THE BIOLOGY OF THE CAPE WEAVER *PLOCEUS CAPENSIS*
WITH SPECIAL REFERENCE TO ITS
POLYGNOUS MATING SYSTEM

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Plate 1.C.
Female

The CAPE WEAVER
PLOCEUS CAPENSIS

Plate 1.A. Adult Male - full breeding plumage.

Plate 1.B.
Subadult Male

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SUMMARY

The study of the biology of the Cape Weaver *Ploceus capensis* was carried out mostly in the winter rainfall area of the S. W. Cape in South Africa. This report shows that the species has conspicuous plumage dimorphism and some physical dimorphism in the sexes, and that the male only achieves full plumage at about 22 months old. The female reproduces at one year of age. Possible reasons for this deferred maturity in the male are discussed. It is concluded that the high competition for mates and the advantage to the young male in nest-building and territorial activities on the periphery of the colony are the main pressures for deferred maturity.

A detailed investigation of breeding seasons in the species is reported and it is shown how aspects of the clutch-size and incubation strategy are apparent adaptations to polygyny and its concomitant fluctuating food source. The ultimate and proximate factors influencing the breeding season are also discussed.

This study presents the first comprehensive study of moult in passerines in southern Africa. The more important findings are that moult is slower than in the northern hemisphere and that there are differences in the start of moult in different age/sex classes.

The food situation in the Cape Weaver is reported and it is shown how the species is adapted to a wide variety of insect and vegetable foods. The chicks are fed almost entirely on insect food except towards the end of the season. Weight fluctuations throughout the year are small and it is suggested that this shows that food fluctuations are smaller and present a much less difficult situation for the passerine in South Africa than in the northern hemisphere.

Evidence is presented which shows a sex ratio of 1 : 1 in nestlings though there are some interesting tendencies revealed in the data. In full-grown birds, there is a slight excess of males probably throughout the year. It is pointed out that this is the opposite to what would be "required" by a polygynous mating system.

Contrary to general theories, it is proposed that males do not suffer higher mortality than females during the breeding season. In fact it is suggested that females suffer higher mortality both in and out of the breeding season, partly as a result of their subordinate social position in all circumstances except at the nest.

The territorial and courtship behaviour of the Cape Weaver are described and it is shown how aspects of the behaviours vary according to the time in the season and the pair-bond circumstances. A social hierarchy study on the species is discussed.

Finally, the special aspect of the study, the unusual polygynous mating system is investigated in detail. A possible evolutionary sequence for the development of polygyny in passerines is proposed. This stresses the importance of the type of food source and the development of coloniality or gregariousness as the primary prerequisite.

A feature of the thesis is the attempt to keep the theme of the adaptations to polygyny in mind through all the studies of the other parts of the Cape Weaver's biology.

SECTION 1 - INTRODUCTION

1.1. Origins

Initial interest in the Cape Weaver Ploceus capensis (Hahn) was aroused because of its unusual pair-bond system of polygyny. At the time that the study was begun, considerable discussion was taking place in the world's journals on the subject of pair-bonds in general and the evolution of mating systems (eg. Crook 1965, Orians 1969, Selander 1965, Verner 1964 and Zimmerman 1966).

A general study, which has since become a classic of its sort, of the Ploceinae by Crook (1964) had also been published. It dealt with the relationship between the ecology and behaviour of this most diverse of avian subfamilies and it pigeon-holed species according to these aspects. But few of the data drawn from Africa involved detailed studies (except Crook 1963, Collias and Collias 1959, 1967 and 1970) and none involved long-term studies. It seemed that the testing of the generalisations expressed by Crook, by the detailed long-term study of one species, would prove interesting.

The ideas expressed by the above authors were brought together in 'Ecological Adaptations for Breeding in Birds', (Lack 1968). In the chapter on the ploceid weaver-birds, it is clear that although there are a number of theories as to the factors affecting the evolution of polygamy, there is little in the way of real supporting evidence. For example the problem of deferred maturity could be related to an imbalance in mortality rates between the sexes but nothing is known of what the mortality rates are in weavers or other polygynous species.

