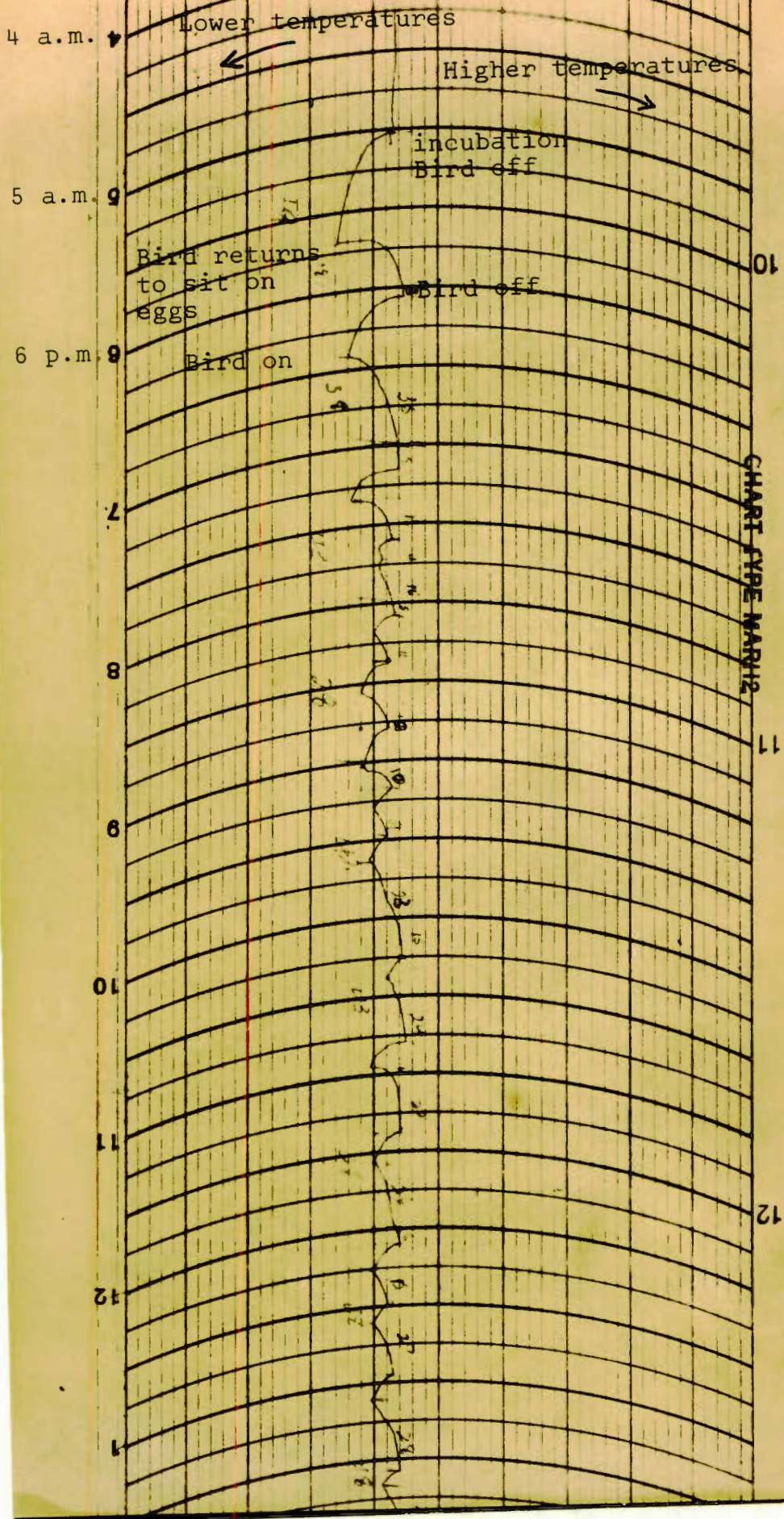


FIGURE 25. Temperature recording through thermistor coupled to recording potentiometer to show incubating pattern.

TABLE 30. Showing details of time spent incubating recorded from a nest with three eggs. Normal incubation for the Cape Sittal is 12-14 days.

Hour of day	1st, 2nd, 3rd egg			Day of incubation														
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	13th	14th	15th	16th		
04-05		60	58	52	52	52	48	55	-	60	54	52	48	46	45	30		
05-06		16	19	38	45	40	40	38	42	-	50	42	38	38	31	28		
06-07		22	33	36	38	47	47	47	44	-	40	38	32	34	26	1		
07-08		37	33	40	26	38	34	48	40	-	34	30	34	45	36	0		
08-09	start	33	28	27	34	35	55	47	56	-	40	40	36	30	34	8		
09-10	0	44	42	40	54	40	54	48	47	-	18	48	50	48	32	0		
10-11	0	43	43	54	51	42	36	48	56	-	41	52	38	38	41	0		
11-12	0	50	48	60	45	50	34	46	60	-	38	40	46	40	34	0		
12-13	0	46	48	33	53	51	50	48	60	-	40	47	54	34	51	0		
13-14	0	34	48	45	45	30	43	53	52	-	40	52	48	38	32	0		
14-15	0	52	48	60	49	34	56	56	56	-	46	32	39	56	53	0		
15-16	0	48	49	36	38	44	60	47	56	-	36	46	53	48	34	0		
16-17	26	56	31	39	44	46	51	47	50	-	40	40	52	45	44	0		
17-18	0	16	10	43	48	33	49	39	50	-	34	42	52	48	43	0		
18-19	0	0	0	36	46	42	49	38	40	(18)	28	41	49	40	39	0		
19-20	0	10	55	60	54	54	56	60	60	46	50	46	50	60	47	0		
20-21	60	60	60	60	60	60	60	60	60	60	60	60	60	60	60	0		
21-22	60	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓		
22-23	60	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓		
23-24	60	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓		
24-01	60	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓		
01-02	60	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓		
02-03	60	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓		
03-04	60	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓		
Start activity		05.32	05.02	04.58	04.50	04.52	04.50	04.42	04.45	?	05.04	04.53	04.46	04.42	04.40	04.35	04.29	
Last activity		19.00	19.05	19.00	19.06	19.10	18.57	18.32	18.45	19.15	19.28	19.13	19.12	19.00	19.11	19.25	08.25	
Total incubation - min.	26	557	610	705	722	675	766	737	824	-	638	700	723	690	637	635	67	
No. attentive periods min.	1	26	22	24	28	29	19	26	18	-	38	35	32	32	47	41	6	
Average " " "		21	28	29	26	23	40	29	46	-	17	20	23	22	15	15	11	
Longest period - min.	26	39	45	130	60	46	70	49	74	-	42	45	22	52	38	34	13	
At what time	16-17	14-15	13-15	10-13	20-22	16-17	08-10	13-14	11-13	-	10-12	08-10	17-19	14-16	16-18	16-18	05-06	
Shortest period - min.		2	4	4	4	4	5	4	8	-	3	4	2	1	2	2	4	
At what time		07-08	07-08	08-09	11-12	07-08	05-06	18-19	13-14	-	14-15	07.00	11-12	05-06	05-06	15-16	06-07	

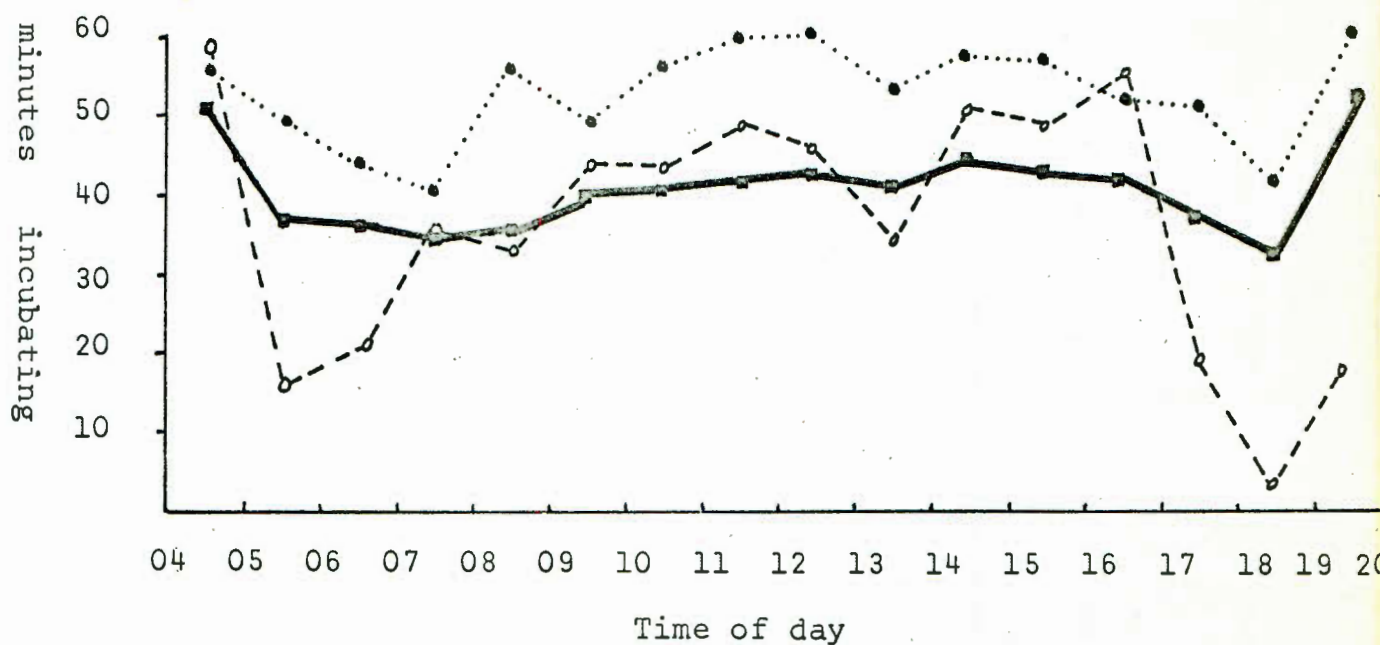


FIGURE 26. The incubation coverage during the course of the daylight period - mean (heavy line), the first day of incubation (line of dashes) and the 8th day of incubation (dotted line).

number of attentive periods is 37 (S.D. 5:6). Applying the student test there is apparently no significant difference between the observations. It is interesting to note on the fourteenth day which should have been the last day of incubation the female was on and off the nest 47 times, this is nine (24%) more than the next highest number of attentive periods during the normal incubation period.

In the House Wren *Troglodytes aedon* (Kendeigh 1952) and in the Cape Sugarbird *Promerops cafer* (Broekhuysen 1959) "there is the suggestion that the attentive time increases during the first three days, after which they fluctuate around a median during the rest of incubation" (Kendeigh 1952 p.27). In the Cape Bulbul the average length of attentive period shows an increase between the 6th and 8th days of incubation with only a minor peak on the 3rd day. In *Pycnonotus cafer* (Dixit 1963) there is a minor peak on the second day of incubation but the highest period is actually recorded the day before hatching occurs. It should be noted here that in none of the recordings taken on the Cape Bulbul was hatching recorded.

The mean duration of the attentive period is highly variable and as Broekhuysen (1959) points out, the standard deviation is such that not much significance can be attached to these figures. Nevertheless, the trend is evident that with the House Wren, Cape Sugarbird and the Song Sparrow *Melospiza melodia* (Nice 1937) the intervals are appreciable shorter than for those of the two species of *Pycnonotus* mentioned. As has already been pointed out by Nice, the Song Sparrow must feed at short intervals and this possibly gives reason for the short attentive periods of that species. Kendeigh makes no mention of this but correlates length of attentive period with ambient temperature. Both factors must play a part in influencing the duration of attentiveness. With the Cape Sugarbird, the nectar feeding and small insects utilized probably requires more frequent feeding activities than might be the case with birds that consume larger animal foods or berries. The Cape Bulbul is able to consume a lot of food at a time and this possibly enables it to have a much longer attentive period. The attentive period of

*Pycnonotus cafer* also agrees with the times for *Pycnonotus capensis*.

The number of attentive periods shows a slight increase in numbers towards the end of incubation in the Cape Bulbul. This agrees with both the House Wren (Kendeigh 1952) and the Cape Sugarbird (Broekhuysen 1959).

Incubation was also recorded for varying periods on other nests but since these came to grief at an early stage or were concerned with a Cuckoo's egg only (for a few days), the results do not prove any additional or contradictory trend to the results provided in Table 30.

As mentioned before only the female incubated. At no time was a male ever seen to sit on the nest when eggs were present. This is also the case with *Pycnonotus cafer* (Dixit 1963). The male was never seen to feed the female on the nest.

Though Broekhuysen (1959) found that the Cape Sugarbird had got off the nest for a short period during the middle of one night, no such activity was noted for the Cape Bulbul.

#### INCUBATION PERIOD

The incubation period was variable. Calculated from the day the last egg in the clutch was laid, the incubation recorded was of two eggs hatched later afternoon of the 11th day - i.e. 11½ days, six eggs in 12 days, five eggs in 13 days and two over 14 days (see Table 33). No obvious factors influenced this variation recorded.

#### BROODING

Brooding of the young birds was done by both sexes but the amount of time spent brooding by the male was very little indeed. The composite figures for the time spent in brooding are given in Table 31, from which it can be seen that the female brooded 18% of the period of observation (1313 minutes) whilst the male brooded for only 3% of this period. The young were covered 21% of the whole.

The changes in brooding pattern with development of chicks can be seen from the data given in Table 32. It appears that the higher percentage brooding periods are all

TABLE 31. Brooded by the male and female at different times of the day

Time of day hrs.	Minutes of observation	Brooding by female minutes.	% of total time	Brooding by male minutes.	% of total time
05 - 06	5				
06 - 07	225	38	17	13	6
07 - 08	251	44	17	20	8
08 - 09	81	12	15		
09 - 10	33	11	33		
10 - 11	61	17	28		
11 - 12	65	2	3		
12 - 13	33	4	12		
13 - 14	117	11	9		
14 - 15	136	30	22		
15 - 16	108	15	14	2	2
16 - 17	131	13	10		
17 - 18	67	37	51		
TOTAL :	1313	234	18	40	3

TABLE 32. Changes in brooding time and feeding of nestlings with progression of their development. The nest (26 W & Y) containing three bulbul nestlings and a cuckoo egg, which was about to hatch when the chicks left the nest.

Age of chicks: Days old	Time of day Hrs. : S.A.M.T.	Minutes of Observation	Brooding interval		Feeding rate		Interval Minutes	Food		
			Minutes	%	Male	Female		Fruit	Insect	Unkn.
2nd	13.00 - 08.52	52	2	( 4)	4	5	5.8	0	3	6
3rd	07.35 - 08.15	40	6 + 20	(65)	2	1	13	0	0	3
	15.30 - 16.30	60	2	( 3)	10	9	3.2	1	5	13
4th	11.25 - 12.30	65	4	( 6)	3	2	13	0	4	1
	14.25 - 15.06	41	0	( 0)	7	3	4.1	1	3	6
5th	09.30 - 10.23	53	25	(47)	2	5	7.6	0	2	5
	15.24 - 16.20	56	0	( 0)	6	7	4.3	1	6	0
6th	8.58 - 9.30	32	5 + 2	(22)	5	4	3.6	1	3	5
	18.34 - 17.34	60	2	( 3)	14	10	2.5	3	1	20
7th	07.25 - 08.24	60	0	( 0)	9	4	4.6	4	5	4
	17.20 - 17.54	34	4	(12)	1	8	3.8	0	1	8
8th	06.55 - 08.00	65	7 + 4	(17)	14	8	3.0	5	1	16
	14.10 - 15.10	60	18 + 15	(55)	6	3	6.7	3	1	5
9th	06.25 - 08.23	118	5 + 2 + 6	(11)	15	16	3.9	7	5	19
	10.22 - 11.30	68	0	( 0)	7	5	5.7	0	0	12
10th	05.55 - 7.00	65	0	( 0)	12	8	3.3	6	3	11
	16.03 - 16.32	29	1	( 3)	6	11	3.6	10	1	6
11th	06.32 - 7.02	30	3	(10)	7	8	2	3	0	12
	12.48 - 14.30	102	15 + 5 + 2	(21)	14	10	2.3	7	3	14
12th	06.23 - 07.03	40	0	( 0)	9	8	2.4	8	1	0
	13.45 - 14.21	36	0	( 0)	6	4	3.6	4	2	4
13th	At this stage 2 sitting on edge of nest one in nest 08.30 same as yesterday. All gone by 18.00									

in the earlier stages of development except where there was dull weather at later stages and on the 11th day when there was some threat to the young. The weather on 8th and 9th day was dull. On the 11th day the Jacobin Cuckoo was nearby and it was suspected that it was trying to check to see if the egg had hatched and this may well explain the coverage at this stage of development and more important, the presence of the male brooding twice in quick succession. It can be presumed that the presence of the Jacobin Cuckoo near the nest stimulated protective and defensive action by the parents. Except for the incidence of the presence of the cuckoo the other trends are normal and conform to the brooding behaviour exhibited by other passerines.

#### FEEDING OF YOUNG

Both parents fed the young from the first. Observations for 1313 minutes at one nest, showed the male fed 159 times and the female 139 times. Detailed analysis of the food brought did not show preference by either sex of any particular type of food.

The food of the young has already been mentioned in Table 11. Of 155 observations, 65 concerned fruits which means that 58% of the food of the young consisted of insect material. From Table 32 it can be seen that of the identified food fed at one nest 64 items were fruit and 50 items were insects (however, only 29% of the food fed was identified). It is likely that much of the unidentified food was small insects. It is also interesting to note that until the sixth day, there was a predominance of insect material over fruit. After the sixth day, more vegetable matter than insect material was fed to the chicks. If these figures are checked statistically, using the studentt test, the differences are significant. This indicates that there was a real difference between the type of food fed to the nestlings at different stages. The younger chicks were fed more insects though not at a high level of confidence (5%) than older chicks. The older chicks were fed significantly more fruit.

Difference between fruit 1st 6 days - last 12 : t=5.1 i.e. .001 level  
 " " " 1st 6 days to insects  
 1st 6 days : t=2.1 i.e. .05 level  
 Difference between fruit 2nd 12 days to insects  
 2nd 12 days : t=8.06 " .001 level  
 Difference between insect 6 days to insects  
 2nd 12 days : t=9.1 " .001 level

### NEST SANITATION

The parent bird keep the nest clean by removing the faeces. Up to the eighth day the faeces were swallowed by either parent. After this stage the faecal sac was removed by the parent which picked the sac up and flew off with it in its bill. The faecal sac was carried at least over the first line of bushes from the nest before being dropped in flight - a distance not less than from five to twenty metres.

It is interesting that Snow (1962) found that seeds were present in the nest and removed by the parents. No seeds were ever found in the nests with nestlings and the Cape Bulbuls' nests were always clean and no debris was to be found below the nest as apparently was the case in the manakins.

## 11. DEVELOPMENT OF YOUNG

## DEVELOPMENT OF YOUNG

The development of the nestling Cape Bulbul can be irregular. Two or three young in the same nest could vary in size and weight - and the presence of a young Jacobin Cuckoo would influence this.

### NESTLING PERIOD

The nestling period was recorded to be between eleven and fifteen days (Table 33). The two chicks which left their nest on the eleventh day were successfully cared for by their parents for they were seen being attended some two weeks later. The two nestlings that left their nest on the fifteenth day were actually observed being fed by their parents back on the nest on the seventeenth day.

It is presumed that the two extremes given are to be considered extremes since thirteen and ~~fourteen~~ days was the normally recorded period in the nest.

### GROWTH

Details are presented in Table 34. The increase in weight of the nestlings is illustrated in Figure 27, and here the different broods and their progress can be seen. It is very interesting to note for example four nestlings dropped weight before leaving the nest whilst four were still increasing in weight when last measured. In many nestlings there is a drop in weight before actually leaving the nest (Liversidge 1955 in press; Broekhuysen 1959, 1963). It is established too that inclement weather can effect the developmental rate of the growing nestling. So these figures merely indicate the normal growth curve and variations found under local conditions.

### PLUMAGE

The newly hatched chick was remarkably unattractive, naked, pot bellied with its head tucked down under its belly. The skin was transparent over the belly and the intestines - pancreas and inside veins could be seen. Within hours of

TABLE 33. Incubation and fledgling times recorded for Cape Bulbul.

	Incubation in days				Nestling period in days				
	11	12	13	14	11	12	13	14	15
No. records in Study area	1	6	5	2		1	3	1	
No. records Western Cape		1	3		1	1	4	1	2
	1	7	8	2	1	2	7	2	2

TABLE 34. Showing maximum and minimum measurements for each day recorded during the growth of the nestling of the Cape Bulbul.

Age - days old	Weight g.	Bill mm.	Tarsus mm.	Wing mm.	longest quill mm.	Tail mm
1	2.7 - 3.9	5.0 - 5.5	7.0 - 8.0			
2	3.3 - 5.9	5.6 - 6.2	7.5 - 9.3			
3	4.5 - 9.5	5.5 - 7.4	8.8 - 11.6		1.0 - 1.4	
4	6.7 - 12.5	6.5 - 7.6	10.3 - 14.0	10.5 - 17.0	1.3 - 3.2	
5	13.2 - 16.6	7.7 - 8.9	12.5 - 15.7	19.0 - 23.0		
6	12.3 - 16.4	7.7 - 8.8	16.2 - 17.5	15.5 - 28.5	9.2 - 14.4	2 - 2
7	16.9 - 25.0	8.8 - 9.4	13.4 - 19.0	29.4 - 38.7	6.5 - 22.0	3 - 4
8	17.6 - 23.6	7.9 - 10.0	18.2 - 20.1	27.0 - 37.4	13.3 - 24.4	3 - 8.4
9	18.6 - 37.5	9.0 - 10.6	17.0 - 22.2	34.0 - 48.3	14.0 - 31.1	5.5 - 9.4
10	22.3 - 26.7	9.0 - 10.3	20.9 - 22.5	40.3 - 54.3	24.3 - 32.5	6.5 - 9.4
11	22.5 - 39.5	10.2 - 10.7	18.5 - 18.6	39.0	17.0 - 18.5	
12	25.8	9.9	22.4	50.6	34.0	10.0
13	35.8 - 45.1	10.8 - 11.7	19.8 - 21.8	50.0 - 53.0	24.0 - 27.0	

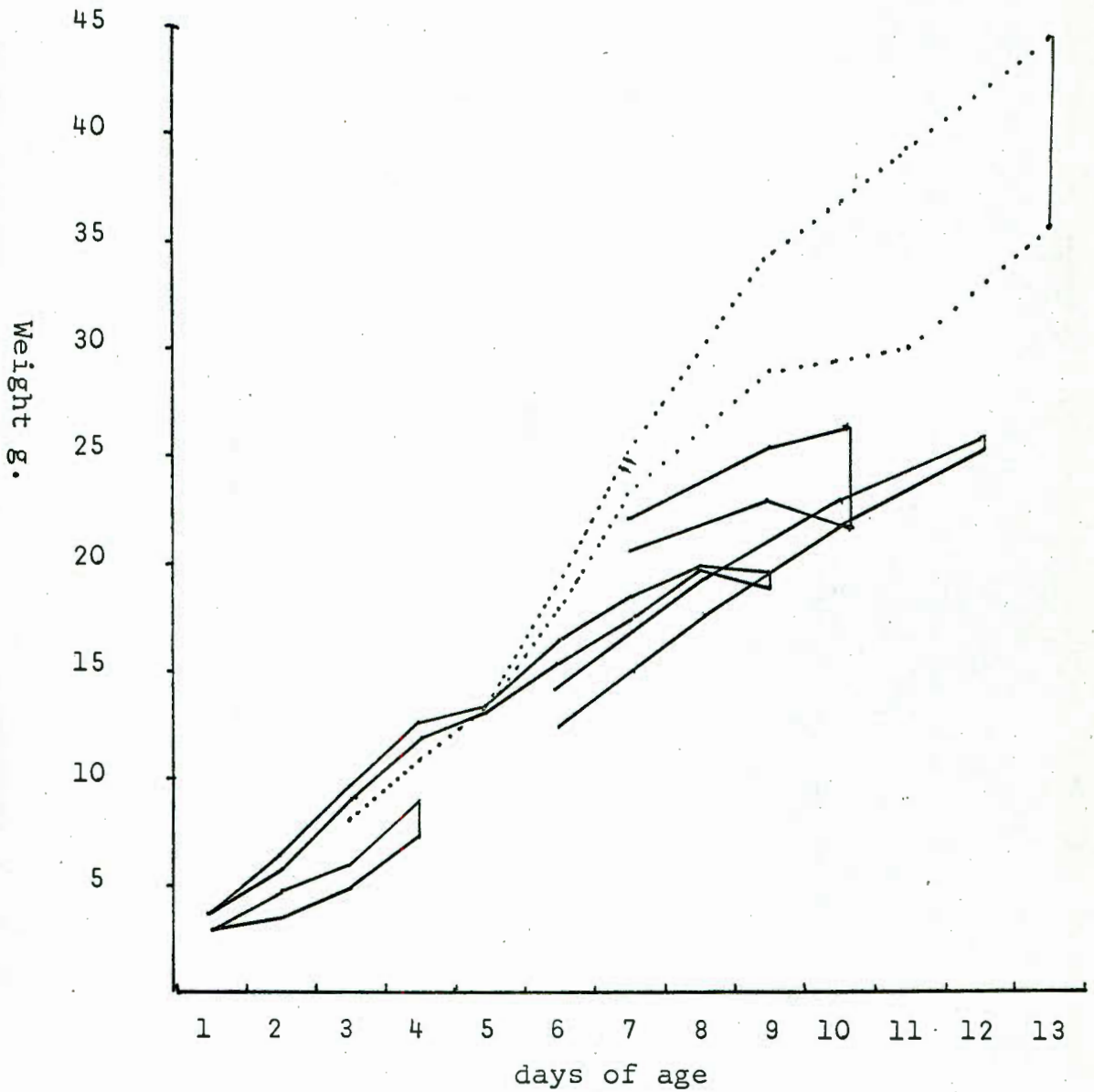


FIGURE 27. Growth by weight of different broods of nesting Cape Bulbul recorded from the study area. Broods are joined by a line.

exposure the chick's skin seemed to toughen up, became opaque and the chick was lying in the nest in a more natural manner with its head forward. The skin became purplish-brown in colour after 24 hours and continued to darken for the first few days.

The body feather tracts were beginning to show through as dark lines by the third or fourth day and the quill-tips broke the surface 24 hours later. The first quills to appear were the remiges and they were measurable on the third day. These quills grew rapidly in length and began to break out of the wax at the tips on the sixth day - at the same time the rectrices appeared.

By the eighth or ninth day the body was more covered by quills and very little skin was visible. The tracts were normal for passerines and no differences were found from the known pattern (Welty 1964). By the ninth or tenth day the quills on the body were breaking into feathers at the tips and by the eleventh day the nestling appeared to be fully feathered.

The eyes were closed when the chick hatched and there was no indication of opening until the third day. The eyes were fully open by the sixth or seventh day though this could be delayed to the eighth day.

The gape was initially pink on the first day. It was recorded as orange in one bird on the fourth day but another nestling showed a whitish gape on the sixth day. Evidently there was some individual variation in the colour of the gape though fledglings were recorded only with yellow gapes. The edges of the gape were paler and the extreme tip of the tongue was black - the amount of black rapidly disappearing so that by the fifth day the black tip had disappeared.

#### DEVELOPMENTAL STAGES

Nice (1943) describes five main stages of development in the passerine young. The Cape Bulbul differs in many respects to the intervals of time given by Nice for the Song Sparrow.

*Melospiza melodia*.

First stage - co-ordinations mainly concerned with nutrition (1-4 days in *M. melodia*). In

the Cape Bulbul this stage required three days. It is during this stage that ordinary response to movement, noise or shadow will induce begging by the nestling.

- Second stage - appearance of new motor co-ordinations (5th and 6th day in *M. melodia*). With the Cape Bulbul this stage was approximately the fourth and fifth day for it was in this period that eyes begin to open; first response was obtained from the parent bird calling the alarm call and the first notes were heard from the nestling during handling.
- Third stage - rapid acquisition of motor co-ordinations (7th - 9th day in *M. melodia*). The most interesting and rapid period of development of the Cape Bulbul was from the 6th to the 11th day. There was now better vision and many responses arose as a result of this new faculty. The first responses to alarm was shown.
- Fourth stage - nest leaving to attainment of flight (10th - 16th day *M. melodia*). As already mentioned this is a stage which was reached by the Cape Bulbul on the 11th day (when flight was possible but limited to short distances and then mainly on a downward path) to the 15th day (when flight seemed more controlled).
- Fifth stage - independence of feeding (17th - 28th day in *M. melodia*). The young of the Cape Bulbul were still fed by parents for at least two weeks after leaving the nest and undoubtedly this period exceeded 45 days. Young were still being partially fed by their parents a month after leaving the nest.

The early two stages would therefore appear to be more rapid in the Cape Bulbul than in the Song Sparrow. The third

stage of rapid acquisition of co-ordination in the Song Sparrow is not so rapid in the Cape Bulbul and development does indeed appear a little slow in this species. In the Cape Bulbul half the period of development to the fledgling stage is taken up with the acquisition of motor co-ordinations whilst in all other species listed (Liversidge in press) this period is a third or less of the time for that stage.

It is interesting to note too that the young seem to be parent dependent for a longer period than in most other species of passerines (Nice 1943 p.70). An exception is the Black & White Manakin *Manacus manacus* studied in Trinidad by Snow (1962) which is dependent on its parents for three or four weeks after leaving the nest. Is the similarity in this respect between Cape Bulbul and the Black and White Manakin due to climatical conditions or is it because both species are fruit eaters? This will be discussed further below.

#### FLEDGLING TO INDEPENDENCE

Once the fledgling has left the nest the parental care and feeding will continue for some time. It is interesting to note that the pair may have built another nest and the female may be incubating a full clutch of eggs while the male is still busy feeding the young of the previous nest. These young birds were never seen to be fed once the second clutch had hatched although they were tolerated near the nest. One was seen at this stage soliciting a parent for food but with no success.

There are several records of young still being fed two weeks after leaving the nest. There is one record of a male feeding young 17 days after leaving the nest while the female was incubating a second clutch of their eggs (October 1960). Another record is of  $\pm$  10 days old young while female was building a new nest - 19th October 1959. On 7th November these same young were being attended to by both parents (29 days later) and the male was still feeding two days later. Another young ringed on 13th November 3 days before leaving the nest was still fed at the rate of nine times in 45 minutes on 5th December (22 days later). It was still begging from its parent on the 12th December, 29 days after leaving its nest.

When the nestling Cape Bulbul left the nest the tail was about half its normal length and its powers of flight were not very strong. Two weeks after leaving the nest the tail was roughly two thirds the size of the adult tail and the flight was strong and purposeful. In between three to four weeks the chick was full sized in all respects but the crest was not as well developed as in the adult and the wattle which although fairly large was still brown. There are six records of ringed chicks still in the nest area between 25 and 43 days after leaving the nest.

One young bird, approximately 40 days out of the nest, was noted to be independent of its parents. This bird was feeding and preening on its own. Another of about the same age was watched bathing in a rain puddle - lifting up its tail too high the bird fell forward into the water!

After the young became independent of their parents, they were still tolerated in the nesting area by the parents. One 'young' bird about three months old was chased out of the nesting bush in the autumn nesting period. The young of the year seemed to come together in loose association and such flocks have been noted from mid December. The majority of the flocks seen until March probably consisted of young birds. The young which left the nest 30 days earlier were heard to call alarm notes which were recognisable but somewhat different from the adult alarm call. After 40 days out of the nest two were heard to call a rather poor version of "piet-my-jol". At this stage they were attempting to sing.

#### MATURITY

Of all the 50 young ringed only three were again recorded over a year later. One was seen a half a kilometre from its nesting area twelve months later. One was seen a similar distance away two years later and a third was seen 17 months later in the same area where it had been reared. The first two birds were presumed to have been paired and breeding at the time.

This would indicate that maturity is reached within the first year.

### SURVIVAL OF YOUNG

If we deal only with those nests in the 20 hectares of the study area we find from Table 28 that 85 eggs hatched, none of these young were recorded to return and breed within the area.

6) Of 85 eggs which hatched only 63 fledged - this is a loss of 24%. This is due to nest predation or the action of parasitism by the Jacobin Cuckoo. Only one young grew up with a deformed leg and though initially this deformity did not hinder progress by the time the other chicks were feathered the handicap of a helpless leg became evident and the chick was ultimately left in the nest to starve to death. Of the 22 nestlings lost four (17%) were lost to natural causes - storms that destroyed the one nest and threw the one chick out from the swaying nest. One (4%) was lost due to deformity. Eight (30%) were lost to nest parasitism by the cuckoo though this is a variable factor and one host chick from one nest survived at least to the fledgling stage with the cuckoo. The remainder (43%) were lost to nest predators.

Taking separately the 63 young bulbuls that fledged. From ringing and observation it is known that three out of five young from two nests perished within the first week of leaving the nest. There were notes made for a further ten nestlings which indicated that they were safely through the first ten days after leaving the nest. A recorded loss of 3 out of fifteen in the first week gives an initial loss of 20%.

It was not possible to ascertain the position four weeks after leaving the nest with any degree of accuracy. Any parent feeding young would have been noted had there been much movement to and from the food source. Unlike the manakin (Snow 1962) the young Cape Bulbul call to parents for food and they can easily be located. There were eleven individuals seen in the study area after a month from leaving the nest. This means that there is a total loss of 82% at this early stage if the observations could be relied upon. This figure must be regarded as an approximation and to err on the high side.

The final figure of three birds identified as returning to the general study area after twelve months can be increased by two birds which were seen once but were not identified. Ringed birds which carried coloured rings were likely to have been ringed as nestlings. From a total of 50 ringed young birds this gives a figure of 10% survival for the first year.

This figure compares with 12.6% average given by Nice (1937) for the Song Sparrow and 12.4 and 8.5 percent for the Pied Flycatcher *Muscicapa hypoleuca* near Berlin (as quoted by Lack 1966). The same source (Lack 1966) gives 2.5 and 1.1% for the Pied Flycatcher and Kendeigh (1937) gives 3% for the House Wren. Both of these last sources indicating that young do not return necessarily to their place of birth. The Cape Bulbul is not migratory and because of its social feeding habits the opinion is expressed that had any of the fledglings returned and settled within a kilometre of the birth site they would have been observed.

The mortality of young Cape Bulbul can thus be summed up as a 24% loss still in the nestling stage. Of those that survive about 20% are lost the first week of leaving the nest. A further 62% are lost in the second to fourth week (which gives 20% a week in the first four weeks of life). Then a further 8% were lost during the next eleven months. Giving a grand total of 90% fledglings that die before reaching the breeding stage.

This figure may seem high. It is indeed higher than the highest figure given by Lack (1954), Kluver's (1951) figure for the Great Tit - 87% mortality between leaving the nest and breeding. It is interesting to note Nice (1937) gives the percentage of fledged young *M. melonatis* that return to breed as 12.6% in 7 years with variations from 4.5% to 20.0% each year. The figure found for the Cape Bulbul studied on a rather small scale is not so far out in comparison with other similar data. Snow's (1962) figure of 67% mortality during the first year after leaving the nest for the Black and White Manakin is considerably lower.

## 12. DISCUSSION

## DISCUSSION

Before discussing the results obtained during the study two points should be stressed. Firstly, the study was carried out on the periphery of the species' distributional range and secondly, the bird studied is typical of the more familiar members of the savanna Pycnonotidae which are predominantly tropical birds.

The question of how much the periphery of a species distribution influences its behaviour and tolerance is indicated by the following three quotations. Mayr (1963) comments that widespread species sometimes display a sharp reduction of their ecological tolerance in areas where their range is overlapped by related species. The case of *P. capensis* and *P. barbatus* is not one of overlap but certainly there is a zone of contact. One can anticipate what Mayr suggests because it is more important that the isolating mechanisms that separate the species will only really become functional in such zones of contact. Then we have the comment by Wynne-Edwards (1962) "Towards the fringe of its range the existence and population-density of any particular species of animal is often overwhelmingly dictated by the physical conditions of the environment". This is more clearly expressed by Haldane (1953 & 1956) as quoted by Mayr (1963) "population size near the periphery of the species range is largely controlled by density-independent factors. Competition with other species would be less drastic under these circumstances and a shift into a new niche facilitated".

Whether these influences apply to the Cape Bulbul population studied, and if so to what extent, is difficult to ascertain but they must be borne in mind. No bird in its widespread distribution is evenly spaced over the whole area and therefore the fact that *P. capensis* occurs in more concentrated populations in more favourable habitats is nothing out of the norm. The study area at Cape Receife was a locally favourable habitat and the population there was as high as any others seen as judged by general impressions. In the final 32 kilometres of the birds distribution the population was

certainly very much reduced. The incidence of the exotic *Acacia cyclops* which undoubtedly had its beneficial effects to the population at Cape Receife extended nearly as far as Sundays River mouth but tailed off except along the coastal dunes. In this narrow coastal area there was an abnormally high population of the Vervet Monkey and doubtless these wiped out any advantages to habitat that the *A. cyclops* would have given. For all practical purposes the population of *P. capensis* in the study area could be considered normal and not typical of an abnormal peripheral population.

The question of whether the Pycnonotidae have any features typical of tropical species is indeed a difficult one to answer. Primarily because so few african tropical passerines have been studied. In some respects there seems no evidence of adaptation to tropical life. Authors like Mayr and Darlington state that with tropical diversified habitats there is a specialisation of niche occupation, thus allowing a greater number of species. The Cape Bulbul does not appear to be very specialised.

The systematic position requires little discussion. There is no doubt that the three species of the *Pycnonotus* group have become reproductively isolated. The few exceptions are not important when one considers how many pairs must remain mutually exclusive and do not interbreed. Mayr (1963) gives the case of an American passerine;- "This hybridization has been known for a century and presumably began some 200 years ago when the natural habitat barrier between the species was obliterated by deforestation and farming. Yet the delimitation of the two parental species is still quite sharp in most areas. There is no evidence of a blurring of the species border except in the zone of overlap". This illustrates that allopatric hybridization need not lead to a breakdown between the species. This is in fact likely to be the case with the *Pycnonotus* group and especially where man has altered the habitat. Such a case as the Carrion Crow *Corvus c. corone* and the Hooded Crow *Corvus cornix* across central Europe, is well known and now accepted without the suggestion that these are one and the same species. There is no reason to my mind why the rare incidence of allopatric hybridization need imply that the three species of *Pycnonotus* in southern Africa need

be considered as one species.

The distribution of *P. capensis* has changed in the last 100 years at its eastern limits. This change has coincided with the increasing settlement and human occupation of these areas. Reputedly there has been considerable clearing of bush, thorn scrub and forest. It can only be suggested that this has somehow affected the species at the previous limit of its distribution. The three members of the Pycnonotus group appear to occupy regions which can roughly be defined as winter-rainfall, arid-summer-rainfall and moister-summer-rainfall. In Grahamstown but not in Kingwilliamstown there is evidence of such "Cape" vegetation typical of winter rainfall as *Oldenbergia* and *Erica* that indicates slightly more humid and cooler conditions. This could well have accounted for the presence of *P. capensis* in that area. The climatic changes have undoubtedly remained unaltered but the habitat and micro-climate have been altered. This would indicate that apart from the overall general climatic condition the habitat and or the micro-climate affects the distribution of *P. capensis*. The fact that the species is not evenly distributed over its whole range but is very much commoner in some areas than in others indicates that habitat is important.

The population-density of *P. capensis* varies as is the case with most avian populations. In this study an attempt has been made to obtain information on the factors involved in the regulation of populations.

There are two theories on the regulation of bird numbers represented by two different schools of thought. On the one hand is the work of Dr. D. Lack - "The Natural Regulation of Animal Numbers (1954)" and "Population study of birds (1966)". Both works advocate density-dependent regulation. Firstly Lack states "in nidiculous birds the normal clutch size is that which, on average, results in the largest number of surviving young" and secondly "in a stable population regulated by density-dependent mortality, a higher reproductive rate inevitably results in a higher mortality rate". These factors all work at the level of the individual. The second approach is in the work of Wynne-Edwards - "Animal dispersion in relation to social behaviour (1962)", who advocates group selection.

According to this author food is the ultimate limiting factor, but overpopulation is never achieved because dispersion through behaviour keeps numbers near to the optimum. In this way food as a proximate factor is not exhausted by a controlled population. There is perhaps a third approach to population regulation and this is by Andrewartha and Birch (1954). They are influenced by work on insects which are essentially poikilothermic and therefore subject to the influence of climate to a greater degree than are the homiothermic birds and animals. The work on insect populations concerns the potential of reproduction and future survival. Work on avian populations are considered from the view point of what has survived rather than what should survive. For these reasons the theories put forward by Andrewartha and Birch are not really satisfactory from the point of view of the present discussion.

The most fundamental difference between the viewpoints expressed by Lack and Wynne-Edwards and the findings in the present study is that the regulation of numbers according to the two authors is density-dependent whereas in the present work it appears to be density-independent. Strictly speaking Andrewartha and Birch (1954) are correct in stating that there is no such thing as density-independence. However, this carries the argument to unnecessary extremes and it is reasonable to refer to factors influencing numbers outside the influence of the biology of the species concerned as density-independent. At least in the study area the immigration or emigration that took place was not concerned with anything to do with the numbers or reproductive biology of resident Cape Bulbuls. It was influenced by climatic changes over quite a large area and changes that occurred not only in the habitat occupied and studied, but also well beyond this area. The question arises whether the study area was too small or whether, if the study area had been large, there would have been population control by density-dependent factors. If natural selection is working at the level of the individual - and I believe it must be - then the area is not too small to indicate the density regulation system. I doubt very much whether a much larger area would have given a different result.

The sample plot appeared to be typical of what was happening elsewhere in the local favoured habitat of the species.

Reverting back to selection at the individual level it is conceded that the work of Kluyver (1951) indicates a socially influenced selection, namely that both clutch size and the proportion of pairs raising second broods in the Great Tit are a little smaller when the birds are more dense than sparse. The effect of greater numbers of breeding pairs is to reduce the reproductive potential a little and if the population drops the reproductive potential increases. So that this effect is only at "optimal" or maximum conditions. Lack points out that the differences are too small to have any important effect on subsequent numbers. So that the advantages of Wynne-Edwards' idea of social-dispersion are not great enough in this instance.

Natural selection must work primarily at the level of the individual.

It is regretted that Lack and Wynne-Edwards have confined their works to conditions apparently so different from those pertaining in Africa. There seems also a desire to use the phrase "density-dependence" when it would seem to me that sometimes this is not really the case. Andrewartha and Birch (1954 p.649) extend this impression by the following sentence. "These generalizations about 'density-dependent factors' and competition in so far as they refer to natural populations are neither theory nor hypothesis but dogma".

It should be noted that not necessarily all bird populations are controlled by density-dependent factors. Allee <sup>1</sup>/<sub>et al</sub> (1949) quoting Nicholson (1933) and Smith (1935) point out "that, by their very nature, density-independent factors operating alone cannot determine and maintain an average population density over long periods of time ...". Without having seen the original article by Nicholson one is not quite certain about the phrase "operating alone". Thinking in terms of the present study, the major density-independent factor was undoubtedly rainfall and the resulting drought (a vague undefined term). Climatic conditions in southern Africa vary not only from time to time but also from place to place. Thus it is believed that the population of *P. capensis* as a whole

was each year affected by drought conditions even though the drought was not being suffered in the study area in all these years. It is believed that if in any year density-dependence factor controlled the local *P. capensis*, that year could be regarded as quite exceptional. The problem here was that it is likely that drought and abundance could operate locally in several areas all within 50-80 kilometres of the study area and this could affect the total breeding population. So for the time being the present study is regarded as an exception to Nicholson's contention. Originally "density-independent" was used as a self-explanatory phrase in place of "catastrophic" but in fact they need not be catastrophic in the dramatic sense of the word.

Clutch size as quoted above by Lack was considered important in density-dependent populations. However, Lack (1968) later shifted the emphasis slightly by conceding that where there was selective advantage in rapid growth rate, the same quantity of food can be used to raise a small brood quickly as can be used to raise a large brood slowly. This was applied in his evidence to differences in passerines between hole nesting (larger clutches and slower development) and open nesting birds (where need to leave nest was more urgent and hence more rapid development had selective advantage from predators). Such a difference does not necessarily explain why clutches in the tropics or warm temperate regions should be smaller in open nesting birds than they are in those from Europe. Lack persists with the concept that food is always a limiting factor in rearing young (p.168) - even though in his previous book (1966) he quotes (p.169) Snow as recording that the *M. manacus* can obtain sufficient food for itself in 10% of the daylight period and that a female only lays two eggs. Lack himself admits that in this instance food is not a limiting factor. It should also be noted that it has been suggested that heat generation by chicks in large broods in cooler conditions conserves energy. This would have a selective advantage for larger clutches in cooler conditions. The converse has also been suggested as a possible selective factor for small clutches in warmer climates.

The clutch of *P. capensis* was two or three eggs though four and five have been recorded in the western Cape where otherwise there are as many clutches of 2(14) as there are of 3(14). The other two members of the Pycnonotus group lay clutches of three or four eggs. So in the genus there is in southern Africa a reversal of the suggested norm of larger clutches with higher latitudes.

It was shown earlier that ten young survived from 45 three-egg clutches whereas fifteen young survived from 29 two-egg clutches. If these figures are treated with the chi-squared test it can be shown that the figure obtained (3.28 for one degree of freedom) gives only a 10 percent probability that the difference between the observations are real or significant. By convention this is not an adequate probability that can be used to make a positive statement. It does, however, indicate a strong trend towards the fact that there may be a possibility that more young are reared from the nests with two-egg clutches.

Of some academic interest is the fact that if the number of eggs are considered when laid in two-and three-egg clutches in relation to the success of nestlings for each group (10 survive from 135 eggs and 19 survive from 58 eggs) there is an important difference. Here the chi-square test gives a highly significant difference (8.7 with one degree of freedom). Thus for effort on the part of the female birds it is more productive when they lay two-egg clutches and the difference is a real difference and not due to chance. This strengthens the possibility that two-egg clutches are more successful than three-egg clutches.

The reason why a two-egg clutch should be a greater advantage over a three-egg clutch is not certain. The fact that there is a difference between the probability of significance of clutch per se and number of eggs in relation to fledgling would tend to indicate that the difference lies between the biological importance of these two issues. Snow (1962) supports Skutch on the idea that few visits to the nest for feeding purposes would reduce the danger of revealing the nest to predators. This would imply a smaller clutch is more likely to succeed. This is not positively shown in this instance even though nest predation is high.

If a clutch of two is adequate what advantage is there in producing more than this number of eggs? Is there not the possibility that conservation of energy is also to the species advantage? It is shown that with those pairs which have two-egg clutches there is a significant improvement of success with the fledging of young when one considers the energy input by the species per egg. Despite the fact that there is apparently no shortage of food there must be some factor giving advantage to pairs with two-egg clutches. The fact that there were more three-egg clutches than two-egg clutches in the study period would indicate that if this is a genetic inherited character there must be times when three egg clutches are more successful. However, since birds appeared to regulate or at least increase or decrease their own clutch size this can hardly be considered a fixed inherited factor. If one refers to energy input per egg it seems possible that the quality of the egg in two-egg clutches must in some way be better than is the case with three-egg clutches and that this advantage is manifest in the success of fledging between these two groups. This at least would provide an explanation of the differences of significance reported above.

The conservation of energy is perhaps more important than one might suspect for the reason that moult occurs along with the end of the breeding season in *P. capensis*. Indeed not only breeding birds at the nest in February and March but also in December were observed to be in full moult.

Moult in *P. capensis* occurs while the birds are still feeding nestlings. The moult continues through a period when the species has a second breeding peak. In general this is an unexpected event if one only considers the example of cool temperate species. Thus Nice (1937) states "But the drought must have brought on the moult of the adults some two weeks or more early and thereby put a stop to nesting". See also Lack with his perennial worry about shortage of food (1966 p.305) "The Timing of the wing-moult raises similar problems to the Timing of breeding, indeed the two sometimes interact. Most species moult just after breeding, and it may be advantageous to finish breeding early enough for the moult to take place when food is plentiful". The recent authoritative work by

Stresemann (1966) says that moult and breeding both have definite cycles which may be independent of each other. He makes no comment on whether one inhibits the other.

If moult occurs during the final stages of breeding activity then it can be appreciated that conservation of energy may well have selective value. Since as already stated moult is reputed to require more metabolic energy than the reproductive cycle.

There is another point of some relevance to clutch size, conservation of energy and in addition the division of labour as found in *P. capensis*. With a second clutch the female is able to continue incubating while the male continues with the feeding of the nestlings. This increases the potential number of broods the pair may rear through intergration and minimum expenditure of energy. Presumably if the male had too many young to feed at this critical stage the parent bird would be weakened. Quite obviously with such an energetic task of rearing young the adult bird would be at a disadvantage to go into a moult if it was not in prime condition.

Whilst all these suggestions fit into an attractive pattern we must be cautious about its validity. Snow (1962) found *M. manacus* stopped breeding at a definite time before it went into moult - whereas it started breeding at no regular time. Here only the female reared the young. But we should again have an exhausted female if she had to rear large numbers of young and then go into the moult at that stage so that there may be an advantage in conservation of energy.

With the suggestion that conservation of energy may influence some aspects of the biology of the bird, the problem of food supply becomes pertinent. It was clearly shown that the availability of food is far in excess of maximal requirements at all times of the year. It therefore stands to reason that the clutch size, number of broods and other events that are so often limited by food supply are not limited for this reason in the Cape Bulbul under the conditions studied. It has been suggested that the small clutch of two or three may be small for the need of conservation of energy. This may not be the only reason for small clutches. It is doubted that the small clutch is an innate tropical adaptation carried

over from the species tropical origins, because the very closely related species of the group have clutch sizes in the tropics that vary from two in the Congo (Chapin 1953) to two to three or even four in East Africa (Praed & Grant 1954). This fact does not support the idea of conservation of energy. But until the ecological life history of those more tropical related bulbuls is available we cannot pass comment. What is known at this stage is that Rhodesian Pycnonotus have only a single breeding peak (Smithers et al 1957) whilst the tropical ones appear to have either two peaks separated by some months or they breed all through the year (Chapin, Praed & Grant loc. cit.). These facts alone would indicate different energy requirements and if only we could establish moult times for these species it might be possible to interpret these points to see how the idea of conservation of energy fits the picture.