Similarly Lack drew attention to the importance of further study of the intermediate ploceine species, i. e. those intermediate ecologically (eating insects and seeds) and behaviourally (both monogynous and polygynus.). The Cape Weaver appeared to be intermediate from the food point of view but not from the pair-bond one, since all male birds were reported to be polygynous although some nested singly (McLachlan & Liversidge 1959).

The species, therefore, was at least partly intermediate and warranted study on that basis.

Examination of the practicality of the study added further points of interest. The bird was considered second only to the Cape Sparrow Passer melanurus as a pest of grapes (especially the valuable export grapes) and of certain cereal crops (e.g. barley). Some farmers claimed to lose as much as 20% of their annual crop to weavers. As a result, a study of the Cape Weaver's behaviour and populations might reveal possible pest control methods or facts relevant to the problem. A further consequence was that the species was declared an official pest and therefore could be collected freely for dissection and analysis, and birds could be kept for experimental purposes in aviaries.

It was also found that the Cape Weaver was very numerous and widespread throughout the south-western Cape. The main problem was to find a place where observations could be conducted without interruption or disturbance and where nest contents could be readily examined. Such a place was, after considerable difficulty, found and studies of the details of the bird's behaviour and ecology became really feasible.

1.2 Scope and aims of the study

The initial aim of the study was to attempt to throw some light on the factors influencing mating systems in weavers and on the pair-bond in general. However, along with almost all other bird species in Southern Africa, only a little data was available on the Cape Weaver's biology. Two papers on the species existed, Skead's (1947) paper being the more comprehensive but a somewhat superficial "natural history" study by modern standards. Rowan (1953) contributed a short note on breeding seasons.

It was, therefore, necessary to carry out a study of the breeding biology of the species while maintaining a special emphasis on factors likely to be influencing the mating system. At the same time, a study of the behaviour of the bird was necessary in order to understand how the polygnous bond became established and to make comparisons with the behaviour of the other weavers with different mating systems.

It quickly became apparent that if the special point of interest in the species was something as fundamental as the mating system, virtually every aspect of the species' biology was of importance. The scope of the potential study therefore became very large. Despite this, efforts were made to restrict the limits of data collection, so that what was collected was meaningful. The study also suffered from a lack of facilities for experimental studies. As will be seen, a few of the latter were carried out, but logistic problems prevented them from being as important an addition to the field work as they should have been.

SECTION 2 - TAXONOMY AND DISTRIBUTION

The type specimen of the Cape Weaver was named *Oriolus capensis* by Linnaeus in 1766 (System. Nat. ed. 12,1 : 163) from specimens collected in the Cape of Good Hope. The standard work by C.M.N. White (1963) shows that there is some confusion about the distribution of the species resulting from taxonomic oversimplification. White gives three races, *P.c. capensis* occurring from the S.W. Cape Province to Algoa Bay; *P.c. olivaceus,* east of last to the Orange Free State, Transvaal and Natal; *P.c. temporalis,* interior of Angola to Mwinilunga in N.W. Zambia. This distribution would in itself be somewhat peculiar with the latter race being entirely allopatric to the other two. The species is not recorded in the Rhodesian Check-list (Smithers, Irwin and Paterson 1957) except as a rejected species, it having been erroneously included in Priest (1936). In the latter, the measurements of adult males is unusually small at 85 mm (mean in the S.W. Cape is 90 mm) although this could be an effect of Bergman's Rule. But the description of eye colour as light red in both male and female indicates misidentification and suggests that the Rhodesian rejection is justified.