The nature of the major mortality factors is most important regarding the control of numbers of the Cape Bulbul population.

The adult mortality of the Cape Bulbul appears to be in the region of 25% from admittedly a rather small sample. This figure is far below that for other passerines as summarised by Lack in his table for species from the northern cool temperate conditions (Lack 1954 p. 91-92). But the figure is only half of that of the tropical *M. manacus* given by Snow (1962). Perhaps it is wrong to emphasise tropical as there are in fact several factors which might be responsible for the difference found. For example *M. manacus* is a promiscuous breeder and this might influence matters as well as the fact that it is a frugivorous feeder. The one thing in common between *P. capensis* and *M. manacus* is that both are fruit eating species and both have low adult mortality rate though not the same for the two (25% and 11%). It is suggested here that the abundance of food at all times of the year was the major factor effecting this low mortality rate for the Cape Bulbul. Another very important point coupled with this is the fact that there was a virtual lack of extremes of climatic conditions that could be considered unfavourable or in any way cause heavy demands upon energy or life of the Cape Bulbul in the study area. It is probable that this abundance of food

and equitable climate applied to the Cape Bulbul over most of its distribution. It is important to stress that these findings apply mainly to the study area and they do not apply to the other two species of *Pycnonotus* which live in areas of greater climatic extremes.

The major mortality losses occur in the reproductive effort of the species. If we take the total number of eggs recorded in the study area and not merely number of eggs in completed clutches we have 233 eggs from which 63 fledglings left the nest - a loss of 73% breeding effort at this stage in the cycle. This means that three quarters of the effort to reproduce is wasted before the young are out of the nest. This figure is far higher than the generalised figure of 43% given by Lack (1954) for cool temperate species of passerines. It is of some interest to note, however, that the second highest figure given in Lack's table is for 10 passerines from Australia. Since this figure is 57% there must be some birds with a higher mortality from among these southern hemisphere temperate birds so that there is a tendency for agreement with the African figure given here. The figure for *M. manacus* (Snow 1963) is 81%. In this last species nest predators are mainly responsible for the losses. In the Cape Bulbul the total loss from the figures given above is 96% due to nest predators (only 17 nestlings lost to natural causes and four eggs added from the balance of loss). It is suggested here that at least portion of the proportionately higher loss during the breeding effort can be fairly attributed to the tropical or warm temperate conditions which provide a wider range of predators such as more snakes and more species of mammals that are potential predators. It is not so much the numbers of predators alone that are important since these will presumably fall in with the classical prey-predator cycle of abundance. But it is the variety of predators all of which are predators and seeking food not so much of a specialised nature as of a random searching. Indeed one is struck by Lack's comments (1966 p.172) "it is impossible that *M. manacus* could provide the main food for any predator". This would imply that predators in the cool temperate regions are far more specialised than those in our regions for it is doubted that

any predators involved with the Cape Bulbul relied upon their food from this source to the extent of even 1% of their diet. The local predators are random feeders and except for the egg-eating snake are unspecialised. The egg-eater does not specialise on any one species of bird quite obviously when one considers the period in which any single bird species could provide eggs for any length of time. The nesting loss to predators of both *P. capensis* and *M. manacus* were both appreciably higher than the average figure of 75% as given by Lack.

Perhaps the most dramatic phase in the mortality of the Cape Bulbul was in the loss of fledglings in the first month after leaving the nest. The figure of 82% loss is derived from a very small sample but it is at least an indication of the magnitude of the loss involved during this period. This loss is similar to figures given for nidifugous species and though it is not strictly comparable the total loss from egg to independence between the two groups nidifugous and nidiculous should be approximately equal. With the Cape Bulbul there is a loss of 20% young still in the nest. The loss of 82% of fledglings plus the number of nestlings lost gives a total loss of young hatched of 87% and this figure is no higher than some of the nidifugous birds listed by Lack (1954). There are unfortunately few records for passerines so that it is not possible to make comparisons with the passerines. It may be argued that the record for the number of young that survived for one month is rather unreliable because the parents may have moved them out of the area. This may be so but with daily observations in the area and the marked parents feeding communally I am fairly confident that their activities would have been observed at one time or another; at least the error is not considered to be very great. The young bulbuls called incessantly for food when hungry and could thus be traced - unlike *M. manacus* which young were silent after leaving the nest (Snow 1962).

The survival rate from fledging to the return the subsequent year is a better documented period for survival. In the Cape Bulbul with 50 nestlings ringed in the study area a

figure of 10% can be accepted as fairly reliable. This figure compares with the 12.6% over 7 years for *Melospiza melodia* (Nice 1937). Of considerable interest here is the fact that *M. manacus* has a 33% survival rate and to quote Lack again (1966) "if a population is stable, a low rate of reproduction must result in a low annual mortality". This is a very interesting statement and I cannot help feeling that this is putting the cart before the horse for surely as Wynne-Edwards states the recruitment rate of a species has been evolved to balance the mortality rate. There is no misunderstanding of Lack since he states in his other book (1954 p.276) that "the view that the reproductive rate of each species is adapted to its mortality is mistaken". In a sense Lack is correct that if the reproductive rate was very high one would obviously have a higher mortality rate to prevent over population. But we must not confuse cause and effect. In the Cape Bulbul there is a low reproductive rate and a high mortality rate. It may be recalled that the actual reproduction fell short of recruitment in two years and was in excess in one year within the study area. Presumably this fluctuation continues providing a long term stable situation through local variation interacting and allowing immigration and emigration to occur locally within the whole area. See especially Kluver (1964). The fact that the Cape Bulbul may have a clutch size of two or three (and there is no evidence that age influences clutch size in the meagre data available) would allow selection to favour the one or other depending upon the competition during the breeding season of adult breeding birds. This would imply that selection pressure is applied to clutch size according to the annual survival rate from one breeding season to the next. This brings in the results from Kluver and Tinbergen already quoted that indicates a lowering of reproduction with increased population. Thus with an increased population the small clutched bird would be at an advantage since it is better adapted to what would be expected to happen under the circumstances of increased numbers. Whilst in years of low numbers the three clutched birds would be at an advantage. This would give a natural variation in clutch size an advantage.

Of some interest here is that in the study it can be seen from Table 28 that there was only one year when there

were more three-egg clutches than two-egg clutches (1961). This was the same year that a substantial emigration occurred in the breeding number of pairs (Table 5). In the two other years and I think one may fairly bring in the 1958 year into this calculation, thus in three years the smaller clutch dominated and coincided with immigration and increasing breeding populations in those years. While it is admitted that the figures are too small for statistical treatment they do show an important trend. This would belie the idea put forward by Lack that clutch size is concerned with the control of the breeding population. For here we have the larger clutches coinciding with emigration when if the birds were self regulating one would anticipate if emigration was occurring smaller clutches would also dominate over larger clutches. What controls the clutch size is not at all clear from the present study but two points emerge; that supply of food has no effect on clutch size in the Cape Bulbul since food supply exceeds demand; that self regulating mechanisms do not apply to influence clutch size in the Cape Bulbul. It was recorded that the same individual female layed either smaller or larger clutches about in equal proportions, but no indication of what influenced these changes was found.

An important aspect of the Cape Bulbul behaviour is its territory or a term which is more appropriate "home range". Territory in this species is a term limited to nesting activities only. The pairs would seem to have a home range which is a loose term indicating that feeding activity and perhaps even the collecting of nesting material can take place over a wide area and often where other pairs perform the same activity. Indeed if the feeding is locally good even the presence of a Cape Bulbul nest will not prevent outside birds coming into a nest territory to feed. It is interesting to find that in *M. manacus* (Snow 1962) the female has a nest territory even though it is a social feeder.

Since Aristotle about 350 B.C. first commented that Golden Eagles established territories for their maintenance (Nice 1953) subsequent writers have stressed the importance of territory for feeding and breeding. The two most important discussions on this topic are those by Nice (1941) and

Hinde (1956) who clearly point out the different types of territories utilized by birds. Nice stresses the territory for purposes of mating but Hinde provides a more satisfactory breakdown. Thus for the Cape Bulbul following Hinde (1956) the type of territory is "Large breeding area not furnishing most food; the behaviour is 'self-advertisement within the area' and the object defended may be 'mate, song post or nest site'. The site attachment is without aggressiveness in the normal use of the word. Certainly song from a song perch acts as some warning to others of the same species but this is normally considered as warning rather than aggression.

Singing male Cape Bulbuls would tolerate others of its own species within the nesting area - whether the stranger was passing through or feeding. There was, however, no suggestion, ever, that any other bulbul pair would build within a song proclaimed territory. The song was sufficient warning to keep other bulbuls away and it did therefore act as a social dispersal mechanism. The functional value of social dispersal in this species is undoubtedly the advantage it gives the Cape Bulbul in regard to nest predation, probably the most detrimental factor in the breeding biology of the species. The spreading out of the nests from each other no doubt reduced predation. This social dispersal probably evolved as a product of the selective value of this behaviour and allowed reproductive success of the species.

This is different from the concept of Wynne-Edwards who suggested the social dispersal acted as a reducing agent of reproductive activity by thinning out the population of breeding pairs.

It should be stressed that the Cape Bulbul is essentially a semi-social species and it remains so particularly in its feeding habits throughout the breeding period. There seems no need then for a mechanism creating social dispersion in a species where the advantage is to be gained from social activities. Social feeding behaviour has evolved for a more efficient utilization of locally abundant food resources. Thus there is a reason for the Cape Bulbul to eliminate social dispersion as a factor for regulation of numbers. Why the

Cape Bulbul has not evolved social roosting behaviour during the non-breeding season as found in Eastern Bulbuls *Pycnonotus caffer* (Ward personal communication) is not certain. It would appear a partial explanation at least is that at no time is there a shortage of food as is the case for *Pycnonotus caffer*. A point which would support the suggestion that social roosting has evolved as a mechanism to utilize limited and very locally restricted food sources more efficiently.

The last point of theoretical interest of the breeding biology of the Cape Bulbul is the effect of the parasitism by the Jacobin Cuckoo. It has been shown (Liversidge in Press) that the Jacobin Cuckoo chooses as host the commonest potential breeding host in the area of its activity. Here it has been shown that the rate of egg laying i.e. parasitism on the host is not related to the number of host nests available in a season. Also an independent variable is the success of the parasitism which is related to the seasonal success of the host. Thus the detrimental effect of parasitism is reduced during years of low reproductive success of the Cape Bulbul. This provides a remarkable balance of relationship between the host and parasite. In this way the parasitism can be maintained in an area on a population of host birds without any danger occurring (under normal conditions) to the survival success of the host population. Indeed it is essential that parasitism should function with this balance but the cuckoo-host relationship regarding host population has not hitherto been established.

1a The findings in this study of the ecological life history of the Cape Bulbul show a number of fundamental differences from birds studied in north temperate conditions. Thus for example regulation of numbers is controlled by density independent factors. A phenomenon which is not unexpected in southern Africa where regular climatic changes do not occur at the same time in the year or to the same degree as is apparently the case in Europe or north America.

The Cape Bulbul do not appear to suffer any period of stress due to food shortage or climatic conditions. This has allowed such energy consuming phenomena as moult and breeding to occur simultaneously and apparently both function quite

independent of each other.

The adult mortality of 25% is low for passerines whilst breeding success in the period studied is also low. The major contributory factor to low breeding success is predation at the nest and loss in the first month away from the nest - this accounts for 82% loss. The survival at the end of the first year is only 10%.

It would appear that the small clutch is adapted to some form of conservation of energy giving greater success to those eggs from nests with lower clutch size. The clutch size is not regulated by food availability or population size and differences in clutch size do not show significant differences in relation to size of clutch and success in fledging.

These results show that theories in regard to various aspects of ecological life histories in passerine birds as applied to north temperate conditions are not universal. This is the first such study for southern African conditions and there are few comparative works from the tropics. It is therefore not possible to weigh the significance of these findings against the mass of data for north temperate species. How normal a Cape Bulbul is in regard to these findings compared to other warm temperate species is unknown.

In the final consideration when one contemplates why the Cape Bulbul does not extend its range northwards there are many fascinating questions to be answered. The Cape Bulbul fits into its ecological niche so remarkably well, it is so well adapted to the local conditions that one can appreciate why it should survive as it does in its surroundings. If it were to suffer extreme climatic conditions or be subject to greater rainfall variation as its congeners do, one wonders how it would cope. If the food story was different as it must be for its congeners - then what adaptations would be necessary for its survival. Would it be compelled to be nomadic as seems the case with *P. nigricans*? One wonders whether predation on the nesting activity by cuckoo or by carnivorae would be as great in other habitats and if not how would this effect clutch size or population changes?

The remarkable results of this study is to show how finely the different facets of the story interdigitate and how well adapted the Cape Bulbul is to survive successfully under the local conditions.

Until we know as much about the ecological life history of the congeners as we do about the Cape Bulbul we shall not know why their distribution is what it is.

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*Alas, that Spring should vanish with the Rose!  
That Youth's sweet scented Manuscript should close!  
The Nightingale that in the branches sang,  
Ah, whence, and whither flown again, who knows!*

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15. SUPPORTING PAPERS

A PRELIMINARY STUDY ON  
FRUIT PRODUCTION IN CERTAIN PLANTS

INTRODUCTION

During the course of an ecological study on a fruit-feeding bird, the Cape Bulbul, *Pycnonotus capensis*, it was necessary to establish, quantitatively and qualitatively, the natural fruit and seed production of the food plants used by the bird. This paper presents the results of a large number of field records taken in an attempt to establish this fruit and seed production in coastal bush near Port Elizabeth.

The concept of an orthodox annual cycle of spring, summer, autumn and winter originated in the northern hemisphere under cool-temperate conditions. There, because of the short and definite seasons, it is assumed that all plants flower and produce seed or fruit regularly. In South Africa where drought is a phenomenon that may exist at all times at one place or another (Wellington 1955) the annual cycle is often disrupted. Consequently the ecological scene is one of irregular flowering, early, normal, late or entirely absent. It is unpredictable from one year to the next and seed or fruit may be in extraordinary abundance or sometimes entirely lacking. When seed or fruit is lacking it is not only because of insect or animal predation, as has been established for cool-temperate regions (Weaver and Clements 1938). Such a state of affairs in Southern Africa is probably brought about through environmental conditions disrupting the normal reproductive rhythm which, in some trees at least may have a two or four year cycle (Phillips 1931).

THE VEGETATION TYPE

The area studied is situated halfway between the town of Port Elizabeth and Cape Recife at the end of a promontory that lies to the south east of the town on the coastal dunes \* (Figure 1). According to Acocks (1953), this area falls under Alexandria Forest complex in subsection called Dune Forest. However, the two indicator species used by Acocks for Dune Forest are absent in the area of study. In fact

\* (Same Figure 1 as in 'The Ecological Life History of the Cape Bulbul').

the "coastal woodland" of Martin and Noel (1960 p.viii) is very much nearer to the vegetation of this area than any other vegetation type described. The plant species mentioned by Martin and Noel under coastal heath are all present. In addition there is a heavy intrusion by the exotic wattle, *Acacia cyclops*, dominant in much of the area.

The main woody plants include *Sideroxylon inerme*, *Rhus crenata*, *Maytenus procumbens*, *Euclea racemosa*, and *Cassine maritima*. Elements of fynbos such as *Agathosma apiculata* and *Coleonema pulchrum*, dominate patches of the shorter coastal heath.

#### THE AREA OF STUDY

The study area is a narrow strip approximately 20 hectares in extent. From the coastal dunes it runs back 100 to 200 metres to the fence of the Humewood Golf Course and approximately a kilometer long. The dunes are from three to ten metres high with a main ridge parallel to the coast above and behind high tide level. Several valleys run at right angles to this ridge, extending inland. This break-up of the dunes and lack of regularity affords numerous slopes which are protected from the fairly strong prevailing westerly or easterly winds. A feature of the vegetation around the promontory is the severe wind-blown appearance of the coastal bush. In the study area the prevailing westerly wind comes over land and the on-shore easterly wind has apparently little effect on the vegetation. Consequently the life-form is normal for the species except perhaps that *Sideroxylon inerme* does not develop into a tree and in fact on some dunes has a prostrate growth, keeping it between thirty and sixty centimetres high though it may fruit prolifically under such conditions. Analysis from aerial survey photographs indicates that 35% of the area is covered by woodland/scrub; 61% cover by coastal heath and 4% is road and roadworks.

The whole study area is on a loamy sand - indeed it forms part of several square kilometers of what was referred to as the Witsands forestry reserve. This indicates the extent of the loamy sandsoil in this area. Rainfall is evenly distributed throughout the year; 48% of the precipitation

has been recorded between October and March, 52% in the other half year. The lowest rainfall figures for the year are generally in January, with the S.E. and S.W. winds predominating and 28½% calm days in July with a westerly wind dominant.

#### FIELD METHOD

The aims of this survey were to establish the availability of fruits eaten by the Cape Bulbul both in respect to seasons and quantities at all times of the year. After trials of various methods, a simple field procedure was adopted which is unrefined but has the merit of being practical and of giving a fair comparative result. Three selected paths were taken to cover different areas - one on the edge of bush and fynbos (120 metres), one from the top of a dune down into the dune valley (110 metres) and the third in a protected valley (100 metres). Detailed notes were made at monthly intervals recording for each bush whether flowers, green fruits or ripe fruits were present. The number of fruits from every bush along the route that lay within 80 centimetres (arms length) of the path, on both sides of the path, was counted or estimated when numerous. The height of each bush was recorded approximately so that the individual bush was recognisable from year to year. During peak fruiting times a number of ripe fruits were taken and weighed on a triple beam balance.

This system would have been more satisfactory if a cyclostyled form had been used indicating each plant on a route and giving height; presence, numbers or absence of flowers; green or ripe fruits; also presence or absence of young leaves.

From a fruit production point of view it is not so important to know the actual number of flowers produced by a plant. Very often if the flowers are "out of season" the correct insect for pollination may not be available (see under *Chrysanthemoides monilifera*) and this will influence fruit production. Another factor is the predation by birds, which often prevents fruits reaching maturity. *Colpoon compressum* always had a few red fruits and only once was a fully ripe, purplish fruit seen on a bush. This was when the fruit-eating birds were attracted elsewhere by the abundance of food on another plant.

While the work was concerned only with the production on those food plants utilized by the bird under study, details were kept of all larger plants. The results concerning all plants are given in Appendix 1.

## RESULTS

The results of the observations on the fruit-bearing plants utilized by the Cape Bulbul are given in tabulated (Table 1) and graphical (Figure 2) form with the details for each species. Viewing these results, it is apparent that flowering and fruiting of at least some of the 24 species discussed occurs throughout the year. Some species show a regular annual cycle, the remainder are irregular in their fruiting. The irregularly fruiting species may have a half-yearly, yearly or biennial cycle which varies slightly according to seasonal changes.

Though records were kept of individual bushes the results are not presented in detail. This is mainly because of lack of regular monthly counts but partly because of uncertainty as to what took place between counts. A minimum of regular fortnightly counts is required to give adequate figures for detailed information. Mention is made under the species of points taken from these chronological records of individual bushes. Some bushes appeared to be heavier bearers than others nearby but the data are too few to prove this point. Indeed, two seasons may show a reversal between two bushes - what was formerly the heavy bearer may the next season have a poor crop compared with the neighbouring bush.

### Flowering

It is assumed that the interval between budding and the ripening of the fruit is more or less constant in individual species. It is self-evident that the fruiting period depends for the most part on the period of flowering. Thus if flowering is early it is likely that ripe fruit will also occur early. Exceptions occur when flowering is out of phase with the pollinating agent (see *Chrysanthemoides*) or when fruit fails to mature (see *Rapanea*) for various reasons mainly connected with unseasonable weather periods.

FIGURE 2. Showing graphically the natural fruit production for the main plant species studied. (Note: the scale of the ordinate is not the same for all species). Climatic conditions also shown.

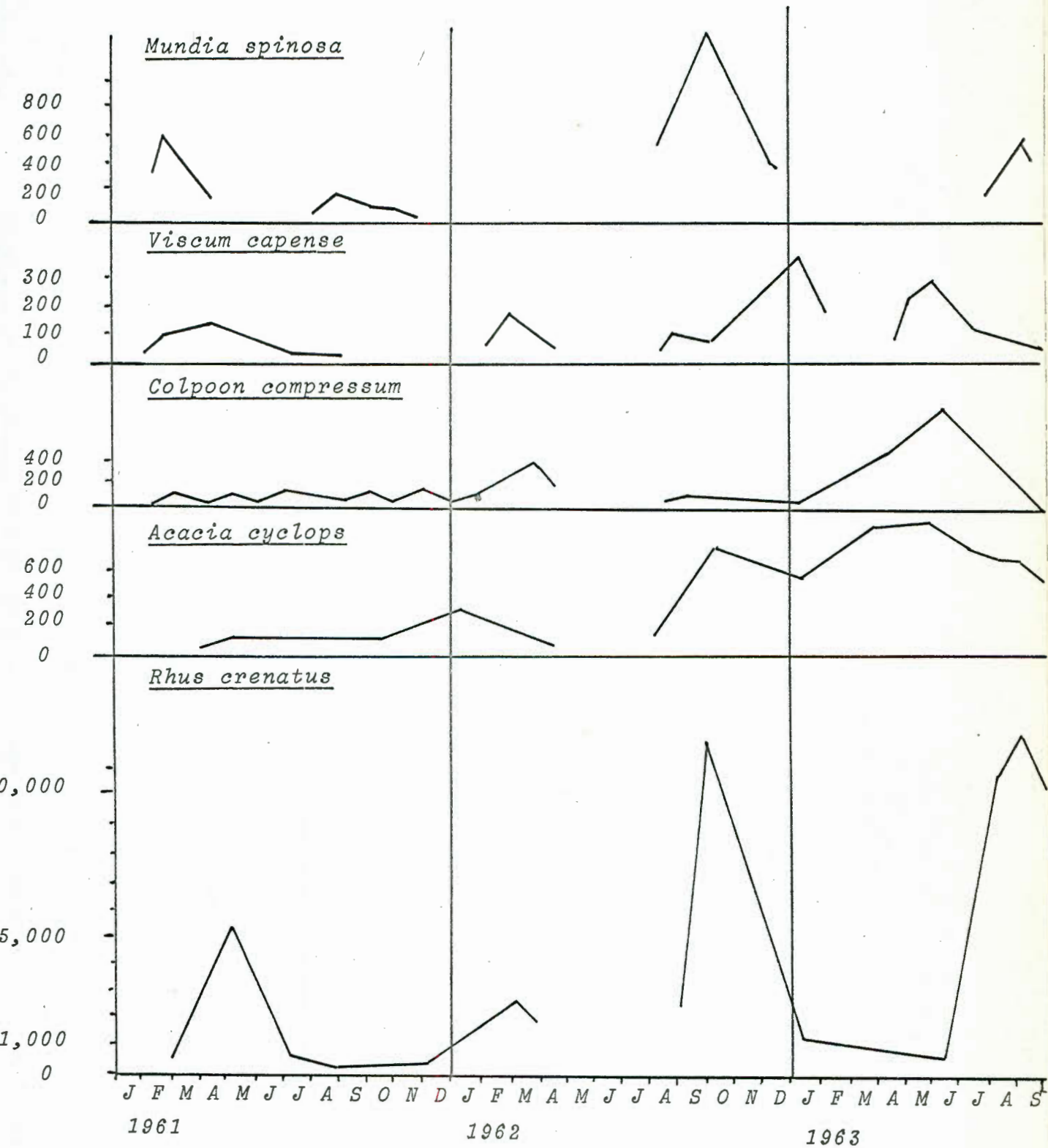


FIGURE 2. (Continuation)