Benson, Brooke, Dowsett and Irwin (1971) also include *P.c. temporalis* as occurring in the Mwinilunga area. This record was based originally on the collection of a single immature male by Benson (1958). Moreau (1960) suggests that on plumage similarities of this one specimen with immature males of *P.c. capensis,* despite the small beak and general body size, *temporalis* should be considered as conspedific with *capensis.* Collias and Collias (1964) point out that the temporalis nest construction is not very similar to that of capensis. The nest specimens obtained were hung in elephant grass (Pennisetum) presumably over dry ground which would be a most atypical site for capensis. I agree with Hall and Moreau (1970) that temporalis, in view of the above differences and lack of evidence to the contrary, should be regarded as a separate species to capensis. Hall and Moreau follow McLachlan and Liversidge (1959), in the distribution of P. capensis, which is recorded as a broad coastal band from the Orange River in the N. W. Cape Province to the Zoutpansberg in the N. Transvaal on the edge of the Rhodesian border. In the north-west of the range, the most northerly observation is from Klipfontein, near Steinkopf, 90 km. inland from Port Nolloth and 50 km. south of the Orange River. The latter and the deserts of the Namib and South-West Africa are likely to form the true limit of the N. W. distribution. In the east of the range, in the Kingwilliamstown region, the breeding range moves away from the coast so that at Durban, the species is recorded as breeding inland above 2000' a. s. l. although non-breeding birds occur at the coast, Clancey (1964).

The exact point at which the species peters out in the N. Transvaal is difficult to determine. The most northerly definite records are from Pretoria (Markus 1964) and the Groblersdal area on the edge of the Kruger Park (Milstein 1962). The distribution must be patchy in the region since the species is not recorded at Loskop Dam (Baker 1970) nor at Naboomspruit (Tarboton 1971).

In conclusion, the distribution of the Cape Weaver extends in a U-shape from the Orange River to the Pretoria region - a total linear distance of about 2400 km. Over this range, there is a clinical gradation in the amount of chestnut on the face of the adult male from pure golden in the west to a heavy chestnut wash in the east and north. The chestnut becomes noticeable in the eastern Cape and the two extremes of the species have been debatably separated into two races, P. c. capensis in the west and P. c. olivaceus in the east.

SECTION 3 - PLUMAGE AND PHYSICAL DIMENSIONS

3.1 Introduction

One of the prerequisites of any field study of a species is to establish accurate ageing and sexing criteria. In full breeding plumage, the Cape Weaver is a strongly sexually dimorphic not only in plumage characteristics but in size as well. (See Frontispiece Plates 1A, 1B and 1C). But the situation is complicated by the male adopting a dull non-breeding dress similar to the female plumage. Furthermore deferred maturity occurs in the male and the subadult male plumage is similar to the female plumage. There is a size overlap between males and females especially between young males and large females.

The aim of this section is to describe plumages and physical dimensions in some detail not only from the point of view of ageing and sexing but also as a necessary basis to descriptions of the species' behaviour.

3.2 Methods

Although the plumages of non-breeding males, subadult males and females of all ages are at least superficially similar, close examination shows that there are differences between the sexes. To establish exactly when these differences develop and how reliable they are, two methods were used: (a) the keeping of birds of known age, under experimental conditions, and (b) the retrapping of wild birds of known age.

(a) Captive Birds:

Chicks were reared by hand (see Section 12) and released into aviaries. Food and water were supplied ad lib. The birds were caught periodically for detailed examination. Each bird was marked with colour rings.

Developmental records were obtained for five birds, three males and two females. Table 3 : 1 shows the changes in iris colour and general plumage of each bird during the month period after fledging. As can be seen, the first detectable difference in iris colour appeared about two months after fledging, when DGBK's eye began to go pale. Only after about six months, had the iris colours of all three males become pale.

The males were taken from nests at the same time but DGBK was between five days and a week older than the other two - this in a normal fledging period of about 17 days. There is thus some variation between individual males kept under these conditions, in the time at which various plumages or soft part colouration are developed.

The plumages of all five birds remained non-descript until about 12 months after fledging, when the yellowing became detectable. At 14 months, detailed examination showed that the forehead and throat were now yellow, these being the last plumage parts to brighten. But the beak was still pale horn-coloured on half of the lower mandible and two-thirds of the upper mandible. Thus the bird could not be described as being in full breeding plumage.