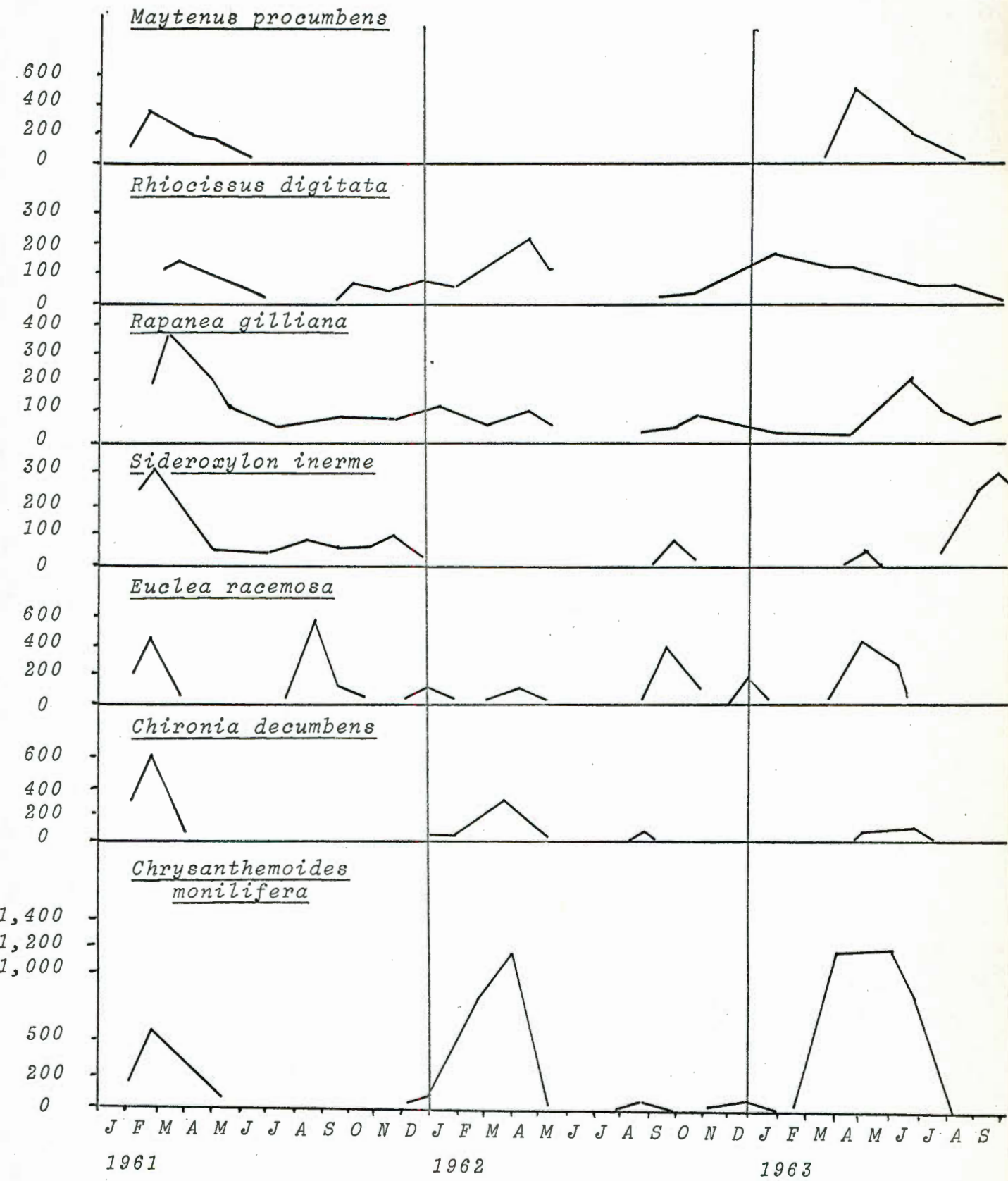
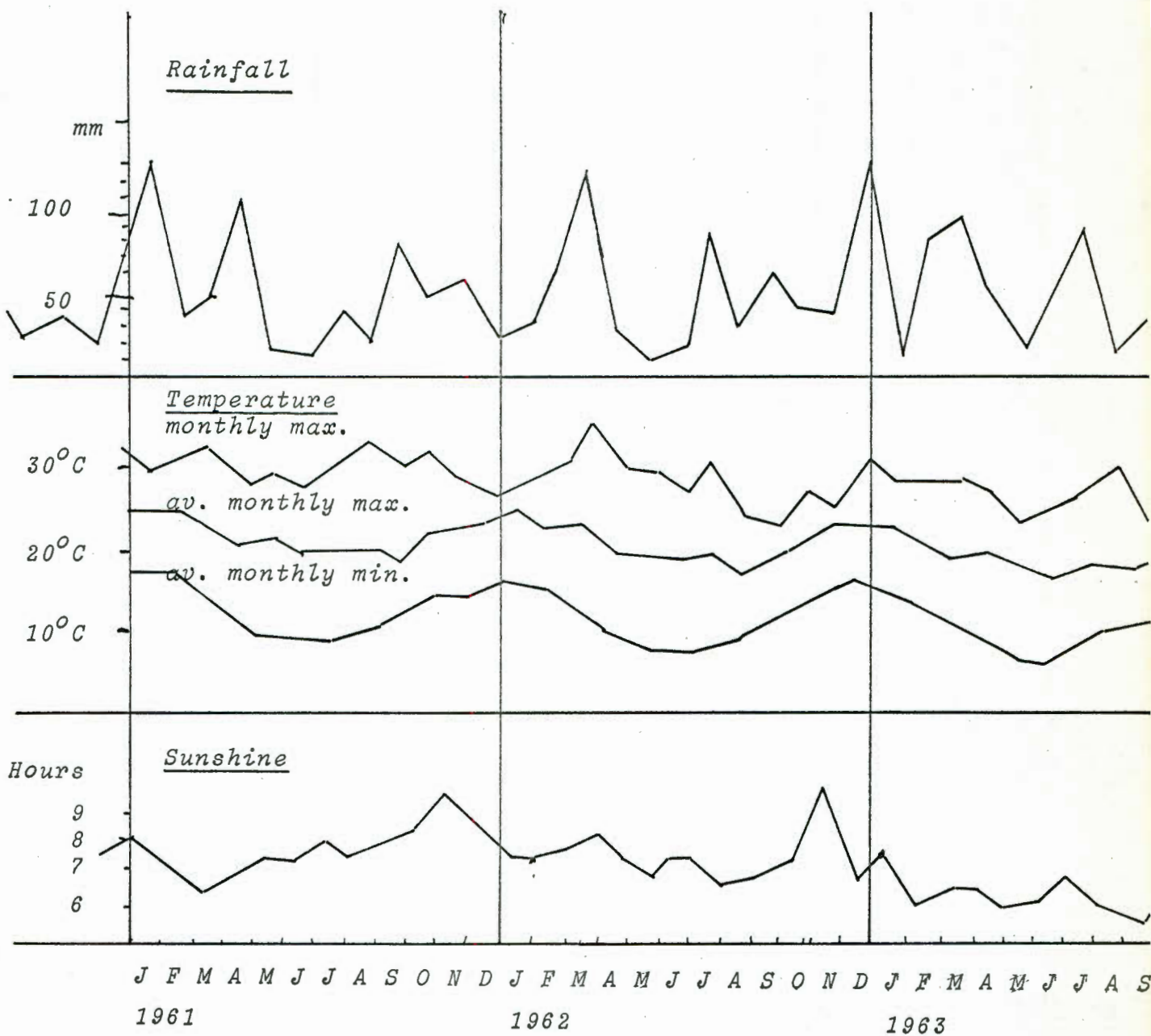


FIGURE 2. (Continuation)



Flowering in the area occurs throughout the year (Table 1). Of the 24 species of plants reported the number flowering each month varied from a minimum of seven to a maximum of 13. The highest numbers per month fell into two periods from July to September and January to March. The length of the flowering period for each species varied from one month to eleven months. Eight species flowered for only one or two months and nine species flowered for more than six months of the year.

### Fruit Production

With the variation in time between budding and ripe fruit from two weeks to eleven months depending on species, it is interesting to find two peaks for the number of species fruiting in a year. Autumn, March to May, is the most prolific period of fruiting and a secondary peak occurs in Spring, from September to November. The average number of plants fruiting agrees closely with the flowering - namely 10.0 per month. The least number of species fruiting in one month was seven and the greatest thirteen.

The variation in fruit production is considerable, both quantitatively and qualitatively. Reference to Table 1 indicates the extremes in number of unripe fruits in any one species along the routes taken to be 60 minimum to 2600 maximum for *Rhus crenata* and 450 to 4980 in *Maytenus procumbens*. For ripe fruits the extremes counted were 40 to 9100 for *Rhus crenata*. The quality of the fruits varied from season to season. While most fell between 34 to 119% difference of fruit weight from year to year, the greatest difference recorded was in *Maytenus procumbens*. In this species 13.4 g for 100 heads was recorded one year and 37.4 g for the next crop two years later (Table 2).

### DISCUSSION

Phillips (1931:245) pointed out that there was practically no information then concerning the biology of the flowers and fruits of the more important trees and shrubs. Little progress has been made since 1931. Phillips himself gives details of 63 species of trees and woody shrubs occurring at Knysna. The only species in his work in Knysna and the coastal-bush under

TABLE 2. The weight of fruits recorded at different times as well as dry weights (oven dried at 10° C for 48 hours) of some fruits.

Species	Date	Weight	Dry	% increase
		of 100 fruits	weight of 100 fruits	in weight over lowest
		grammes	grammes	rec.weight
<i>Viscum capense</i>	9. 3.64	12.5	-	-
<i>Acacia cyclops</i>	-	17.3	4.69	-
	6.12.69	8.9	5.12	-
<i>Acacia cyclops:</i> aril only	-	7.3	1.27	-
	6.12.69	7	1.63	-
<i>Mundia spinosa</i>	30.11.62	57.3	-	-
	6.12.69	49.5	11.36	16
<i>Rhus crenata</i>	31. 7.61	1.37	.66	-
	30.10.62	2.10	-	53
<i>Maytenus procumbens</i>	27. 3.61	13.4	8.29	-
	3. 5.63	39.4	-	194
<i>Cassine maritima</i>	31. 7.61	18.2	4.67	-
<i>Rhiocissus digitata</i>	30. 3.62	28.7	-	-
<i>Rapanea gilliana</i>	31. 7.61	43.6	5.87	-
	3. 5.63	72.2	-	66
	3. 6.63	76.2	-	75
<i>Sideroxylon inerme</i>	27. 3.61	7.6	-	-
<i>Euclea racemosa</i>	30. 1.63	9.6	2.59	-
	30. 3.62	13.1	-	37
	9. 3.64	14.0	-	46
	27. 3.61	17.1	2.59	78
	26. 4.63	22.0	-	130
	3. 6.63	28.8	-	300
<i>Olea exasperata</i>	27. 3.61	22.0	8.05	-
	3. 6.63	28.8	-	31
<i>Chironia decumbens</i>	27. 3.61	10.3	-	-
	30. 3.62	13.4	-	30
	9. 3.64	13.7	-	33
<i>Chrysanthemoides</i> <i>monilifera</i>	30. 3.62	15.0	-	-
	26. 4.63	19.4	-	29
<i>Solanum sp.</i>	6.12.69	61.9	8.37	-

study are *Euclea racemosa* and *Sideroxylon inerme*.

It is shown above (Table 2) that the timing, quantity and quality of fruits varies from year to year. Phillips (loc.cit. p. 246) has shown how complex these matters are:- "Individual plants near the sea flower and fruit several weeks to months before their relatives in the inland plateau or mountain kloof (forest) patches". Coastal conditions are usually slightly warmer and rather drier than inland. Flowers are sometimes further advanced and more prolific on individual plants on the warmer northern or north-western aspects. Species near the coast flower more prolifically than those inland, a point which can be correlated with the observation that trees in the drier forests usually bear richer crops than those in moist forests - bearing in mind that this is relatively speaking, since all the forests are moist forests in the region discussed. These differences would explain several of the differences in flowering time as recorded in the study area from those of the Albany and Bathurst division (taken from Martin & Noel 1960).

Details of fruit production in relation to climate are given in Figure 2. If, in fact, these two can be correlated it becomes possible to predict fruit crops in advance. The problem is not so much correlating peak of crop with peak in weather but why peak in weather does not always result in peak in crop. A rest period for the plant (which need not be required at all times of the year) would probably explain some observations. Flower production at periods when pollinating agents are unavailable would also influence fruit production.

The difference in size of fruit available is not so easily correlated with climatic factors. If we refer to Figure 2 it can be seen that actual rainfall one month prior to fruit production in general was very much less in 1961 than 1962. Also temperature were ascending at this time in 1962 and warmer weather may have helped.

It is unlikely that degree of pollination differed markedly. *Rhus laevigata* is poorly pollinated by *Apis mellifera* and *Apis caffra*. Ants are active on *Rhus crenata* throughout the year. The two months of probable pollination had good rainfall but the minor peak of fruit production in the autumn

of 1962 occurred when the rainfall was rather low. Predation on buds and young ovaries in these plants is known to take place in the area of study, particularly by members of the seedeater family, *Fringillidae*. This, however, is unlikely to have a significant influence on the fruit crops of such heavy producers as were studied.

The observed facts are too limited to be able to suggest reasons for seasonal variations in fruit production. They do, however, show the irregularity of season and production from year to year. From an ecological point of view it is desirable to determine the variables that affect fruit production, and the time of fruit ripening.

#### ACKNOWLEDGEMENTS

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## APPENDIX

Details of flowering and fruiting of plants presented in order according to that used by Martin & Noel 1960.

### AMARYLLIDACEAE

Brunsvigia sp.: Common in open areas of coastal heath, this spectacular flower appears from February to April, the leaves appearing from June to August.

### LORANTHACEAE

Viscum capense L.f.: The Cape Mistletoe is a fairly common parasite in the area. Flowering and fruiting occurs in the spring and autumn; the fruit is ripe in a couple of weeks. Flowers and berries were not produced in spring, 1961 and autumn 1963.

Viscum (species unknown): This is a larger leafed plant with larger fruit. Recorded in fruit in September, 1962, only.

### SANTALACEAE

Colpoon compressum Berg: a fairly common tall shrub usually occurring in clumps within the bush. Recorded flowering throughout the year in the study area, though only from April to October in the Albany and Bathurst flora. There is a period of about three months before fruit is ripe and the main fruiting season is from April to July. No green fruits were recorded in May.

The only occasion fully ripe purple fruits were recorded was on 26th April, 1963. This month, *Chrysanthemoides*, the favourite food of the Cape Bulbul and *Maytenus*, the favourite of the Sombre Bulbul, *Andropadus importunus*, were at peak fruit production. Both birds feed upon *Colpoon* normally but during this time they fed elsewhere, this allowing the *Colpoon* fruits to ripen. This is the only period in three years when this was noted.

There was no major production of fruit in the autumn of 1961 such as there was in 1962 and 1963.

### LEGUMINOSAE

Acacia cyclops Cunn.: this alien wattle (*Rooikrans*) was introduced into the area to bind the sand dunes. It has become dominant in the general area and several patches occurred within the study area.

Flowering occurs prolifically and simultaneously throughout the area at the time the pods ripen. This is from October through to February. A few flowers may be present at other times though none were recorded for March and June. Young pods are noticeable from January though more were recorded from March onward. By June the pods are almost full sized and green.

The pods become brown in Spring and by October they begin to crack open, showing a red fleshy aril. The dry pods open with quite a loud crackling noise during January and February, ejecting the dried red aril and seed. The peak period of abundance of ripe pods varies; January in 1961, December in 1961 whilst there was an extended period from October 1962 to January 1963 - evidently a "good" year.

This plant is frequently cut for fire wood and most trees under study were eliminated so that individual bush records were not available.

### AIZOACEAE

Carpobrotus edulis (L) N.E.Br.: the "hottentot fig" is a common ground cover on the sandy areas where it sometimes forms solid patches. Flowering occurs from late July through to September with fruits from September onwards. This species appears to have a more regular annual cycle than many other local plants.

### RUTACEAE

Agathosma apiculata G.F.W.Mey apud Bartl. & Wendl.: common on the flat areas of coastal heath. Flowering begins in late June and extends through to October in the study area, though it is recorded until January in the Albany and Bathurst areas. Fruits do not remain much later than the flowers, being recorded from August to October.

Coleonema pulchrum Hook.f.: present in patches, this attractive little shrub is in flower most of the year, though few flowers were present from November to March. Seed heads were recorded from September to November.

#### POLYGALACEAE

Mundia spinosa DC: the "waxberry" is a common low bush on the sand dunes and was locally abundant enough to form the supply for a small wax industry in the early days of Port Elizabeth. Flowering is recorded from April to October, with the height of blooming in July in each year. The waxy fruit ripens about three months after flowering. For reasons which are not apparent, for the facts do not fit in with flowering times. The berry crop has two distinct seasons, March to May, and the more important spring crop October to December. Timing of flowering and berry production is uniform and simultaneous in the study area. Crops were produced in the spring of 1961, 1962 (no observation - spring 1963) and autumn 1964. One bush which produced a good spring 1962 crop produced a poor autumn 1964 crop whilst 2 which had poor and good crops respectively in spring 1962 had good crops in autumn 1964. Individual variation thus occurs.

#### ANACARDIACEAE

Rhus crenata Thunb.: perhaps the commonest indigenous shrub, it is widely distributed throughout the study area. Though not clearly shown in Table 1, this species has two flowering seasons each year and consequently two fruiting seasons. The fruit ripens in three to four months. Berry production does not occur every spring and autumn. Very poor berry crops were produced in the spring of 1961 and autumn of 1963. Furthermore, the autumn crops of 1961 and 1962 were very much lower than those of the springs of 1962 and 1963. Not only was there a quantitative difference but also a qualitative difference between crops. Thus 100 berries in the autumn of 1961 weighed 1.37 g whereas the same number of berries weighed 2.10 g in the spring of 1962, an increase of 53% by weight.

Individual bushes may flower twice in a year whilst another bush may miss out a flowering period and thus have

three crops in two years. One bush had only one good crop in two years. There is thus much individual variation between plants. This results in a wider flowering and fruiting period than other plants.

Rhus glauca Desf.: this larger-leafed *Rhus* is less common than the previous species and tends to occur in the coastal heath areas. Only one specimen was subject to observation. This individual flowered in May 1961 and had fruits again two years later in June and September 1963. This indicates the possibility of a species which flowers every second year. In view of the variability shown by *Rhus crenata* this needs confirmation. Fruits ripen about 3 months after flowering.

#### CELASTRACEAE

Maytenus procumbens (L.f.) Loes.: common but not dominant except in localised patches of growth. Flowering was noted from February to May, green fruits from March to June and ripe fruits from April to September. In the area under study flowering and fruiting occurred in 1959, 1961 and 1963 indicating a two year cycle. Of some interest is that all the plants in the surrounding areas had the same season. In other words fruits were only produced alternative years and as a food source for berry-eating birds this would have disadvantages.

Fruit production in 1963 was more prolific than in 1961. It should also be noted that the fruits too were larger and weighed nearly three times as much in 1963 - 100 fruits being 13.4 g in 1961 and 37.4 g in 1963, an increase of 193%.

Cassine maritima (Bol.) L.Bol.: not uncommon tall shrub with small edible fruits. The flowers were recorded in January with fruits from March to July. This species only produced fruits in 1961 and 1963 and it is therefore believed to have a two year cycle.

Cassine tetragona Loes.: there were only three plants along the paths taken for these counts; these three plants produced flowers and fruits only during the one summer, December to April 1962. It is probable that this species has a cycle longer

than one year but the exact period is not determined. It should be noted that flowering is recorded in July in Albany and Bathurst.

#### VITACEAE

Rhiocissus digitata Gilg et Brandt: this creeper is commoner growing on vegetation with a sheltered northern aspect, thus it occurs in patches. The flower is short lived and for this reason flowering was recorded only from November to March. Berries were recorded every month of the year but these may take several months to develop and ripen. On the one path where this species was common there was a peak production in the summer 1961/1962 and the next peak was in winter 1963.

#### THYMELAEACEAE

Passerina rigida Wikstrom: this tall shrub is widely scattered in the survey area. Flowering occurs from September through to January with fruit recorded from October to January. It flowers annually regularly, with flowers and buds recorded 21st September 1961 and buds only on 21st September 1962.

#### MYRSINACEAE

Rapanea gilliana Mez.: this little bush is subject to considerable variations in its fruit production. The flower is short-lived and though flowers were only recorded May to July there appears to be a double crop of fruit each year. The fruit apparently requires rain for final development. During one dry period the fruits remained on the bushes for two months longer than normal, during which time they became sunburnt.

One bush had 100 fruits March 1961 and its second crop in September was only 16 fruits. In a stand of this species beyond the route recorded, prolific flowering was noted in August but no fruit was set, possibly because this flowering was abnormally late. Yet this same patch produced unusually numerous and large fruit seven months later. The fruit itself varies from crop to crop. Thus on 31st July 1961, 50 fruits weighed 21.8 g whilst on 3rd June 1963 the same number weighed 38.1 g, and increase of 75%. The size of a ripe fruit varied

from 6-8 mm in diameter to 12 to 15 mm, on the same dates mentioned above.

#### SAPOTACEAE

Sideroxylon inerme L.: locally a wind-formed low shrub, not uncommon. Buds and flowers were recorded from late August to late January. This plant would seem to flower annually with fruits taking about 9 months to develop from small and green to ripe. A peak production occurred in March 1961 and again in November 1963 and although the figures are inadequate to draw any conclusions there appears to be a difference quantitatively from year to year in peak fruit production.

#### EBENACEAE

Euclea racemosa Murr.: a fairly common shrub which grows, in this area, up to 2.20 m high. The same plant carries two crops of fruit in one year. Flowering occurs in August and again in March and the fruits ripen within four to six weeks. The seasons may vary from year to year by a month forward or a month later. There is also a considerable difference in quality of fruit from season to season - thus 50 ripe fruit weighed 6.34 g in March 1962; 11.0 g in April 1963 and 14.0 g in June 1963 - a total increase of 119%.

#### OLEACEAE

Olea exasperata Jacq.: this shrub, which grows up to 2.20 m high, is patchy in its distribution. In exposed positions it remains only 6cm tall. Recorded to flower in Albany from August to November, under local conditions it seems to flower most months of the year. Despite this prolific flowering fruits were recorded only in March and May 1961 and again in December/January 1961/1962.

#### GENTIANACEAE

Chironia decumbens Levyns: this attractive low bush grows up to 60 cm high in patches in semi-open sandy spots. Though a definite flowering period occurs from December to March, the odd flower was recorded in other months. The flowering period

is four months earlier than that recorded for Albany and Bathurst. The fruits take about four months to mature and thus ripe fruits occur for the most part from March to June.

There is some difference in quantity and quality of fruit crop from year to year. Thus a bigger crop of smaller fruits appeared in March 1961 and a smaller crop of bigger fruits was produced in April 1962 while in 1963 the crop was even later. Weight of 100 fruits on 27.3.61 was 10.3 g and 35 on 30.3.62 weighed 4.70 g, which represents an increase of 33%.

#### LABIATAE

Salvia africana-lutea L.: locally this shrub occurs within patches of mixed species of shrubs about 1.20 m high. Flowering occurred from July to September in 1961 and 1963 and from September to October in 1962.

#### SOLANACEAE

Solanum quadrangulare Thunb.: this creeper was not common and its appearance seems short lived. Flowering occurs over a long period from February through to August. Ripe berries were only recorded in August probably because they are quickly eaten by berry-feeding creatures and have little opportunity to ripen on the plant.

#### COMPOSITAE

Chrysanthemoides monilifera (L.) T. Norl.: perhaps the commonest indigenous shrub, this plant grows up to 2.40 m high and is dominant in the vegetation. Flowering occurred annually from September (as early as August in 1963) through to March. The fruit took from three to five months to ripen.

Differences in season and quantity of flowers and fruit varied enormously from year to year. The heaviest flowering occurred in March 1961, when no insects were seen on the flowers and the subsequent fruit crop was the poorest of the three years. In 1962 the peak fruit production was recorded in April, while in 1963 this extended from April to June. 100 fruits on 30.3.62 weighed 13.7 g while on 26.4.63 the

same number weighed 19.4 g, representing an increase of 34% by weight. It is interesting to note that a beetle, *Melyris interstitialis*, occurred on the flowers from October to December and a green *Melyris* sp. from January and February. Individual bushes may not produce fruit each season.

## THE BIOLOGY OF THE JACOBIN CUCKOO

### *CLAMATOR JACOBINUS*

For a period of five years a detailed series of bird observations was maintained in 50 acres of coastal bush near Port Elizabeth (for details of site and habitat see Liversidge 1966). The following account presents the results of these observations on the Jacobin Cuckoo and its host species the Cape Bulbul *Pycnonotus capensis* in this study area.

#### ARRIVAL AND DEPARTURE

The Jacobin Cuckoo is a summer visitor to the study area. First arrivals were noted on 5 October 1957, 28 September 1958, 1 October 1959, 22 September 1960 and 1961 and 2 October 1962. These dates indicate the arrival here to be the last week of September to early October. This is of particular interest in view of the fact that the earliest of nine first records given by Skead (1951) from Albany is the 3rd October. The birds possibly come down the coast and spread inland since Albany lies some 30-odd kilometres inland and on higher ground.

The departure of the species is not so clear cut because the birds do not usually call after the breeding ends. As Skead (loc.cit.) so aptly comments they "more or less fade from the scene". The records for the summer 1962/63 illustrate the point:- birds seen regularly until 12 November, then a pair seen again on 28 December, 29 January and from three to 20 February. For the most part the birds have disappeared as regular residents by the end of November - 27th in 1960, 29th in 1961 and 12th in 1962. Odd records within the study area occur until as late as 28 March 1961 and the latest for the Port Elizabeth division was on 16 April 1959. Skead records his latest date on 20 May for Albany.

A report was made by Maj. E. Woolley that the Jacobin Cuckoo overwintered in the coastal area near Port Elizabeth. Though a thorough search was made no evidence was forthcoming to confirm this. A positive approach was made to investigate this problem by playing the taped call of the species through a 10 watt portable amplifier from various vantage points.

Nothing was ever attracted by this experiment during the winter months though it must be admitted summer experiments elicited curiosity rather than alarm or mild attraction to the call.

### COLOUR PHASES

There is no need to discuss the taxonomy of the two colour phases - the black phase and the black/white phase (the black/grey phase of some authors). What is of interest is the relative abundance or complete absence of each phase in different areas of the species distribution in southern Africa as well as the difference in sex ratio between the phases. The incidence of black to pied birds recorded in the study area was 17 to five for observations where more than one bird was seen at a time. This preponderance of black over pied occurs mainly along coastal regions in southern Africa.

There are 163 skins of this species in the Transvaal, Bulawayo, East London and Durban Museums of which only 26 are black-phase birds. Eighteen of the 26 records can be considered as coastal or at least lower altitude records. The black phase is not recorded in Botswana and is rare in Rhodesia, Zambia and Malawi.

Of the 163 specimens collected there are 95 males and 66 females (1.4 : 1). This selection of more male than female birds is probably due to the fact that the male tends to sit in more prominent positions than the female. Notwithstanding this difference it is interesting to note that in the black phase there were 13 males collected and only six females. In the pied phase the ratio is little different from the overall ratio 1.3 male : 1 female.

### TERRITORY AND PAIRBOND

The determination of territorial activity depended upon the ability to recognise individual birds in the following ways. One pied bird was identified in two successive years in the same area by its white neck spots. The possibility that these may have been two different birds is not ruled out, but is unlikely. However, the female birds could be recognised by markings present on newly-laid eggs. It was found that although the eggs were white, within the first 24 hours a

distinct pattern of translucent and opaque striations was easily discernible. Eggs laid by one female could be identified in one territory because this pattern was identical in several eggs found. Baker (1942) also noted the ability to identify different individual females of the genus *Clamator* by their eggs. Using this means of identification it was found that one female occurred in the same area in three successive years.

There is no doubt that females have fairly well defined territories which they normally use for selecting host breeding birds. This territory is rather one of familiarity to the bird than a set area defended from other Jacobin Cuckoos. Indeed two or three females may range over the same territory and may lay an egg in the same host nest. These birds may also feed together. Thus it would appear the function of territory in this species is not for the reservation of a feeding zone nor reservation of a supply of host nests for reproduction.

The female must be familiar with the territories and individual pairs of host species to be able to find their nests for breeding purposes. The study area was used by at least three female Jacobin Cuckoos in one year. On one occasion five birds were seen together, several times four were seen together and three were commonly recorded at once. From this it is assumed that female territories overlap. The size of any one bird's territory was not fully established but with none of the three females did the 50 acres seem to occupy much of their range. One female was known to lay eggs along at least one kilometre of coastal dunes. Her territory was in all probability longer and possibly the same extent landwards, giving an area of (at the very minimum) one sq. kilometre. In 50 acres the average number of host pairs was 15 and, assuming an equal density over the whole of the female cuckoo's territory, she would have about 50 pairs of host species to parasitise. This is considered far in excess of the number required or even used. Restricting the area of activity by the individual female Jacobin Cuckoo may have survival value by limiting the number of potential host breeding pairs. The female

cuckoo requires time to observe a host species and to familiarise itself with the individual host's habits. If a territory has too many host pairs the cuckoo may be side-tracked while watching one pair and have its nest-finding effectivity impaired. Egg-laying by the cuckoo at the correct moment increases the breeding success.

The part of the male in territoriality is less well established. Without marked birds it is not easy to be certain of the true relationship between two neighbouring males on territory occupied by any one male. Single cuckoos were less often seen during the active breeding period, there being 28 records of single birds to 50 records where two birds were seen together. On the other hand, females usually laid eggs on alternate days and they remained quiet and inactive between days of laying. The impression was gained that the male was polygamous, consorting with the female after she had laid her egg and choosing neighbouring female the next day. In this species the male does not have a regular call perch as does the Red-chested Cuckoo *Cuculus solitarius*. On arrival in spring the male calls vigorously and frequently throughout the day for several days from various vantage points over an area more than one square kilometre in extent. Thereafter he will call from any vantage point for short periods unless disturbed. Persistent calling does occur after the first arrival but not regularly and seems to accompany egg laying activities.

The territory of this species is discussed by Friedmann (1948) who is influenced by the suggestion of Bradfield (1931) that the Jacobin Cuckoo may pair for life. This implies that the species is monagamous. At least in the area of study there is no evidence of monagamous behaviour nor of life pairing. It is suggested that, because individuals (probably male birds) call vigorously on return to the breeding area, and that, because initially these calling birds are single, the species does not pair for life. Bradfield may have recognised an individual bird in the same area on successive years and recording normally only paired birds he would have drawn the conclusion that they are paired for life. That individuals return to the same breeding area in subsequent years has been indicated above.

period it is usual to see two or three birds spread out over a couple of hundred square metres each seeking food, usually below the canopy of the vegetation and calling only an occasional single low note.

When the sun is up the birds sit hunched up on a high branch on the sunny side of a bush, as though to dry out and warm up. If there has been no dew they still appear to enjoy the routine of a quiet rest before commencing the days activities. Telephone wires are often used during this period if available and it is possible that the opportunity to watch the activities of the host species is also taken during this quiet period.

If there is no dew the male will call quite frequently during the rest period but the male called much more actively about two hours after sunrise. Windy weather would reduce the calling heard, sometimes to as little as one call only in the morning. During this same period the female would either watch within sight of the hosts' nests or would watch a host with a view to finding a nest.

After egg laying the pair would fly away from the nest area and remain together for another half an hour or so. After this the pair would break up, the male flying off with an occasional call in flight and the female to feed. Feeding, preening and resting occupy the middle of the day. Towards late afternoon the female might be seen working around a host bird's territory. Feeding again seemed to be the last activity of the day and usually there were two or more birds together at last light. Roosting was not observed.

#### BEHAVIOUR

The Jacobin Cuckoo is a conspicuous bird in flight. It may be seen perched during the breeding period especially when searching for host nests but otherwise it creeps quietly and unobtrusively through the scrub. Typically its stance in a bush is horizontal with head and neck raised at a slight angle, crest erected and the tail raised above the level of the primaries which protrude well beyond the body. When perched in the open the tail usually hangs down, perpendicular to the ground, the body at an angle of  $45^{\circ}$  from the horizontal

with crested head more or less horizontal.

### ALARM

When alarmed the crest is erected; the tail is raised and lowered deliberately and repeatedly. Such movement is often accompanied by a low grating "chuka-chuka-chucka-chucka" call. If put to flight in alarm such a rattling note is followed by a "kleeeuu" or a "clooo". Possibly the former ending is used by the male and the latter by the female but this difference needs confirmation.

### COMMUNICATION

Single birds may call a quiet "treee" or more often "clue" and the latter is used when a bird flying through the territory calls the longer call notes. The male whilst flying may call a "chit-it-chee" repeatedly or a repetition of the "clue" note in bursts of four or five.

### COURTSHIP

Calling presumably by the male will attract a female or if the birds have been feeding together the calling will stimulate courtship. The call used is usually "kruu-kru-kru-kleeeuu". If uttered in flight the male usually exhibits what is best described as a butterfly flight - with a slow irregular wing beat - more gliding than flying and with tail well fanned. When calling in such flight his head and neck is thrown up, the wings fluttering below the level of the back.

There is a special display in the courtship that seems to be a prerequisite for copulation. On all observed occasions, copulation took place when the male had presented the female with food. Godfrey (1939) records the same occurrence twice within ten minutes. Food on all occasions observed was in the form of "de-haired" caterpillars.

After courtship flight with both birds calling, there is a period when the male disappears from view - presumably in search of food. The female remains on some conspicuous perch and after a period of quiet she actively starts to solicit the male. She flicks her wings and slowly raises and lowers

her tail. The sudden movement and flicking draws attention to her whereabouts. The tail moving up and down at about 5-second intervals pin-points the place from which the sudden movements came. Her head with crest erected may be held up initially and jerked from side to side but as the male approaches the head is lowered and stretched a little forward while the crest is flattened. The male then stands on the back of the female and feeds her the caterpillar, copulates and then drops off to a perch below. After momentarily preening the bird flies off calling the "kruuu" note frequently. The female was frequently observed to solicit between courtship flights and presumably on such occasions the male could not find a caterpillar or some other event prevented him from participating.

#### AGGRESSION

It is not uncommon to see two or three birds together, sometimes two males. If there is any indication or provocation of courtship by a female the two male birds will immediately become antagonistic. Obvious excitement and quickening of activity is then accompanied by excessive but irregular calling - usually the "chit-it-chee" or repeated "clue" notes. With increasing intensity the wings are flicked frequently, the body jerked and the crested head is moved in jerks often to one side. Such behaviour is also carried out by the female in courtship but in aggression her movements are more jerky and stylized; her tail is moved up and down in courtship but in aggression the tail is fanned open. The female in courtship does not fan her tail. This activity usually culminates with one bird attacking the other followed by pursuing flight and calling. During such flights both birds fan their tails. Such attacks can lead to physical contact as mentioned above.

#### HOST SELECTION

It is no coincidence that within a few kilometres of each other populations of Jacobin Cuckoos choose the nests of different host species in which to lay their eggs. Thus in the study

area the host was the Cape Bulbul; four kilometres away in the Baaken's River valley the host was the Sombre Bulbul *Andropadus importunus*. Still further off in the drier areas, where neither bulbul was common, the Fiscal Shrike *Lanius collaris* was parasitised. Baker (1942) states that individual cuckoos always keep to the same foster parent and this seems to be the case in the Jacobin Cuckoo under local conditions. While Chance (1940) agrees with Baker he also believes "that a cuckoo tends to lay her eggs in the nest of that species by which she herself was reared". There are several reasons to support this idea in the Jacobin Cuckoo. Perhaps one of the strongest is that in the study area 50 Jacobin Cuckoo eggs were recorded and all were laid in the nests of one host species.

Within the study area the Jacobin Cuckoo had the choice of ten different host species, which it has been recorded to parasitise. Indeed, female cuckoos were seen to inspect the nests of both *Lanius collaris* and *Andropadus importunus* within the study area but no use was made of any species other than the Cape Bulbul. That the adult cuckoos return to the same territory in subsequent years and that they parasitise only the Cape Bulbul, suggests that the individual Jacobin Cuckoo parasitises only one species and probably the species which reared it. One tantalising observation of a cuckoo with a possible blue ring was made the year after blue rings were applied to all young of that year. Unfortunately the sighting could not be confirmed, but the indication was there that the young cuckoo returns to its area of birth.

It seems that the young cuckoo learns the habits, calls and nesting sites of its host. Such information is subsequently vital to the successful finding of sufficient host nests needed for survival of the species. As both Chance and Friedmann point out, the cuckoo normally seems to choose only a few host species to parasitise but eggs may be laid in otherwise strange host nests under special circumstances. Such chance parasitism would ensure utilization of the best host available in the area.

There is one curious point regarding choice of host which appears to have been largely overlooked and that is compatibility of food between cuckoo and host. The Cape and

Sombre Bulbuls are essentially fruit eaters. Although very small bulbul chicks are fed on insects, young feathered bulbuls are fed almost entirely a berry diet. The result with the young Jacobin Cuckoo is that the faeces are liquid. Normal nest sanitation is impossible and it is easy to see when a cuckoo chick has been reared from a bulbul's nest.

The Cape Bulbul is the commonest species parasitised by the Jacobin Cuckoo in the study area. In the Baaken's Valley the Sombre Bulbul is the commonest breeding host species. The same can be said for the Fiscal Shrike where this is known to be host to the Jacobin Cuckoo - the shrike breeding population was unusually high compared to other areas. Unfortunately no figures are available to confirm these subjective observations. If the premise is accepted that the Jacobin Cuckoo utilises the commonest breeding host species in its territory and if there is a local change in population of one host species or another, this fortuitous habit of utilizing an occasional new host by the Jacobin Cuckoo would be to its advantage in the long term. If for example the Cape Bulbul in the study area was decimated for one reason or another, chance laying in say a Sombre Bulbul's nest would probably have led ultimately to the change-over of host species in the study area, because there would have been more of the latter host's nests than the former and one female laying several eggs in a season would probably give rise to a population of cuckoos parasitising the "new" host. The hypothetical prey-predator relationship would apply in such circumstances except perhaps the "prey" population i.e. the host species could not be reduced too drastically in view of the probability of a change of host if another potential host was common in the area. Table 1 indicates the populations of the prey and predator during the years of study.

There is no doubt that birds in general are aware of the Jacobin Cuckoo and, whatever may be the cause of enmity, alarm is created by the cuckoo's presence. Thus for example in the study area both the Tchagra Shrike *Tchagra tchagra* and the Fiscal Shrike actually chased the Jacobin Cuckoo away from their nesting areas. These two species were not parasitised by the cuckoo in the area. There are many records of host

species pursuing and attacking the Jacobin Cuckoo and the writer has observed the Fiscal Shrike, the Sombre Bulbul and the Cape Bulbul pursue the cuckoo away from nesting bushes in areas where these three species were parasitised. In one instance an adult female cuckoo was attacked so severely by Sombre Bulebuls that she was rescued and picked up by hand.

#### POPULATION VARIATION

It was not possible to be precise about the number of individual cuckoos present in the area. Suffice it to say that groups of up to five birds were seen in 1959 and only pairs in 1962. The number of eggs laid each year as shown in Table 1 would seem a fair indication of the proportions of the population of birds present. With this assumption it can be seen that the population is locally subject to enormous variation from year to year. This is indeed the general impression one gets with this species, namely that in some years it is more common than in other years.

Assuming that this fluctuation in numbers is a real one, the question arises as to whether it is due to purely local conditions (i.e. the host population has an influence on the parasite's numbers) or to climatic conditions, food supply or some other factor which will draw the birds away to some other area. From Table 1 it can be seen that there is no evident correlation between cuckoo numbers as reflected by number of eggs laid and number of breeding host pairs. It could be that the period of four years is inadequate to show such a change. The years 1959 and 1960 of higher population were more successful for the number of both host and cuckoo fledglings that left the nest. It would seem from these figures that the cuckoo population varies at least in part according to whether it is a "good year" or not.

#### NEST LOCATION

It was quite remarkable how many Cape Bulbul nests were found through seeing the Jacobin Cuckoo "nest watching". There is something in the manner of the cuckoo which reveals its intentions of locating a host's nest. This is difficult

TABLE 1. Data on nesting results of the Jacobin Cuckoo and Cape Bulbul for the years 1959-1962 recorded from 20 hectares of coastal bush.

YEAR	Jacobin Cuckoo				%	Cape Bulbul		
	No of eggs		No of young			No of pairs breeding	No of eggs	No of young
	laid	lost	lost	fledged			laid	fledged
1959	20	12	5	3	15	13	35	15
1960	17	7	4	6	35	19	93	23
1961	9	7	1	1	11	13	29	2
1962	4	1	3	0	0	15	58	9
TOTAL	50	27	13	10				

to express in words. The cuckoo, invariably the female, sits quietly in a conspicuous position - often on a telephone wire. There is a slightly plump appearance which is exaggerated by an apparent absence of neck since the head is drawn in close to the body. Usually in association with this attitude is the song of a male bulbul from a perch near the nest or a bulbul flying in a "suspicious" manner and this indicates what is taking place.

Situated in a good position the cuckoo can watch the activity of the birds around. The easiest way the writer found to locate bulbuls nests is to watch from a high vantage point about two hours after sunrise when the bulbuls are most active in their nest-building activity. A bird carrying nesting material will use the same flight path repeatedly and usually there is a fluttering flight used which indicates a special activity. It is no problem for either man or bird that knows the secret to locate the nest. Indeed on one occasion, to the alarm of the cuckoo, the writer and cuckoo came round the same side of a bush in which both suspected (rightly) that a bulbul was nesting. On this occasion the cuckoo had dropped down into the bushes below her perch and worked her way towards the nest beneath cover. This was in fact their normal mode of final approach. If the host was near the cuckoo would search around as though for food and gradually work its way to the nest.

If a cuckoo was not particularly watching for nest building activity or feeding and a bulbul flew past it with a "going-to" or "coming-from" nest type flight the cuckoo would follow immediately to investigate. On one such occasion a newly fledged bulbul was located in this way. Under these circumstances the male was once recorded to follow a nest building bird though the female seemed mainly responsible for locating nests.

#### EGG LAYING

While Jacobin Cuckoos were seen to inspect many nests of the Cape Bulbul and occasionally that of other species, such inspections were usually done while the host species was away from the nest in the afternoon. Two records exist of

the cuckoo actually sitting on the bulbul nest before it was completed. It is obvious that the cuckoo must inspect the nest regularly since the cuckoo lays her egg at the best time to take full advantage of the parasitic habit. Of 50 eggs recorded within the study area, 11 were laid on or before the first day on which the host laid her own egg (see details below). There is usually a day or two after completion of the nest before the bulbul lays her first egg. The Jacobin Cuckoo was not known to lay during building and never more than one day before the host's first egg.

The pair of cuckoos work in close co-ordination when an egg is to be laid. Prior to laying the female will usually sit quietly for an hour or so within sight of the nest in her plump "nest watching" attitude. She will then move to the male who is feeding nearby or call the male up using a quiet "chuka" note. The pair will then work their way indirectly towards the nest; as they get closer the male makes himself more conspicuous. He will call from the tops of bushes and almost assumes a provocative manner. It is as though he is deliberately drawing the hosts to himself. Ultimately he will perch above the nest and await attack by both host birds. While the hosts are distracted the female cuckoo will slip on to the nest for the briefest moment, lay the egg and fly off after the male (see Appendix for details of one event). There is much variation on this simplified scheme. One pair trying to parasitise a nest situated next to a road were interrupted for nearly two hours at the critical moments by passing pedestrians or vehicles, this pair only succeeded in laying on the sixth pass at the nest (see Appendix 1). Another pair had four passes at the nest; on this occasion the writer had put a false nest with blown bulbul eggs near this site the day before. The female cuckoo had sat on the false nest the day before and did in fact sit on it the day she laid but possibly the cold eggs put her off. At any rate she finally did lay in the correct nest on the fourth pass. Sometimes the female may sit for a reasonable period on the nest, but more frequently she seems more to pass over the nest than actually to sit on it. On one occasion it was reckoned she was on the nest for only ten seconds. On

another occasion the writer felt that his presence too near the scene of activity unsettled the pair; after two unsuccessful attempts to lay they left the one pair of bulbuls and proceeded to parasitise another nest in the same stage of laying some 366 metres away.

Chance (1940) suggested that disturbance may prevent a female cuckoo from laying in the chosen nest and then compel her to select another host. This situation could well happen with the Jacobin Cuckoo. The bird can be put off her chosen course. It has also been shown that the female cuckoo will inspect nests of species other than the normal host. However, in five years of close study no egg was recorded within the study area in any host other than the Cape Bulbul, so that in the Jacobin Cuckoo, given reasonable conditions, it is unusual to lay in a host other than the normal one.

There was no indication that the birds would remove any hosts egg nor was any cuckoo seen to carry any egg in its bill. One nest which had three hosts eggs lost a host's egg on each subsequent day that a cuckoo egg was laid, two being laid in the one nest. However, a cuckoo egg disappeared on one day and three days later all eggs had been taken. So evidently it was not the cuckoo female removing the eggs when she laid.

It is suggested by Friedmann (1964) that all members of the genus *Clamator* remove host eggs. There is no evidence in southern Africa for this habit in *C. jacobinus*. Indeed the mere fact that hosts with a normal clutch of two or three may be found with as many as seven cuckoo eggs in a nest indicates that the hosts eggs are not normally taken.

On ten occasions that egg laying was observed, the host bird returned quickly to the nest and settled on the eggs as normal. Most certainly the incubating host bird looked down at the eggs before settling but no more so than is their normal behaviour. It has been suggested by several writers, Baker (1942) in particular, that rejection of egg by host species plays an important role in successful host selection. Such a theme is contradictory to the evidence of the Jacobin Cuckoo which deposits a large pure white egg in a nest with eggs of a strikingly different colour. There is no suggestion that these bulbuls hesitate or are in the least put off by

such an event. Yet by and large the Cape Bulbul has a reputation of deserting more readily than most small common birds. There are records of as many as three cuckoo's eggs in a bulbul's nest. In the study area two cuckoo eggs were recorded several times and the normal clutch for the bulbul is two to three.

The majority of eggs were laid between 7 a.m. and 9 a.m. (sunrise 6 a.m.) and a few were laid later when circumstances thwarted the cuckoos from laying in their first attempts.

#### TIMING OF EGG LAYING

It is a source of amusement that in two of the five years, the first egg recorded within the study area in a bulbul's nest was a Jacobin Cuckoo getting its egg in before the host!

Of 50 eggs recorded within the study area, three were laid before the bulbul's first egg, 16 were laid during the laying period of the bulbul, ten were laid within two days of the host clutches completion (see Table 2). This means that 58% of the eggs were laid in time to allow the cuckoo chick to hatch before or at the same time as that of the host. Two other eggs laid on the third and fourth day after incubation commenced were close enough to put the cuckoo chick to advantage over the host and thus 62% of the eggs laid should have been highly advantageous for the parasitic habit between these two species. Of the remainder, details of 15 eggs were unknown but of some interest are three eggs laid 11, 16 and 11 days after completion of host clutch. These eggs and one other were laid 13, 16, 12 and 11 days after the first cuckoo egg in the same nest.

The three late eggs are of more than passing interest. The most remarkable was the female that laid in the same nest she had laid in 16 days previously. This female was seen in the vicinity of the nest from the twelfth day after it laid its first egg. For four days it was seen about, on one occasion coming out of the nest bush. On the sixteenth day a new egg was laid. The implication is that the cuckoo knows the incubation period of its egg and that there is some post-laying interest in its activities. That three other eggs should be

TABLE 2. Showing the time of egg laying by Jacobin Cuckoo in relation to the laying period of the host Cape Bulbul.

No of eggs laid			No of days after host clutch completed	No of days between 2 cuckoos egg in same nest
Before host laid	During host laying	Unknown		
3	16	15	1 - 1,1,1,1, 2 - 2,2,2,2,2,2, 3,4,11,11,16.	1 - 1,1,1, 2, 11, 12, 13, 16.

laid subsequent to the first egg at an appreciably later period - a period equivalent to the cuckoo's own incubation period - lends support to the idea that some post egg-laying interest exists.

#### EGG LAYING - FREQUENCY, CLUTCH AND SEASON

The same individual female was not known to lay more frequently than at 48-hour intervals. There are three definite records of 48-hour intervals between two eggs laid by the same female. One individual laid eggs in two days twice in succession and her next known egg was five days later.

There is a period of maximal activity of egg laying when for example 15 eggs were laid in 31 days. It has been suggested that cuckoos may lay in clutch rhythms. The evidence for this is morphological and based on follicle eruptions in the ovary. However, the plotting of known egg-laying does not indicate any rhythm. It is true there are several records of a run of two eggs at 48-hour intervals, but the impression gained in the field is that the cuckoos lay immediately after arrival and that high activity in this regard remains for the first two or three weeks, after which the eggs are apparently laid when the bulbuls provide the opportunity.

It seems no mere coincidence that the arrival of the cuckoo coincides with the commencement of the bulbul's breeding activity. Though the bulbul's breeding period is subject to change according to local conditions (Liversidge 1966) it always extends over the normal period of sojourn of the cuckoos. At least under local conditions there is not sufficient field evidence to indicate a clutch rhythm in the Jacobin Cuckoo.

Egg laying is over a short six-week period mainly from the last week in October to the first week in December. The earliest egg recorded in the four years was on 7 October. Table 3 shows the figures for each month for the study area as well as records from elsewhere taken from the S.A.O.S. nest record scheme. It can be seen firstly that the overall egg-laying period is from September to May, which more or less coincides with the bird's presence in its summer quarters. Table 3 shows also that the laying period is slightly earlier

TABLE 3. Recorded months of egg laying of the Jacobin Cuckoo.

AREA	S	O	N	D	J	F	M	A	M
Study area alone		13	29	8					
Whole Eastern Province		13	30	10					
Eastern Escarpment	1	2	14	20	9	2			
Highveld		2	4	7	0	3	1		
Rhodesia & Zambia		1	17	21	8	6	2	0	1
S.W.A. & Botswana				1	1				
TOTAL	1	18	65	59	18	11	3	0	1

in the south eastern portion of the birds range than elsewhere. This is in fact to be expected since the birds breeding period and thus presumably the host-availability on the highveld and in Rhodesia are later than those in the south eastern escarpment area. The point of interest here is that the species appears to be in a breeding state during its entire summer sojourn in the south.