Individual Colour-ring Combinations	Sex	2.11.70	22.12.70	14.1.71	22.1.71	23.3.71	19.8.71	18.11.71
DGBK	M	brown	pale brown	pale brown	pale brown	pale white	pale yellow	pale gold
WR	M	brown	medium brown	medium brown	medium brown	pale brown	pale yellow	pale gold
0	M	brown	medium brown	medium brown	medium brown	pale brown	pale yellow	pale (not gold uniform)
BP	F	brown	dark brown	brown	brown	brown	chestnut	brown
DG	F	brown	brown	brown	brown	brown	brown	brown
Plumages		"non-descript"						first male plumages developing - Oct. 71
Age (weeks, months, years)		1½m.	fledging/2m 1wk.	4m	4m 1wk	6m 1wk	11m	1y 2m

TABLE 3 : 1 - The changes in iris colour with age of Cape Weavers kept in captivity. in relation to their plumage appearance and their age.

Table 3 : 1 shows that at 14½ months the full iris colour, pale gold is developed. Once developed, the iris colour is retained and does not revert to brown. The plumage state reached by DGBK on 18th November 1971 was, however, the maximum development achieved in the breeding season after hatching by any of the three males. On 18th November 1971 primary moult had just begun and subsequently the bright poumage was lost, and an eclipse plumage adopted.

It was noticeable that DGBK achieved a brighter plumage than either 0 or WR before going into eclipse. This again indicates that there is a variation in the timing and degree of adoption of adult male plumage in different males under these conditions.

During the whole period covered so far, the plumage of the females remained the same and the warm brown colour of the iris was retained.

The three males remained in eclipse until June when again a yellowing of the plumage was noticeable. By mid-July DGBK had reached full adult plumage, including the complete blackening of the beak. By the end of July all three males were in full plumage. The time elapsed between fledging and achieving full adult male plumage was about 22 to 23 months.

It should be pointed out that under the conditions of captivity, stress factors may be having an effect. Woehler (1953) found that repeated catching of young pheasants increased stress and retarded plumage development. A similar effect seems to have operated in the Cape Weaver studies, since the results given below on wild birds show slightly faster plumage development than that given above.

(b) Retraps:

Of 251 retraps made at the main study colony between 1968/72 30 were of birds ringed as pulli and identified on retrapping as males. Of these, 11 were retrapped as First Year Males, i.e. males hatched in the immediate past breeding season; 15 were retrapped as subadult males and four as adult males. The exact range of time elapsed between ringing as pulli and retrapping is shown schematically in Fig. 3.2. In all cases it is assumed that birds fledged very soon after ringing since only nearly-fledged birds were ringed. First year males were identifiable on physical dimensions (see section 3 : 5) and can be seen to be identifiable within two weeks of fledging. The gaps in the record are due to insufficient retraps. The earliest retrap of a pullus reaching adult plumage (17 months) was for a bird in eclipse plumage. From the available evidence, it seems that in the wild the minimum elapsed period for acquiring full plumage would be about 18 - 19 months.

3.3 Cape Weaver Plumages

The above investigations show that the Cape Weaver has four identifiable male plumages, namely adult breeding, adult eclipse, sub-adult, and first-year. The female plumage characteristics remain broadly the same throughout its life. These different plumages are described below in some detail. The difference between the male age groups, and between the sexes have repercussions not only in the behaviour and displays of the species but in the social system as well.