#### INTENSITY OF PARASITISM

As shown above, nine out of 41 nests (21%) parasitised by the Jacobin Cuckoo had two eggs. This figure is close to the 24% given by Feidmann (1964, p.47). However, at least one of these nine cases was the same individual laying a second egg in the same nest because, it is believed, the first egg failed to hatch. It has been suggested that three others of the nine might have been laid for the same reason. It thus becomes somewhat risky to put too much significance into these figures. Indeed it is the writer's opinion that no importance can be attached to these figures because there are so many inponderables such as the number of females cuckoos in the territory and the time difference between egg laying.

What is of some interest is the incidence of parasitism from the host's viewpoint. Thus referring to Table 4 the incidence of parasitism in the host species varied from 72% of the nests in 1959 to 12% in 1962. The mean of these figures is 41%, considerably higher than the 25% given by Reed (1968) for the Diederik Cuckoo *Chrysococcyx caprius* in the Transvaal.

This high average incidence of parasitism is quite remarkable but ultimately it is the effect that this has on the reproductive rate of the host which is important. It is doubted that, if 100% success of eggs to fledglings occurred in <sup>the</sup> cuckoo, the low clutch size of the host would prove adequate for survival of the host species. There is therefore apparently a necessary factor of failure in the success of the cuckoo fledgling to allow the status quo to persist. Comparing figures of successful fledgling, the incidence of successful parasitism varies from 0 to 50% with an average of 24%. The 50% can be considered somewhat high since only two bulbul chicks fledged in 1961.

TABLE 4. Intensity of parasitism showing the relative number of hosts nests used and success of fledgling.

Year	Jacobin Cuckoo				Cape Bulbul			
	No of eggs laid	No nests with 2 eggs	para-sitised nests	No young fledged	No of nest attempts with eggs	No young fledged	% nest with cuckoo egg	% cuckoo young fledged to host young fledged
1959	20	4	16	3	22	15	73	20
1960	17	4	13	6	39	23	33	26
1961	9	1	8	1	21	2	38	50
1962	4	0	4	0	33	9	12	0

### EGG COLOUR AND SELECTIVE ADVANTAGE

The weight of the Jacobin Cuckoo's egg varies from 5.7 to 7.95 g and the measurements of 63 eggs from the general area of study are 23.4 - 29.0 x 20.5 - 23.5 with a mean of 26.3 x 21.8.

The egg of the Jacobin Cuckoo is pure white; when freshly laid the shell is slightly pinky and translucent and thus perhaps not so noticeably different from that of the host as it is after 24 hours when the white is conspicuous.

Much has been written about mimicry in cuckoo eggs. Friedmann (1964) has not emphasised enough the volume of words and bad influence on theoretical biology written about *Cuculus canorus* which is a highly evolved and specialised cuckoo. In southern Africa we have nine species of cuckoos which are fairly common. Five of these lay marked eggs and four lay normally plain eggs of which the Emerald Cuckoo *Chrysococcyx cupreus* and Jacobin Cuckoo lay white eggs. It must be pointed out that both lay other types of eggs too although only white is known for the Jacobin south of the Zambesi-Cunene Rivers.

It is suggested here that the white colour of the egg of the Jacobin Cuckoo is not a primitive condition as put forward by Friedmann (1964, p.51) but that it has definite selective advantage. In a reference that the writer has never been able to find again there was comment that the white egg in tropical America has selective advantage in that white eggs were not subject to predation by snakes to the same degree as coloured eggs. This was a subjective comment by an observant naturalist and put forward as an idea rather than a proven fact. The comment provided the germ of the idea that white eggs have survival value. It should be mentioned, however, that the egg-eater snake *Dasypeltis scabra* was positively identified as one of the egg-predators of the cuckoo so that colour in this specialised species of snake is not so significant.

Inspection of Table 1 provides some interesting facts which must be dealt with in detail before further discussion. There are details concerning 50 eggs of which 23 hatched. Of the 27 eggs lost, four were left as addled and four were deserted so that we have to account for 19 eggs destroyed.

Five of these eggs were lost from nests where the bulbul eggs were destroyed and the cuckoo eggs were not destroyed but found out of the nest. In three nests the host eggs were eaten before the cuckoo's egg and in one nest the sequence was reversed by a Striped Mouse *Rhabdomys pumilio* eating the cuckoo egg first. Thus we have one case where the cuckoo egg was taken first, three where the bulbul's eggs were taken first and a further five where the cuckoo eggs survived the predation, but were lost out of the nest. Note here Bradfield's (1931) comment that this species "lays many eggs, most of which are laid on the ground and abandoned". This statement will be discussed below but it is likely that this observation also refers to cuckoo eggs which have survived destruction (see also below under "Egg-Predators").

It has been shown with admittedly rather poor figures, that the white cuckoo egg has a greater survival rate than the host bulbul egg. The fact that three records exist in the study area of Cape Bulbuls incubating single cuckoo eggs for a period of more than a week shows the possibility of such survival. It should be mentioned that these last three records were of nests where no bulbul eggs were recorded but in fact these could be cases where the bulbul eggs were taken by predators before being recorded and the cuckoo egg survived predation. This would in fact further increase the ratio of survival of cuckoo eggs over host eggs taken from the nest.

It has been suggested that a white egg may be a contributory factor leading to rejection by desertion or ejection. Such a possibility must be remote for the habit to survive. Of all the cases recorded in the study area, desertion only occurred once immediately after the cuckoo egg was laid. Indeed this happened only after the second cuckoo egg was laid in a nest already having three bulbul's eggs. The normal host clutch is two or three and with a fifth egg it is probable that the number of eggs had more effect on the host than the colour of the egg.

There were nine nests where two cuckoo eggs were laid and 32 nests in which one egg was laid. There are many records in the literature of three eggs and even four to seven cuckoos in one host's nest. No doubt more cuckoos' eggs in the nest

increases the chance of desertion but this is surely due to clutch size rather than egg colour.

#### EGG-PREDATORS

Rodents (Bush Otomys *Otomys irroratus*, Forest Dormouse *Claviglis murinus* and Striped Mouse *Rhabdomys pumilio*) were responsible for the destruction of several cuckoo eggs and there is a record of the Egg-eater Snake taking two cuckoo's eggs out of one nest (plus two bulbul eggs). The Vervet Monkey *Cercopithecus aethiops* was responsible for destroying two of the nests where whole cuckoo eggs were subsequently found on the ground. The monkey is typically destructive when taking eggs or chicks and it is quite usual to find the whole nest lifted out of its site and pulled to pieces. The observation by Bradfield (1931) was possibly of eggs lost through the action of monkeys, since, if there had been nests remaining in the vicinity of where the cuckoo's eggs occurred on the ground, Bradfield would surely have commented upon the fact. He was a very observant naturalist.

#### POST-LAYING BEHAVIOUR

After the egg has been laid the pair of cuckoos fly off calling with more than normal characteristic "post-laying" calls. The male calls repeatedly and in answer to the female calls with the "chit-it-cheee" and "cluepo" note. The female calls a loud, rapid series of gurgling notes. Such calling can go on for ten minutes and often another cuckoo will be drawn in by the calling (see Appendix).

Courtship leading to copulation normally takes place late morning or early afternoon and in one instance took place within an hour of the female having laid an egg. Although only seen once soon after egg laying it is believed this was normal from behavioural evidence and the pre-incubation embryonic development.

#### INCUBATION PERIOD

A new-laid cuckoo egg has in fact an embryo 17-20 hours advanced in development compared with the normal domestic

fowl's new laid embryo (Liversidge 1961). Even with this advantage the embryonic development must be remarkably rapid since although the egg is more than twice the weight of its host egg, development is two days shorter. The stages of development of the newly hatched chicks are approximately the same - perhaps the bulbul is even less advanced since its head and eyes are proportionately larger compared to body size in comparison with the same parts of the cuckoo.

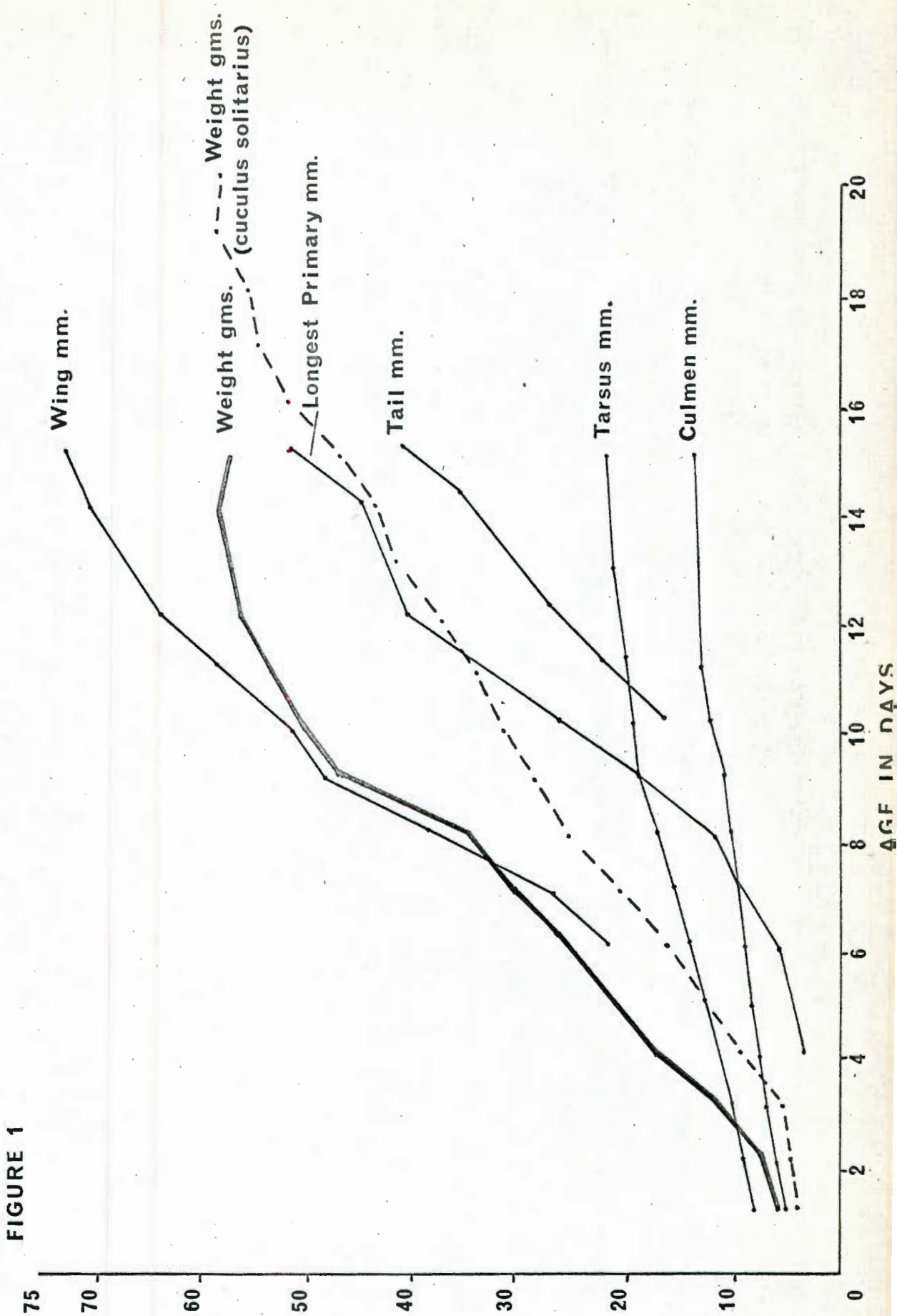
There are six detailed records of incubation from laying to hatching. One egg took between ten and 11 days and, in view of the other records, this is probably 11 days. One recorded was for 11 days  $\pm$  3 hours; three for 11 days  $\pm$  12 hours and one for 12 days  $\pm$  12 hours. This last egg took appreciably longer to hatch than the other eggs so there is some degree of variation in the period.

#### DEVELOPMENT OF YOUNG

The newly hatched chick is naked with an orange-flesh coloured skin, a bright orange gape, a small black point at the tip of the tongue and a white egg tooth. The skin turns a dark purplish-brown on the back after 24 hours and after 48 hours the whole body is a dark purplish-brown colour. The gape remains orange during the whole nestling period but after six or seven days there is a narrow yellow rim around the edge of the gape.

The weight of a newly hatched chick varies between 5.8 to 7.3 g. This is appreciably heavier than the Red-chested Cuckoo *Cuculus solitarius* which weighed 4.9 g. The developmental rate of the Jacobin Cuckoo was appreciably faster too as can be seen from Figure 1, though the weight of the chick on leaving the nest was very similar. The nestling period of the Jacobin Cuckoo varies from 11 days (twice) to 14 days (twice) and 15 days (once). The two records of 11 days were considered abnormal since the chicks were unable to fly and in the one instance the chick perished the subsequent night probably on account of rain and cold.

The development of behaviour falls into the stages as used for the Red-chested Cuckoo (Liversidge 1955) although the Jacobin Cuckoo develops more rapidly than the former species.



Showing the growth rate of the nestling Jacobin Cuckoo reared by the Cape Bulbul. Also comparing growth rate of Red-chested Cuckoo reared by Cape Robin.

Initially begging is upwards and either movement of the branch, nest or a whistled note stimulates immediate response. By the third day of the chicks existence (this convention is used throughout the discussion on development - thus the third day is a two-day old chick) begging occurred only when the nest was touched. Begging occurred up to the fifth day if the parents called even if the chick was in the hand. The eyes could be partially opened on the fourth day and fully opened on the fifth day. Directional begging coincided with the full opening of the eyes on the fifth day. The first indication of fear was recorded on the eighth day when the chick crouched in the nest on being disturbed. On the ninth day threat occurred in the form of a forward-thrust orange gape. The first note heard was also uttered on the ninth day. The first indication of co-ordination of muscles was by the 11th day when the chick was able to flick its wings and tail; by the 15th day the opening of the gape in threat was accompanied by the erection of the head feathers. On the 16th day weak flight had developed and by the 24th day the chick which was  $\frac{3}{4}$  full sized was able to fly strongly. On the 27th day the chick was almost full sized, noticeably browner than the adult, and with shorter tail. Flight was inadequate to cope fully with a strong wind on the 29th day. The chick was still begging with fluttering wings on 28th day and was still being fed by foster parents on the 33rd day.

The one chick weighed 56.5 g the day before leaving the nest and (as appears usual) the weight dropped at the end of the nestling stage. An adult female weighed 82.4 g so that the chick weighed 69% of adult weight on leaving the nest.

Comparing this development with the developmental stages of the Red-chested Cuckoo (Liversidge 1955) and the Song Sparrow *Melospiza melodia* (Nice 1943) the Jacobin Cuckoo falls in between the two (Table 5). The initial stage of co-ordination for nutritional needs is similar to the passerine. The second stage of new motor co-ordination in five days falls between the two days for the passerine and eight days of the Red-chested Cuckoo. The third stage of rapid acquisition of motor co-ordinations takes four days in *Clamator* and *Cuculus* and two days in the passerine. From this it can be seen that

TABLE 5. Showing comparison of rate of development of nestlings in days from day of birth.

STAGE	<i>Melospiza melodia</i> (Nice 1943)	<i>Cuculus solitarius</i> Liversidge 1955	<i>Clamator jacobinus</i>
I Co-ordination concerned with nutrition	1-4	1- 5	1- 4
II First motor co-ordinations	5-6	6-14	5-10
III Rapid acquisition of motor co-ordinations	8-9	15-20	11-15

the appearance of new motor co-ordinations is the critical period of difference between *Clamator* and *Cuculus*.

The newly hatched Jacobin Cuckoo chick already has the fourth (outer) toe laterally placed and, though the feet cannot be used effectively initially, this fourth toe inclines backwards under pressure. It is interesting that with the Red-chested Cuckoo the newly hatched chick has three toes forward and one back, after 24 hours the fourth toe is lateral and on the third day the permanent cuckoo foot form is achieved.

The feather tracts are shown in Fig. 2. The feather tracts appear as dark lines on the second day and on the same day the wing quills are already breaking through. General body quills break through on the fifth day. By the sixth day the wing quills measure 6 mm. The tail feathers break through the quills on the tenth day and the wing quills break out on the 11th day. The general body feathers begin to break through the quills on the 11th day and by the 12th day the general appearance is of a feathered chick. On the 15th day the chick is completely covered with feathers except for the nape which has a quill covering. It is interesting that the appearance of quills and break through of the feathers happen roughly about the same period of time after hatching in the two species Jacobin Cuckoo and Red-chested Cuckoo.

#### BEHAVIOUR OF NEWLY HATCHED YOUNG

There is no evidence of the young newly hatched chick evicting or attempting to evict host eggs or young. In newly hatched chicks the writer was unable to elicit any reaction to pressure on the back except in one instance. In this one case pressure from a finger appears rather to have induced avoidance rather than any directional movements as occurred in the *Cuculus solitarius* studied.

It was noted that the young Jacobin Cuckoo was invariably spread-eagled over eggs or young in the nest. The wings and feet holding down or resting on top of the host chicks. Thus on one occasion the day-old bulbul chicks were unable to lift their heads to beg for food when the parent came in to feed. It is believed that this spread-eagled attitude was too often

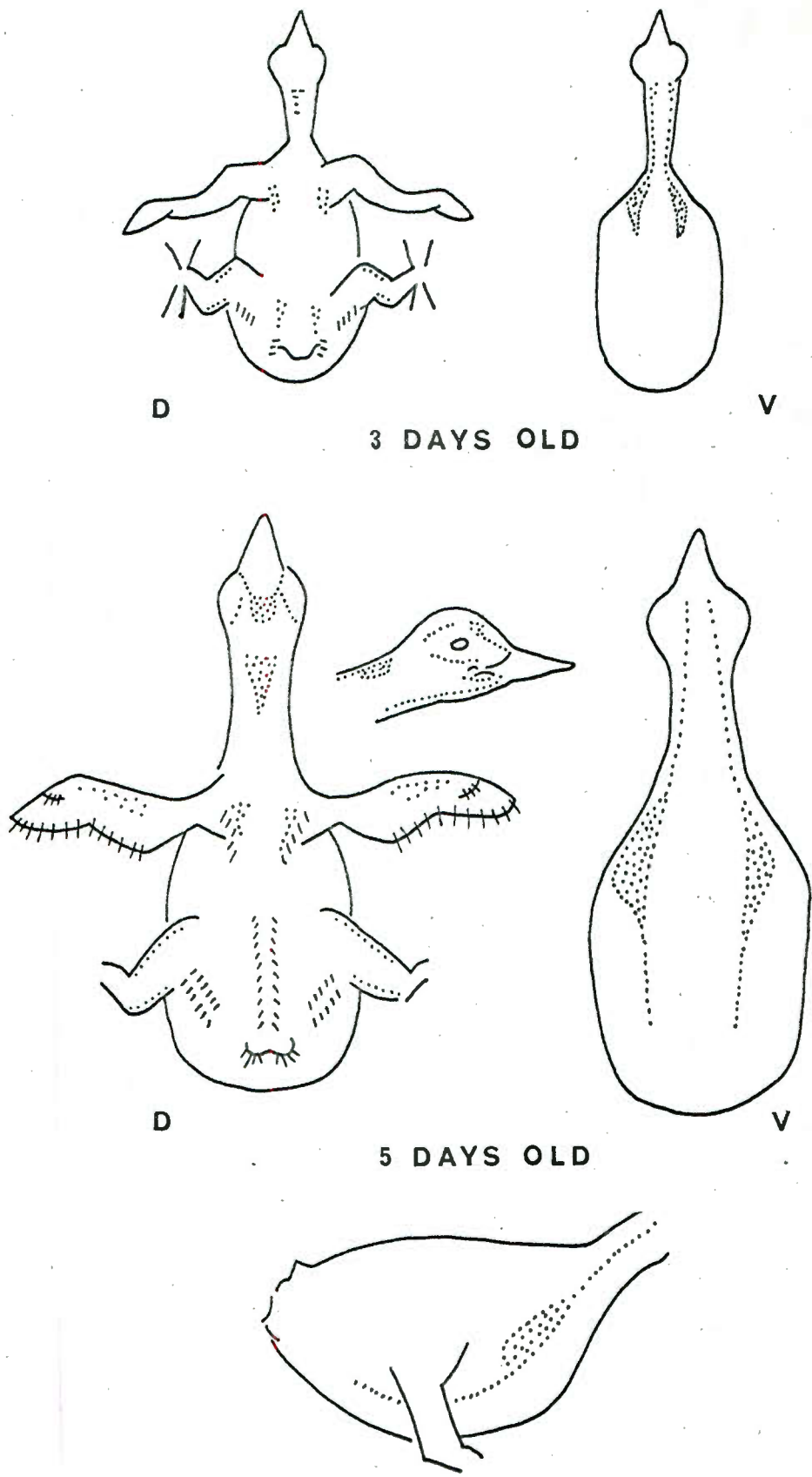


FIGURE 2. Showing feather tracts of the nestling Jacobin Cuckoo.

D = dorsal

V = ventral

seen to be mere chance and that this habit of the cuckoo chick contributes to its successful survival.

In one nest the host bulbul chicks were found out of the nest at intervals. Thus in a nest with two host young hatched at the same time of day as the cuckoo, one bulbul chick was found on the ground after 24 hours and the second chick was found hanging dead (being eaten by ants) in a branch below the nest on the fourth day. There is no explanation to this, other than that either the cuckoo chick deliberately evicted the host chicks or that the parent birds evicted their own dying chicks. This is not impossible because a cuckoo chick which was small and under nourished compared to the feathered host chicks in the nest, also disappeared under abnormal circumstances.

It is of some interest to note that there are several records of young cuckoos being successfully reared along with young of the host. In the study area and period only one such situation occurred. There was also a record of two young cuckoos being reared in the same hosts' nests - and by coincidence one young was black-phased and the other black-and-white. Since both of these chicks were identical in size the eggs must have been laid simultaneously and two cuckoos must have parasitised the same nest on the same day.

#### FOOD

Though frequently observed searching for food in fynbos, *Rhus* bushes and wattle, only two types of food were observed eaten. The most important source of food is undoubtedly the various species of hairy caterpillars. These hairy caterpillars are "de-haired" in the normal manner before being swallowed. Nine records of positive identifications of swallowing hairy caterpillars were made. One was a small orange hairy caterpillar and another a large black one with long white tufts of hairs. The cuckoo was observed to hawk flying termites on four different occasions.

The young nestling was observed to be fed insects (termites (36 times), a beetle, a green locust with all legs taken off, a long-bodied insect with transparent wings *Rhus crenatus* berries (six times) and ripe berries of *Chrysanthemoides monilifera*. These last were purple in colour and usually left

a permanent colour on the nest (and hands of the person handling the chick).

### DISCUSSION

Much has been written about cuckoos and it is not possible to carry out a study of this nature without commenting upon some of the theories put forward. This is of especial interest in this study because the genus *Clamator* has been suggested Friedmann (1964) to be a primitive cuckoo genus with somewhat uncertain origin. At least from the divergent viewpoints of its origin, it can be said the origin is uncertain.

Having studied the development of a young bird of the genus *Cuculus* (Liversidge 1955) it has been possible to make several comparisons between the two genera (*Cuculus* and *Clamator*). All comparisons tend to confirm the point made by Stresemann (1969) that *Clamator* is isolated from *Cuculus*. Thus, for example, in general behaviour most of the *Cuculus* group have definite song perches whereas the *Clamator* have no such defined call posts as far as behaviour in southern Africa is concerned. The egg laying procedures as far as have been described show that most females of the *Cuculus* group lay their eggs without male assistance, whereas this study of the *Clamator* shows that the pair co-operate closely. The development of the chick of *Clamator jacobinus* is appreciably more rapid than that of *Cuculus solitarius*. The chicks of most of the *Cuculus* group evict hosts eggs or young but there is no evidence of this behaviour pattern in newly hatched *Clamator jacobinus* young.

It is suggested by Friedmann (1964) that *Clamator jacobinus* is the most primitive member of the genus. A variety of reasons are given for these ideas but they are by no means convincing. If, as suggested here, white egg colour has survival value - and indeed it must have to have survived, even if the writer's theories are incorrect - then it need not be a primitive condition but merely a secondary adaptation. Another point is that *Clamator jacobinus* have only been recorded laying eggs with male and female birds partaking in the activity. This is probably because the pair consort during much of the day; there is no solitary male activity as in the majority of the

*Cuculus* group and indeed most of the parasitic birds in other families. It can be argued that the pair bond is more primitive but it seems a stronger argument that the parasitic habit has arisen through the neglect of the males' normal breeding activities. It is the writer's belief that the pair bond in *Clamator jacobinus* is a secondary evolutionary development from the normal cuckoo behaviour of independent females laying on their own as in *Cuculus canorus*.

Friedmann (1964, p.14) said that when *Clamator jacobinus* spread from southern Africa to central Africa and India it turned from bulbuls and shrikes to babblers as chief fosterers. With respect to Friedmann's argument it would seem that parasitising babblers is potentially more primitive than bulbuls. Since some African babblers have uniform pale-coloured eggs, it would seem that this is the initial and longest evolved adaptation. From this host to the bulbuls seems a more logical step since the eggs would surely match the original hosts' if they do not match the new one (using Friedmann's own argument against Voous' (1959) suggestion that *C. glandarius* originated in the south).

A lot of nonsense has been written about cuckoo egg colour. This has mainly been concerned with *Cuculus canorus* where colour mimicry has evolved to a fine degree. Nobody has really experimented sufficiently with the host birds and their reaction to foreign eggs and colours of eggs. Work on reaction to colour has produced some interesting results and, at least in some passerine species, there is some reaction against certain colours. On the other hand this study concerns a bird, the Cape Bulbul, which is reputed to desert its nest far more readily than many other local passerines. Yet it accepts a pure white egg appreciably larger than its own, even though it has a comparatively small normal clutch of two to three eggs. Another point already mentioned is the very fact that seemingly incongruously coloured eggs are accepted by a number of different hosts from different parasitic cuckoos, indicating that there is some survival value in the existing state of affairs. Why it should be regarded as necessary for some cuckoo species in some portions of their range to have remarkably similar egg coloration to their hosts' and in other parts of their range to be so different has not been explained. One imagines that

egg predation plays a far greater role in this subject than has previously been suggested, since the host species appear less meticulous about accepting a strangely-coloured egg than has been implied. However, this is as much conjectural as the discussion on colour and mimicry of egg-colour in cuckoos' eggs. Until experimental work has been carried out on the behavioural aspect of the host's reactions to foreign eggs we cannot do more than guess.

#### ACKNOWLEDGEMENTS

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#### SUMMARY

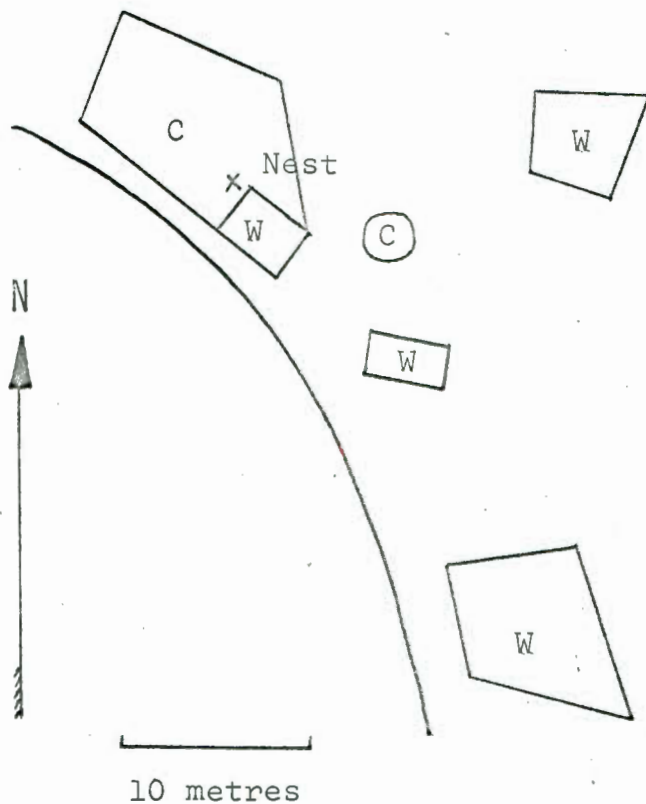
A detailed study of the Jacobin Cuckoo *Clamator jacobinus* over four years is presented. Differences in colour phase and sex ratio are mentioned. The birds are apparently not paired for life. They are mildly polygamous and return to the same area in subsequent years. Territory and its function are discussed. Behaviour is discussed including the special prerequisite to copulation of the male feeding the female with a caterpillar. Host selection is partially dependent upon the female cuckoo's own foster parents; this aids the cuckoo in finding the host nest at the most advantageous time. Degree of parasitism is given. Egg laying is described showing the part played by the male and the female cuckoo. Most eggs are laid during the host's laying period or after an interval equivalent to the incubation period. The selective advantage of white eggs is suggested. A total of 50 cuckoo eggs are dealt with. Predators and causes of loss are given. Development of young is outlined and comparisons with development of *Cuculus solitarius* are made. Observations on food are given.

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APPENDIX

Field notes of the detailed activity during which a cuckoo egg was laid in a bulbul nest. Nest No. 24, 5 December 1960. This egg laid 16 days after previous cuckoo egg by same female in same nest. (C = Jacobin Cuckoo; B = Cape Bulbul).



Map showing position of nest in relation to scrubs in the vicinity.

W - *Acacia cyclops*

C - *Chrysanthemoides monilifera*

- 8.00 a.m. Passing lorry frightens ♂ C from nest bush to 45 metres off.  
♂ C flies to edge of nest bush to attract ♂ B.  
♀ C emerges from 27 metres W. flies toward nest sees ♀ B sitting on nest.  
♀ C hovers about .61 metres off nest then returns to 27 metres W.
- 8.05 ♂ C joins ♀ C.  
♀ C drops into bush and works way to solitary *Chrysanthemoides monilifera* and sits in lower branches.

- 8.06 a.m. ♀ C joins ♂ in wattle.
- 8.13 Both cuckoos disappear into bushes.
- 8.18 Man walks past nest. ♂ B moves away.
- 8.21 ♂ B returns to nest bush.  
♀ B flies off nest - B chicks gaping.
- 8.23 ♂ B feeds chicks and remains on nest rim.
- 8.24 Both cuckoos preening in full view.
- 8.26 ♀ B returns to top of nest bush.  
♂ B flies off immediately.  
♂ B returns onto nest feeds chick - ♀ flies off.
- 8.28 ♀ B returns and broods on nest.  
Cuckoos disappear
- 8.30 ♂ B returns to feed chick, ♀ B to top of nest bush.  
Bulbul 26 comes to nest bush and is attacked by  
♂ and ♀ B of 24.
- 8.31 A cuckoo 13 metres from nest.
- 8.33 Pair 24 attack 26 bird and cuckoo moves closer.  
Sitting ♀ B calls alarm "Churrrr".
- 8.36 ♂ B comes to feed chick, ♀ B off.
- 8.39 ♀ B returns and settles on chicks.
- 8.41 ♂ C onto nest bush and is attacked by ♂ B.  
♂ C takes refuge within leaf canopy of nest bush.  
♀ C moves up closer, her position prevented site  
of ♂ C actions.  
♀ C flies to nest, sees ♀ B on chicks and hovers  
with spread tail over nest.  
♂ B attacks ♀ which flies off to 9 metres W.
- 8.43 ♂ B returns to nest bush perch.  
♂ C flies out with evasive twists and turns and  
settles conspicuously 9 metres off.  
♂ B is drawn by ♂ C evasive actions and settles  
.30 metres from ♂ C.  
♂ C jumps off with same exaggerated flashes and  
twists ♂ B calls rattling alarm but does not follow  
♀ C joins ♂ C 13 metres off.
- 8.45 Both cuckoos fly off 27 metres away.  
♂ C calls and moves off.
- 8.49 Both cuckoos fly right away.
- 8.59 ♂ B feeds large insect to young.  
♀ B to nest bush perch, preens then off.

- 9.02 a.m. ♂ B feeds chicks again and remains on nest edge  
1½ minutes.
- 9.03 ♀ B returns feeds chick and then settles on nest.
- 9.19 ♂ B returns to nest bush.  
♀ B flies off and ♂ B feeds young and sits on rim.
- 9.24 ♀ B returns and feeds chick then settles, ♂ B flies c
- 9.35 Cuckoos call 91 metres away.
- 9.36 ♂ B returns to 9 metres W and preens.
- 9.42 ♂ B leaves perch to return ½ minute later.
- 9.44 Both cuckoos return to 27 metres W.
- 9.48 Both cuckoos to 9 metres W near nest.  
♂ B sits within canopy, threatening with crest  
flattened.
- 9.50 ♂ C onto near open perch.  
♂ C moves to several nearby points.
- 9.54 ♂ C into W. 2 metres from nest.  
♂ B above cuckoo - silent.
- 9.56 ♀ C flies to other side of nest bush, ♂ B in  
hot pursuit.  
♀ C then appears on top of bush.  
♂ B goes above nest.
- 9.58 Four men walk past.  
Both cuckoos fly off ♀ 27 metres W. and ♂ B to  
9 metres W.  
♂ B initially pursues cuckoos but settles back  
quickly.
- 10.00 ♂ flies to ♀ C.  
Both cuckoos move to 13 metres W.
- 10.01 ♂ B feeds chicks but ♀ B stays on nest.  
Bulbul from 26 sits 9 metres away preening.  
Bulbul ignored by 24 ♂ and ♀.
- 10.05 Cuckoos moving about.
- 10.09 Cuckoos moving about.
- 10.10 Cuckoos move towards nest.
- 10.13 Bulbul 26 collects *Chrysanthemoides monilifera*  
berries from nest bush.  
Bulbul 26 flies to 27 metres W. Crest up and  
normal stance all time.
- 10.15 ♂ C flies and settles .61 metres from nest.  
♂ B attacks and drives it to 9 metres W. and  
returns to above nest.

- 10.15 a.m. ♂ B feeds chick as ♀ B flies off to 13 metres W. sits above ♀ C.  
 ♀ C preening nonchalantly.
- 10.17 ♀ B away and quickly returns to 9 metres W.
- 10.20 ♀ B returns to feed chicks  
 ♀ C to nearby *Chrysanthemoides monilifera*.  
 ♂ B to nearby *Chrysanthemoides monilifera* and remains
- 10.28 ♂ B chases bulbul 26 from 9 metres W.
- 10.36 ♂ C flies to near nest bush then into nest bush.  
 ♂ B follows ♂ C.  
 ♀ C into nest bush near nest, ♀ B drawn off to attack her.  
 ♂ C now flies to nest and both ♂ and ♀ B attack him.  
 ♂ C now flies off with exaggerated flashy flight not too far or fast.  
 ♀ C seems to pause a tantalising interval then onto nest.  
 ♀ B flies onto ♀ C on nest, wings fluttering tail spread.  
 ♂ C flies back over nest pursued by ♂ B.  
 ♀ C flies off 13 metres followed closely by ♀ B which returns to nest rim.  
 ♀ B crouches on rim for  $\frac{1}{2}$  minute then settles on nest  
 ♂ C flies off, ♂ B remains.  
 ♂ C calls a lot, a third cuckoo appears and the two fly to 27 metres W. where ♀ C joins.
- 10.40 Cuckoo off and all is over - a warm fresh cuckoo egg in nest.

## FURTHER NOTES ON BIRDS OF THE BLOEMHOF DISTRICT, TRANSVAAL

D. M. Skead & H. D. Brandt

The following observations supplement data in Skead (*S.A. Avif. Sér.* 26, 1965), adding a further 34 species to the list for the Bloemhof District. The authors are grateful to Mr. T. J. Steyn, Director of Nature Conservation in the Transvaal, for permission for one of us (D.M.S.) to publish this paper, Mr. S. S. du Plessis for checking the manuscript, and to Mr. R. Liversidge for supplying the information on the Wattled Crane *Bugeranus carunculatus*.

Squacco Heron *Ardeola ralloides*

Seven at the Big Pan on the S.A. Lombard Nature Reserve, 4 March 1967.

Saddlebill Stork *Ephippiorhynchus senegalensis*

An immature bird at a small vlei on the farm Kalkfontein near the Bloemhof/Hoopstad bridge over the Vaal River on 2 January 1967. Seen at the same place on 12 January 1967 by Mr. A. Speier.

Hadedah *Hagedashia hagedash*

Two flying up the Vaal River at Bloemhof, 17 July 1966. Five roosted overnight in Cape Willow *Salix capensis* trees on a small island in the Vaal River, 24 September 1966, at Klipdrift, Verlatenkraal.

Maccoa Duck *Oxyura punctata*

At small vlei on Kalkfontein, and recently on the S.A. Lombard Nature Reserve.

Lanner Falcon *Falco biarmicus*

One on the S.A. Lombard Nature Reserve.

Western Red-footed Kestrel *Falco vespertinus*

A large concentration arrived at the Lesser Kestrel *Falco naumanni* roost in Bloemhof in the second half of the 1966-67 summer where they remained for several months.

Black Kite *Milvus migrans*

An occasional visitor. One flock of 22 birds on the S.A. Lombard Nature Reserve.

Little Sparrowhawk *Accipiter minullus*

One in bush along Vaal River at Verlatenkraal.

Chanting Goshawk *Meliërax musicus*

Several sightings on the S.A. Lombard Nature Reserve.

African Marsh Harrier *Circus ranivorus*

Occasional at dams and vleis.

Moorhen *Gallinula chloropus*

Once at reedbed in the Vaal River at Bloemhof, and recently on the Big Pan, S.A. Lombard Nature Reserve.

Wattled Crane *Bugeranus carunculatus*

Although this is certainly not a bird of the area today Liversidge, *in litt.*, kindly supplied the following information: "Ludwig Krebs, an early German Naturalist, collected a specimen and eggs at Oppermansdrift in 1838." Oppermansdrift is about one mile above the town of Bloemhof.

African Jacana *Actophilornis africanus*

One on the Vaal River at Bloemhof.

<i>Hyphanturgus ocularis</i>	...	A.	21.10.63	Male 34.0, female 43.9, 40.0
			1.12.63	36.0
<i>Ploceus capensis</i>	...	P.E.	9.4.63	Female 47.8, 37.1, 44.8, 40.9, 33.2, 32.7 M, male 41.3 M, 43.3 M, 40.0 M, female 31.9 M, 34.8 M, 34.4 M, 41.9 M, imm. male 38.9 M
			24.6.63	Male 47.8, 45.2 M, 48.7 M, 46.6, 54.6 M, female 40.6, 44.9 M, 52.1, 38.6, 44.9, 51.5, 46.7 sex unknown 46.5, 41.0 44.0, 38.6
		A.	21.10.63	Female 44.0, 46.6, 44.2, 51.5, male juv. 43.7, 52.5
		H.	8.10.63	Male 45.8, 47.9, not sexed 39.1, 38.7, 35.0, 40.1, 41.8, 37.7, 37.1, 39.0, 46.5, 44.8, dead weight 44.1, 38.3, 35.2, 38.5, male 49.4, female 35.9, 36.5, 35.9
<i>Ploceus velatus</i>	...	K.N.P.	27.2.63	Male 24.5, 23.6, 23.3, 24.7, 23.2, female 19.7, 17.8, imm. 17.4
		A.	26.4.63	Female 23.6, 24.7, 27.4
<i>Quelea quelea</i>	...	K.N.P.	27.2.63	Female 16.0 M
		Kly.	28.8.66	66 weights min. 17.4, max. 23.3, mean 19.4 S.D. 1.47
<i>Euplectes orix</i>	...	Kly	24.8.66	Male 24.7
			28.8.66	25.2, 26.3, male 23.7
			24.9.66	20.6 M, 24.3, male 22.1
<i>Diatropura progne</i>	...	H.	8.10.63	Male imm. 46.9
<i>Amadina erythrocephala</i>	...	K.N.P.	27.2.63	Male 22.8, female 22.9, 21.0, 21.7, 20.7, 20.1
<i>Lagonosticta senegala...</i>	...	Kly.	30.10.66	8.7, 8.4, 7.4
<i>Granatina granatina</i>	...	Kly.	4.9.67	10.3
<i>Ortygospiza atrocoelis</i>	...	Kly.	28.8.66	12.9
<i>Vidua macroura</i>	...	Kly.	30.10.66	Female 13.6
<i>V. regia</i>	...	K.N.P.	27.2.63	Male 14.3, female 14.9
<i>Crithagra sulphuratus</i>	...	P.E.	23.3.61	27.8, 29.4, male 27.6, female 29.1
<i>C. flaviventris</i>	...	K.N.P.	27.2.63	Male 14.9 M, 15.0 M, 16.8 M, 14.6 M, 13.2 M, 12.5 M, 13.2 M, 13.8 M, 14.6 M, female 16.0 M, 14.8 M, 15.5 M, 12.5 M, 12.7 M, 13.3 M
		Kly.	24.8.66	Male 16.0
			28.8.66	17.4, male 16.8, female 16.8, 15.1
			24.9.66	Male 16.9, 16.8, female 16.8, 15.9, female 19.4, 17.4, 17.9
<i>Poliospiza gularis</i>	...	A.	1.12.63	24.7, 20.2, 20.2
		P.E.	14.8.61	22.9
<i>Fringillaria impetuani</i>	...	Kly.	28.8.66	14.8 M, 14.3 M, 15.7 M, 14.3 M, 13.8 M
			24.9.66	15.3 M, 15.0 M
			20.6.67	12.4, 15.4 M, 12.0, 15.2, 13.1, 15.1
			4.9.67	16.2, 16.9, 16.1
			10.9.67	18.6, 18.9

R. Liversidge, Alexander McGregor Memorial Museum, Kimberley, C.P.

<i>Sylvietta rufescens</i>	...	...	K.N.P.	27.2.63	11.5 f.p.
<i>Apalis thoracica</i>	...	...	P.E.	12.9.62	11.4
				23.3.60	10.2 M; 10.4
<i>Prinia flavicans</i>	...	...	Kly.	28.8.66	9.9
<i>Prinia maculosa</i>	...	...	P.E.	23.3.60	10.3 M, 10.5 M, 10.0 M
				14.8.61	11.2
<i>Parosoma subcaeruleum</i>	...	A.		1.12.63	13.9
		K.N.P.		27.2.63	12.8 M, 15.7 M, 13.0, 12.8 f.p., 13.6 M
		Kly.		28.8.66	14.1, 15.0
				30.6.67	16.1
<i>Bradornis mariquensis</i>	...	...	K.N.P.	27.2.63	23.5 M, 20.8 M
<i>Sigelus silens</i>	...	...	A.	21.10.63	27.9
			P.E.	22.3.60	22.5, 23.0
			Kly.	30.10.66	24.4, female 26.6, 26.8
<i>Batis pririt</i>	...	...	Kly.	30.6.67	Female 8.7
<i>Macronyx capensis</i>	...	...	P.E.	16.5.63	54.4 M
<i>Lanius minor</i>	...	...	K.N.P.	27.2.63	41.3 f.p. 42.8 M
<i>L. collaris</i>	...	...	P.E.	16.5.63	49.2 M
				17.5.63	Male 44.0, 48.9, female 40.5, 42.6
			A.	21.10.63	44.6
				1.12.63	Male 46.6 f.p.
<i>L. collurio</i>	...	...	K.N.P.	27.2.63	27.9, 23.8 f.p.
<i>Laniarius ferrugineus</i>	...	...	A.	21.10.63	57.5, 69.5, 63.0
				1.12.63	59.1
<i>Tchagra tchagra</i>	...	...	A.	21.10.63	50.6, 54.3
<i>T. australis</i>	...	...	Kly.	30.6.67	34.3
<i>Nilaus afer</i>	...	...	Kly.	30.6.67	26.9, 23.9
<i>Creatophora cinerea</i>	...	...	H.	8.10.63	68.9 M
<i>Lamprocolius nitens</i>	...	...	K.N.P.	27.2.63	69.3 M, 74.9 M, 65.3 M, 68.4 f.p., 85.4 M
<i>Spreo bicolor</i>	...	...	A.	17.5.61	103.0, 98.0, 94.5, 91.5, 100.5
			H.	8.5.63	101.4, 104.4, 93.6
				8.10.63	98.8 M
			A.	1.12.63	96.5 M
<i>Nectarinia famosa</i>	...	...	P.E.	18.8.61	15.4
<i>Anthobaphes violacea</i>	...	...	P.E.	16.5.63	9.2, 9.3
<i>Cinnyris afer</i>	...	...	A.	24.5.63	Male 12.7, 12.3, female 11.3 (all dead weights)
				1.12.63	Female 9.8
<i>Zosterops pallidus</i>	...	...	Kly.	28.8.66	9.5, 9.0, 9.7
				30.10.66	10.1, 9.4, 9.4, 8.7, 10.3, 10.5
				30.7.67	8.7, 8.5, 9.1, 8.5, 8.6, 8.4, 9.0, 9.5, 9.7
<i>Plocepasser mahali</i>	...	...	K.N.P.	27.2.63	43.5
			Kly.	24.2.62	47.3, 40.6
				10.9.67	48.8, 43.9
<i>Philetarius socius</i>	...	...	K.N.P.	27.2.63	26.9 25.6, 27.1, 26.2, 26.6, 24.1, all in moult imm.
					25.4, 24.2, 24.6, 22.7
<i>Passer iagoensis</i>	...	...	K.N.P.	27.2.63	Male 31.1 M, female 31.6, 30.5, 32.5, 33.6, all in moult
<i>P. melanurus</i>	...	...	P.E.	10.8.61	Male 17.4, female 17.3
			Kuru-	3.3.63	Male 18.4, 21.4, 20.4, female 19.1
			man		
			Kly.	28.8.66	Female 24.4, 24.6, 23.6, 21.4 M
				20.6.67	19.5, 21.0
<i>P. diffusus</i>	...	...	K.N.P.	27.2.63	20.4 f.p., 23.6 f.p., imm. 18.6
<i>Sporopipes squamifrons</i>	...	...	K.N.P.	27.2.63	11.0, 11.0, 11.0, 10.0, 11.5, 11.0, all in moult
			Kly.	28.8.67	10.0 M, 11.3
				4.9.67	11.8

<i>Urocolius indicus</i>	...	...	K.N.P.	27.2.63	53.1, 51.7
			Kly.	30.6.67	51.9, 41.0, 47.2
<i>Megaceryle maxima</i>	...	...	P.E.	26.11.63	sick bird 233.5
				4.6.63	332.7 M
<i>Corythornis cristata</i>	...	...	P.E.	6.4.63	14.9
<i>Halcyon albiventris</i>	...	...	P.E.	26.11.63	sick bird 61.7
				1.12.63	Male 68.2, female 72.6
<i>Coracias caudatus</i>	...	...	K.N.P.	27.2.63	122.1
<i>Upupa africana</i>	...	...	A.	17.5.61	Male 59.0, female 47.5
				21.10.63	66.7
				1.12.63	Male 63.0
<i>Rhinopomastus cyanomelas</i>	...	...	K.N.P.	27.2.63	Male 38.8 M
<i>Tricholaema leucomelas</i>	...	...	K.N.P.	27.2.63	29.3 M
			Kly.	28.8.67	36.2
				30.10.67	36.0, 33.4
<i>Indicator minor</i>	...	...	Kly.	30.6.67	26.6 37.2
<i>Dendropicos fuscescens</i>	...	...	Kly.	30.6.67	35.7
<i>Mirafraga africanoides</i>	...	...	K.N.P.	27.2.63	24.5
<i>Tephrocorys cinerea</i>	...	...	Kly.	24.9.67	25.7
<i>Hirundo rustica</i>	...	...	A.	9.4.63	18.9-24.0 mean 21.0 S.D. 1.4 (30)
			Kly.	Mar. 67	juv. 21.0-26.4 mean 24.6 S.D. 1.4 (34)
					ad. 23.9-27.3 mean 25.6 S.D. 1.2 (9)
<i>Petrochelidon spilodera</i>	...	...	Kly.	24.9.67	19.8
<i>Riparia paludicola</i>	...	...	H.	8.10.63	13.2, 11.5, 10.9
<i>Campephaga hartlaubi</i>	...	...	A.	1.12.63	Female 39.7
<i>Oriolus oriolus</i>	...	...	Kuru-	3.3.63	Female imm. 66.3 M
			man		
			area		
<i>Corvus capensis</i>	...	...	H.	8.5.63	697 M
<i>Parus afer</i>	...	...	K.N.P.	28.2.63	18.0
			Kly.	28.8.66	20.7
				30.10.67	22.4
<i>Turdoides bicolor</i>	...	...	K.N.P.	27.2.63	77.3 M
<i>Pycnonotus capensis</i> : see figure 1					
<i>Pycnonotus nigricans</i>	...	...		20.6.67	31.3, 32.4, 28.1, 32.1, 38.4, 28.4, 29.0, 28.0, 31.5, 32.8, 32.9, 30.6, 30.0, 35.5, 29.3, 35.6, 30.3, 28.7, 27.0, 30.6, 28.1, 28.2, 31.5, 26.5, 28.3, 34.1, 29.0, 30.8, 31.6, 26.6, 28.2, 28.2, 30.1, 32.8, 29.6, 35.9, 35.7, 39.1, 32.4, 32.5, 30.3, 32.1, 35.1 26.5-39.1 mean 31.4 S.D. 3.1 (43 birds)
<i>Andropadus importunus</i>	...	P.E.		14.8.61	38.6
				23.3.61	34.6 M
		A.		21.10.63	39.2, 33.5, 38.8, 31.5, 35.5
				1.12.63	37.0, 34.6, 36.8, 37.4, 35.8, 33.7, 37.2, 30.3
<i>Turdus olivaceus</i>	...	...	A.	21.10.63	72.0, 85.0
			Kly.	30.10.66	74.2, 74.7, 70.2, 64.0, 69.2, 80.8, 77.3, 77.9, 74.2
				30.7.67	78.2, 86.4, 83.2, 72.7
<i>Turdus litsitsirupa</i>	...	...	K.N.P.	27.2.63	72.4, 75.6
<i>Cercomela familiaris</i>	...	...	K.N.P.	27.2.63	18.4
<i>Saxicola torquata</i>	...	...	P.E.	16.5.63	15.8
			H.	8.10.63	14.7
<i>Cossypha caffra</i>	...	...	A.	21.10.63	27.4, 29.0
			P.E.	23.3.61	27.0
			Kly.	30.10.66	28.9, 27.7, 29.3, 33.2
				30.7.67	27.5, 30.1, 27.2, 24.3, 31.9, 28.6
<i>Hippolais icterina</i>	...	...	K.N.P.	27.2.63	12.4
<i>Calaniocichla gracilirostris</i>	...	...	H.	8.10.63	17.2

various authorities. There are too many to whom thanks are due for such help to name them individually, but credit goes especially to the members of the Eastern Cape Wild Birds Society and Northern Cape Nature Conservation Society, who have helped in the ringing programmes from which much of this information was collected.

<i>Phalacrocorax africanus</i>	...	H.	8.5.63	655
<i>Melierax musicus</i>	...	K.N.P.	25.2.63	500.8
<i>Francolinus natalensis</i>	...	Kly.	30.6.67	554.9 ad., 369.3 juv.
<i>Charadrius pecaurius</i>	...	Kly.		35.1
<i>C. tricollaris</i>	...	Kly.	24.9.66	33.2, 35.0
<i>Stephanibyx coronatus</i>	...	K.N.P.	2.3.63	158.3
<i>Capella nigripennis</i>	...	H.	8.10.63	109.8, 106.3
<i>Calidris testacea</i>	...	C.	18.12.48	45, 46
<i>Calidris minuta</i>	...	C.	21.12.48	21, 21, 22, 24
<i>Tringa glareola</i>	...	H.	8.10.63	55.9; A. 21.10.63 58.5
<i>Burhinus capensis</i>	...	K.N.P.	27.2.63	427.2
<i>Pterocles namaquensis</i>	...	K.N.P.	27.2.63	170.7 M; 179.4 M
		Kly.	29.7.66	Male 171.8, 185.7, 181.4, 183.1, 183.3, 176.8, 166.0, 177.3, 191.3, 177.7, 188.4, 190.8 Female 149.1, 176.7, 180.9, 181.9, 183.3, 178.7, 181.9, 192.2, 164.9, 182.9, 149.8, 142.6, 192.6
		Kly.	24.8.66	Male 167.8 Female 167.3, 156.3
		Kly.	24.9.67	191.4 M; 188.8
<i>Pterocles burchelli</i>	...	Kly.	29.7.66	Male 192.7
<i>Streptopelia capicola</i>	...	P.E.	19.4.63	155.7
		K.N.P.	Feb. 63	119.4 imm; 122.8 imm; 130.1 ad; 136.8 M. 124.2 ad; 136.9 ad; 114.0 ad M
		A.	21.10.63	156.5, 148.7, 159.0, 153.0, 148.4
			1.12.63	129.0, 141.2, 124.7, 127.1
		Kly.	24.9.67	147.1, 124.7, 175.7
<i>Stigmatopelia senegalensis</i>	...	A.	1.12.63	97.6, 77.5, 108.2, 99.2, 99.7, 114.2, 95.0, 111.0, 92.5
		Kly.	24.8.66	76.1
			28.8.66	99.5 M, 99.2 M
			24.9.66	89.1, 90.2
<i>Oena capensis</i>	...	K.N.P.	27.2.63	Male 35.4 M; Female 38.8 M; Female imm. 35.3 M, imm. 30.9, Female 40.6 M
		Kly.	24.8.66	imm. 40.0, 38.1, 39.9, 39.7, 39.4, 39.4, 43.6, Male M. 46.0, 41.2, 46.6 gms Female 36.8
			28.8.66	imm. 38.9, Male 42.8, 48.2, 41.4, 43.8, 43.2, Female 43.0
			24.9.66	Male 41.6, 38.2, 36.2, 43.5, 46.2, Female 41.3, 38.6 M
			20.6.67	40.1
			4.9.67	40.1, 42.2, 42.4
<i>Turtur chalcospilos</i>	...	A.	1.12.63	imm. 48.4 M; 52.8 ad, 62.5 M
			1.12.63	ad. 60.0, 63.4, 61.4, 67.7, 70.7, 65.0, 66.2, 64.4, 68.4, 66.6, 63.1, 59.7, 67.2
<i>Cuculus cafer</i>	...	A.	21.10.63	91.5
<i>Clamator jacobinus</i>	...	P.E.	1.11.63	82.4
<i>Caprimulgus europaeus</i>	...	K.N.P.	27.2.63	50.6
<i>Apus apus</i>	...	K.N.P.	27.2.63	31.2
<i>Colius striatus</i>	...	P.E.	12.9.62	58.4
<i>Colius colius</i>	...	K.N.P.	27.2.63	52.4
		Kly.	28.8.66	41.8
			30.6.67	47.9, 38.3, 44.1, 43.6, 38.2, 48.3, 43.6, 46.3
			30.10.67	47.6

## BIRD WEIGHTS

R. Liversidge

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There is very little recorded on the weights of birds in Southern Africa. Thus, during the course of netting for ringing opportunity has been taken to weigh all species caught. Although this has necessarily resulted in a haphazard collection of information (presented below), it nevertheless appears that there is geographical and season variation in bird weights, as well as individual variations within the species; and the data seem worth placing on record.

All birds have been weighed alive, except where otherwise stated, using a triple beam balance (Ohaus), correct to 0.1 gm. Initially birds were placed in cloth bags, the bags being weighed before and after each individual bird. Later paper cones were used with a check before and after of the weight of the cone. The list uses names from *Roberts Birds of South Africa* (McLachlan and Liversidge 1957), and the following abbreviations: A=Amanzi, Uitenhage; H=Humansdorp; Kly=Kimberley area; K.N.P.=Kalahari National Park; P.E.=Port Elizabeth area; M=bird in moult; f.p.= bird in fresh plumage. All weights are given in grams.

To show variation during the course of the year, weights for collected (dead) specimens of the Cape Bulbul *Pycnonotus capensis* are present in graph form (Fig. 1).

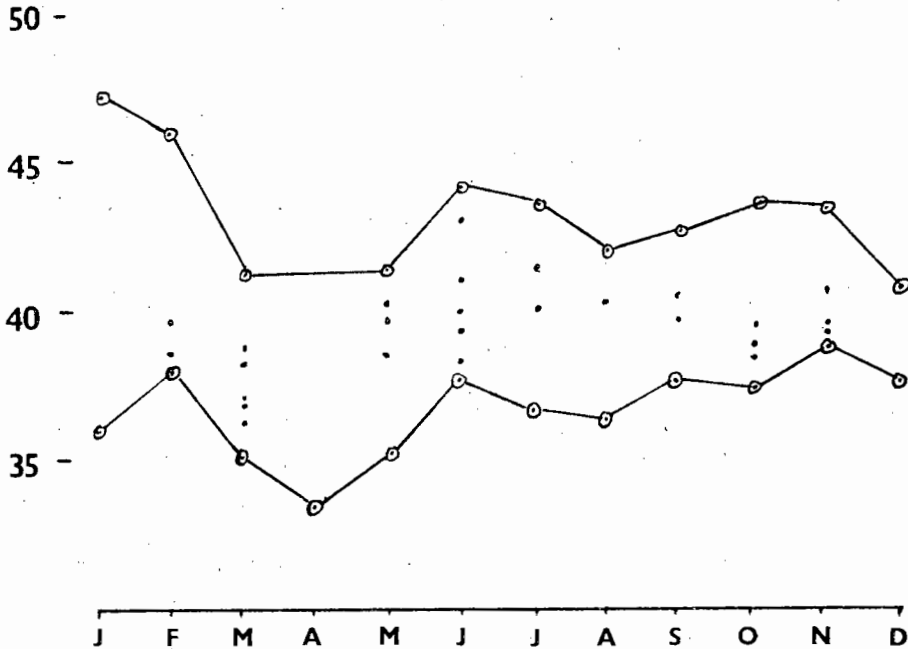


Fig. 1. Dead weights (gm.) of *Pycnonotus capensis* collected in each month of the year. (x axis=months, y axis=weight)

In a small series of weights taken of *Quelea quelea* flying in and out of a nesting colony, an attempt was made to establish whether there was any significant difference between weight of male and female; or between birds with full crops coming in to feed young, and birds with empty crops leaving the colony. Using the t test for significance on the following data no significant differences were established.

No. of birds (female) 13 without food mean 18.7 gm. S.D. 1.22

No. of birds (male) 18 without food mean 19.3 gm S.D. 1.19

No. of birds (male) 21 with food mean 20.8 gm. S.D. 1.13

Catching live birds needs the co-operation of many individuals and permission from owners and

species were represented by more than one breeding pair; whereas during the drought year 1960 the same species might have been seen, and in the case of *Turdus olivaceus*, were seen, carry nesting material to a site well outside the area.

The different species do not all react the same way to conditions. Table 2 shows data for one species and it can be seen that the most successful year from the point of view of number of fledglings was 1960 with 23 against 2 in 1961 and only 9 in 1962. This is different from the combined result of all species (Table 1). Parasitism by a cuckoo in *P. capensis* was greatest in 1960 too.

No mention has been made of the breeding activity outside the August to December period. December is normally a quiet period and post-nuptial moult often takes place at this time. However, if there are good rains, breeding will commence again. It has been shown in *Pycnonotus capensis* that breeding will take place irrespective of the stage of moult. Breeding occurred in several species in March after good February rains. Thus the facts and tables presented here do not give the complete picture for the year.

It is thought that the 1962 population, with 115 breeding pairs within 50 acres, is probably a "normal" breeding population for the habitat. And that after very good years the numbers and variety will increase further. What the limiting factors are, is not fully understood. It is very doubtful that food was a limiting factor for any species during the period of study. For *Pycnonotus capensis* it has been worked out in detail that there is more than enough food for the small population present even within the 50 acres. The impression gained is that at no stage during the study did the population reach a point where density dependant factors came into operation. Density independant factors operate and rainfall appears to be the most important factor involved even here where conditions are more stable than elsewhere in Southern Africa.

## SUMMARY

Details of 519 nesting attempts by 30 species over a three-year period are tabulated showing annual variation in numbers of species and numbers of individuals. Changes in seasonal activity are discussed. It is concluded that density dependant factors do not operate under local conditions and that rainfall and its effect are the most important density independant factors.

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## DISCUSSION

The results of 519 nesting attempts in three years have been summarized above. It has been shown that drought years have some effect upon the birds and their breeding efforts. What could well be stressed in this regard is that the south coastal belt is one of the more stable, climatically speaking, and the changes given can be regarded as almost minimal if not the minimum change that can be expected in southern Africa. It is interesting too in this respect to note that locally, whilst the rainfall differed from the pattern of the region (say a 50-mile radius), the population changes seemed more influenced by the region than by the immediate local conditions. This is important since it has been generally stated that birds in the Western Cape breed earlier than in the Eastern Cape.

This change in season must be dealt with, with caution and it is essential to take consideration of the local conditions when making such a comparison. Table 4 concerns one species that breeds in the Western Cape and the Eastern Cape and shows that the peak period each year for the species in the one area varies and that birds nesting 500 miles away vary to a different degree. It can be clearly seen that no two years are alike and thus any generalization is not permissible. Thus nesting seasons cannot easily be compared.

TABLE 4

NUMBER OF NESTS RECORDED FOR EACH MONTH IN THREE DIFFERENT YEARS FOR THE *PYCNONOTUS CAPENSIS* IN THE WESTERN PROVINCE AND EASTERN CAPE

Year		Aug.	Sep.	Oct.	Nov.	Dec.
1960	W.P.	0	1	0	1	1
	E.P.	0	0	13	23	3
1961	W.P.	2	4	3	1	0
	E.P.	0	0	6	14	1
1962	W.P.	0	11	6	2	0
	E.P.	2	17	7	6	1

There is some indication that the peak of the nesting activity occurred in each year in the month after the peak rainfall. In 1960 major rainfall was in August and September with the nests increasing in October and peak in November. In 1961 the peak rains fell in August with nesting activity increasing appreciably that month and the following month. In 1962 there was a high August peak rainfall with a high nesting peak in September.

Another aspect of rainfall effect is that on the vegetation, particularly with berry production for the frugivorous species. Peak berry production varied with the rainfall but the effect took longer, depending upon the species of plant it was between two and four months. The flowering period, of course, had to coincide with the insect population needed for pollination and if the rains were too early or too late this would affect the berry production. However, the birds seemed more effected by direct rainfall than the indirect factors of rainfall.

Before making final comments about the various aspects of this paper it is worth noting that the area of the sample plot—50 acres—is probably on the small size. Campbell (1953) has discussed suitability of area and inclines to favour an area of 100 acres. It would not have been possible to include every detail of all species in such a large area. An interesting aspect of sample size is that in the good year, 1962, nearly all local species nested within the 50 acres and several of the

TABLE 2

THE DETAILED NESTING ACTIVITY OF ONE SPECIES *PYCNONOTUS CAPENSIS* FOR COMPARISON WITH TABLE 1, TO SHOW HOW ONE SPECIES MAY DIFFER FROM THE GENERAL PATTERN

Year	No. of breeding pairs	No. of nesting attempts	No. of eggs laid	No. of eggs in completed clutches	No. of completed clutches	No. clutches that hatched	No. of eggs hatched	No. of young fledged
1960	19	39	93	72	30	13	32	23
1961	13	21	29	19	7	1	2	2
1962	15	33	58	50	20	10	23	9

## NESTING URGE

The nesting urge as represented by the number of nests found varied from 117 in 1960 to 253 in 1962. This represents a drop of 53% in nesting activity in drought years. This drop is in part due to population change but not entirely, since a crude estimate of number of nesting attempts per pair was 1.5 in 1960 and 2.4 per pair in 1962. The nesting urge is apparently less in drought years than in better years.

## BREEDING SUCCESS

The greatest change that occurred was from 104 fledglings in 1961 to 165 in 1962, an increase of 37%. This does not agree with the figure for nesting urge but it is apparent that there is something different with nesting success since 1961 is lower than the drought year 1960, despite the fact that the breeding population increased 13% and the nesting urge in the same period increased 27%. The reason for this curious anomaly is not clear. It will be noted that the number of eggs hatched that survived to the fledgling stage is approximately the same. There were less completed clutches in 1960 and the average clutch size was smaller. It was noted that predation upon the nests at the egg-laying stage was highest in 1961.

## SEASONAL VARIATION

The peak nesting periods in the three years showed a shift from November in 1960, October-November 1961 and September in 1962. There seems to be some correlation with average rainfall in these years with peak nesting following after the rainfall. (See Fig. 1.)

TABLE 3

NUMBER OF NESTS RECORDED IN EACH MONTH OF EACH YEAR INDICATING THE SEASONAL DIFFERENCE IN PEAK NESTING ACTIVITY

Year	Aug.	Sep.	Oct.	Nov.	Dec.
1960	1	6	40	62	8
1961	5	17	60	60	7
1962	4	122	61	61	5

is a "good" one. This error is considered less than that using the number of completed clutches as an indication of breeding activity.

## RESULTS

From the mass of information gathered four tables are presented below summarizing details of breeding activity. For the purpose of these tables, the month in which the first egg was laid or estimated to have been laid has all information from that particular breeding attempt. Incomplete clutches have not been included in the figures and where fledglings or nestlings were found, the assumption has been made that the number of eggs hatched and the clutch size, equalled the number of young unless an unhatched egg was found.

### NUMBER OF BREEDING SPECIES

Of the 76 species recorded within the 50 acres, 30 were known to breed. Another eight species nested in similar habitat nearby but were not recorded within the study area. In the three years the number of breeding species varied from 20 in 1960 to 28 in 1962. This change was probably due to the prevailing drought in the earlier year and the successive years of better conditions. *Sylvietta rufescens* was present only in the drier years. *Turdus olivaceus*, *Zosterops pallidus*, *Sigelus silens*, *Coliuspasser capensis* and *Serinus flaviventris* which were all absent as breeding birds in 1960 increased in numbers with the better conditions.

The increase of 27% in variety of breeding species is considered due to difference between drought and "normal" conditions.

TABLE 1

DETAILS OF NUMBERS OF SPECIES, PAIRS AND THE NESTING DATA ON ALL BREEDING ATTEMPTS FROM AUGUST TO DECEMBER

Year	No. of species breeding.	No. of breeding pairs.	No. of nesting attempts.	average per pair.	No. of eggs of completed clutches.	average per pair.	No. of eggs from complete clutches hatched.	ditto as %	No. of young fledged.	% of eggs to fledglings.	% mortality of nestlings.
1960	20	79	117	1.5	243	3.1	146	60	113	46	23
1961	24	89	149	1.7	222	2.5	126	57	104	47	21
1962	28	115	253	2.4	336	3.3	236	64	165	45	30

### NUMBER OF BREEDING PAIRS

Not only were there more species under moister conditions but the number of breeding pairs increased appreciably from 79 in 1960 to 115 in 1962. This represents an increase of 46%; perhaps this is better expressed as a drop in the breeding population of 31% due to drought conditions. Many birds were present in 1960 although they made no attempt to breed e.g. *Sigelus silens*. Perhaps more noteworthy in this respect is *Turdus olivaceus*, present in 1960 and 1961 but in 1962 four pairs bred within the study area indicating that this species is subject to considerable population fluctuations.

termed a social association. Indeed 18 of the 30 breeding species were recorded at one time or another tolerating their own species within their nesting or song proclaimed territory. Quite apart from this problem there is also the complication introduced by the so-called mimics. Mimics in song, not only introduce a source of error but could take up considerable time in the field merely checking up on all birds heard. For this reason, the normal census methods proved inadequate.

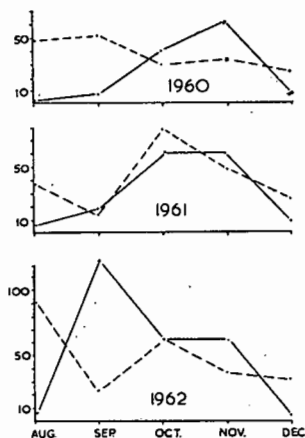


Figure 1. Comparison between rainfall in mm/month (broken line) and the number of nesting attempts (solid line).

The presence of all breeding pairs was established by the time consuming method of following the activities of all birds. A small number of birds were colour banded. The area was visited most mornings during the period August to December. In 1961, 118 visits were made covering a minimum of 171 hours. Whilst all attempts at nest building may not have been recorded, the observer feels satisfied that no fledglings were reared that were not recorded. Of the 30 species nesting, 13 were uncommon enough to know all nesting attempts. Fourteen of the remainder possibly had a maximum error of two in ten whilst for three species the error may have been greater than this because of their secretive habits. The writer does not feel that the error was as great as this and whatever error there was, was a constant error. Such error as admitted, falls well within the limits of error using the "singing male" technique.

### BREEDING ACTIVITY

It is normal to give the number of clutches or young hatched or some similar standard as the measure for breeding activity. Under the local prevailing conditions predation upon nests was unusually high; at least higher than for figures quoted for temperate regions. Predation upon eggs especially was high during the laying stages with monkeys, rodents and egg-eating snakes leaving abundant tell-tale evidence of their visits. One colour banded pair of bulbuls attempted eight nests in one year and three nests the following year without ever hatching any eggs. In this paper the number of attempts at nest building is used as an indication of the level of breeding activity. The major drawback, of this method of presentation is that if the first attempt to nest is successful, the time and energy taken to produce fledglings reduces the probability of an immediate second brood unless the season

# FLUCTUATIONS IN A BREEDING POPULATION IN THE EASTERN CAPE

R. Liversidge

Coldstream, E.C.P.

## INTRODUCTION

It is perhaps topical that with an apparent diminution of numbers of birds in at least some parts of southern Africa this drought-stricken year, the fluctuations in breeding populations should be discussed. This study will show what happens during a recovery period from drought in a region where drought conditions are comparatively mild. The work presented here was a by-product of a detailed study carried out on the Cape Bulbul *Pycnonotus capensis*. For a period of five years the detailed activities of this species were recorded in an area of 50 acres near Port Elizabeth, Eastern Cape. At the same time extensive notes were made on all birds within this area. The first two years are not presented since there was a necessary period of learning when the probability of error made the results not too reliable. The final three years (1960-62) breeding of all species, for the period August to December only, are here presented.

## HABITAT

The vegetation type in the area along the coastal sand dunes is referred to as coastal or maritime heath (Martin & Noel, 1960). Wind-eroded shrubs and dwarfed trees dominate the dunes but a fair proportion of exotic wattle, *Acacia cyclops*, exists and outside the area of study it is a dominant in the whole region. The windward aspect of the dunes are covered with xerophytic prostrate shrubby forms and the valleys on the leeward side with tree forms. Open areas extend between the dunes which have fynbos or prostrate vegetation. This habitat forms a narrow strip along the whole southern coast line.

Compared to other portions of southern Africa, the coastal area of the Eastern Cape is climatically more stable than elsewhere and rainfall occurs throughout the year. Generally the Eastern Cape suffered a drought period which was broken in 1960. Although in the general surroundings rainfall increased from 1960 to 1962, in the area of study the 1960 rainfall was highest with a gradual lessening each year (Fig. 1).

## METHOD OF OBSERVATION

A lengthy discussion on the merits of various theories regarding census work on breeding populations cannot be given here. Enemar (1959), however, has written an excellent review article which shows clearly that much reliance is placed upon "mapping singing males". In fact the only point at dispute in the literature appears to be the relative proportion of singing males to the breeding pairs present, or to the population as a whole. This presupposes a strict territorial behaviour in all birds present. Such an assumption cannot be made under local conditions.

With social or semi-social species it is obviously not possible to rely on numbers of singing males as an indicator of population. With frugivorous species and those that fed on seeds or flower heads there was often need to feed in, what may be

## SHORT COMMUNICATIONS

### PRE-INCUBATION DEVELOPMENT OF *CLAMATOR JACOBINUS*

The incubation period of parasitic cuckoos is very short for the size of the bird compared to that of their host. Nice ('Ostrich' 1952, 23 : 223) states that she was unable to find a single, properly authenticated published record of an incubation period of any species of bird of less than eleven days, and expresses doubt about Skead's record for the incubation period of the Bronze Cuckoo *Chrysococcyx cupreus* of 10-10½ and 10-11 days. In recent work on the much larger Jacobin Cuckoo *Clamator jacobinus* the incubation period was determined in four instances to be between 11 days ± 14 hours and 12 days ± 12 hours. Such short incubation must contribute to the successful habit of parasitism and it was decided to determine the extent of any embryonic development occurring in *Clamator jacobinus* before the egg was laid, that might account for this.

An egg was laid by a Jacobin Cuckoo between 7.00 and 9.15 a.m. The embryo was fixed at 10 a.m. and had thus been laid 2 hours ± 1 hour prior to fixing. However, if a domestic fowl's egg cools to room temperature (about 80 °F.) development ceases (Barth 1953 'Embryology'). The nest in which the Jacobin Cuckoo had been induced to lay was deserted by the host the previous day, so that it is assumed no incubation took place and it seems reasonable to consider the fixed embryo as newly laid. A whole-mount slide showed quite clearly the primitive streak on the pear-shaped pellucid area and indication of the headfold below the proamnion. Cross sections also showed the primitive groove quite clearly. No somites had yet formed.

The embryo of a domestic fowl develops for about 20 hours before being laid (Barth *loc. cit.*) in the period between ovulation and laying, the ova being fertilized by the sperm present as it erupts; but the state of the development of the embryo is usually expressed in days and hours only from the time incubation started. Following Witschi (1956 'Development of Vertebrates') the development described above is comparable to 17-20 hours *post*-incubation development of the domestic fowl and it is possible to say that at laying the development of the embryo in the Jacobin Cuckoo is approximately 17-20 hours advanced on the normal chick embryo. This is not unexpected since the species lays at intervals of not less than 48 hours (Liversidge, in press) as is also the case with the European Cuckoo *Cuculus canorus*.

The Jacobin Cuckoos' behaviour between the laying of the eggs is normally quiet, and the sexes very often hunt food separately; whilst on the mornings on which the eggs are laid there is considerable display and only on these mornings were attempts at copulation seen, always after the egg had been laid. It is therefore possible that fertilization takes place about 48 hours before egg-laying, giving the advantage over the host species of extra time for embryonic development. In the chicken the next ovulation occurs soon after laying, and fertilization follows very quickly, but copulation at this time is not necessary for fertilization of each egg in the chicken and at least some other species. It remains to procure a small series of female cuckoos which have just laid in order to see whether ovulation and fertilization do in fact occur nearly 48 hours before laying.

Nice ('Centaurus' 1954 : 349) states that the critical factor determining the length of incubation is the rate of development of the embryo. Witschi (*loc. cit.*) compares the chicken development with that of the House Sparrow *Passer domesticus* without making any comment on any great difference between the two. In the case of the Jacobin Cuckoo (12 days) and the chick (21 days) it is obvious that the factor determining the length of incubation is the stage of development at which the embryo hatches, rather than the rate of development, which latter may be assumed to be not greatly different in the two species.

Museum, Snake Park and Oceanarium,  
Humewood, Port Elizabeth, S. Africa.

R. LIVERSIDGE.

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