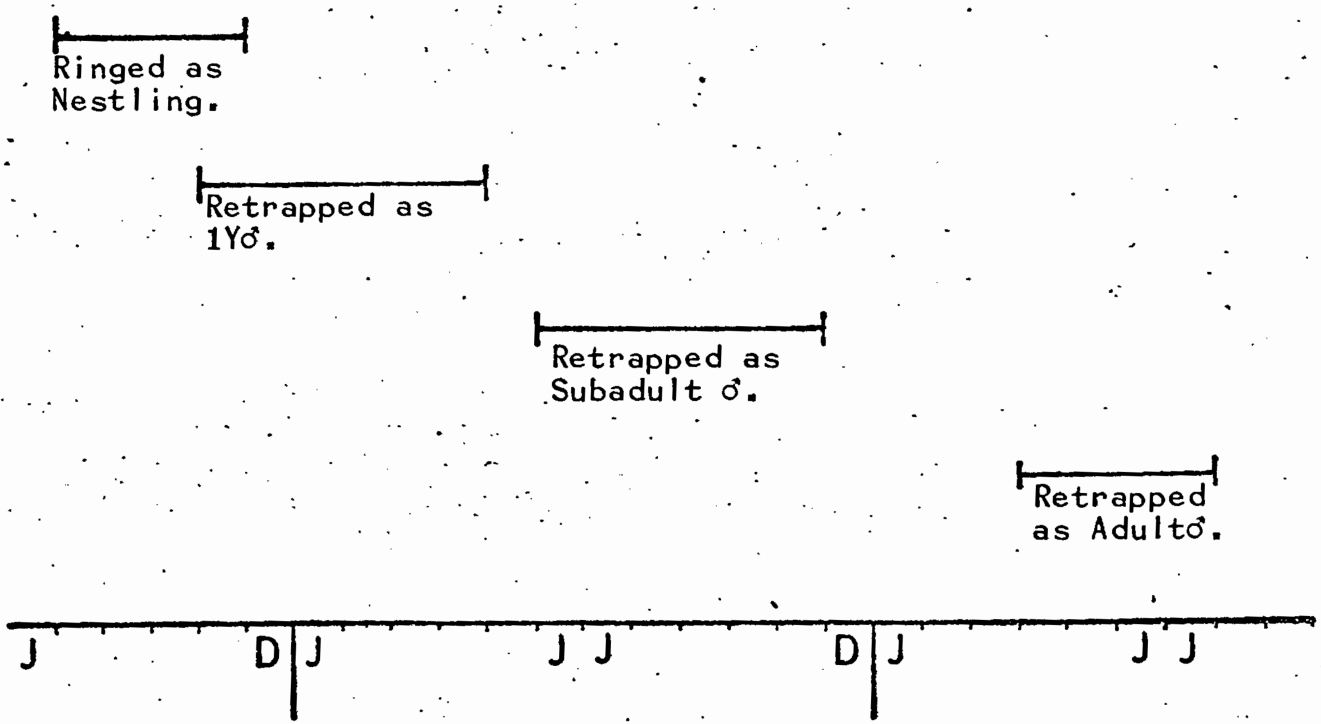


FIG. 3:2 The change of age classes in males according to retrapping information, showing the time elapsed between ringing and retrapping in successive plumages.

(a) Adult Male:

The overall impression is of a golden yellow bird with a dark yellow-olive back, a conspicuous coal-black, sharp-pointed beak and bright golden eyes (see Plate 1A). In detail, it is seen that the whole of the underside is golden yellow from the base of the lower mandible to the tip of the tail coverts. The underside is an even yellow but the breast and throat region of the nominate race P. capensis capensis becomes suffused with a deeper orange/yellow, giving a touch of the chestnut wash which is more conspicuous in the eastern race P. c. olivaceus .

The beak is entirely black. Moreau (loc. cit.) mentions that there is a dark shadow on the sides of the face, which he suggests indicates evolution from species with more facial melanin. There is indeed such an olivaceus wash over the lores and ear coverts, although to suggest its origin, is highly speculative. The forehead and crown are deep golden and being composed of small compact feathers have an almost velvety sheen. The nape and remainder of the upperparts to the tip of the tail are a dark golden-olive. The centre of each back feather has a dark mid-line giving a scalloped appearance to the plumage.

The upperside of the wings is a dark olive with the outer edge of each remex and its covert being bordered with a narrow yellow line. The underside of the wing is a shiny pale grey with a tinge of yellow. The underwing coverts are similar and there is a bright flash of yellow on the under edge of the wing at the base of the ninth primary. The tarsi and the feet are flesh coloured.

Each individual golden feather is in fact only golden for half its length. The inner half of the vane is dark grey. When the feathers are parted or fluffed out, as they are in certain postures, the dark bases of the feathers are exposed and a black line can appear in the throat and upper breast region.

The breeding plumage of the adult male is therefore one of contrast, the yellow underparts contrasting with the olive upper-parts. The dull olive upperside of the wing contrasts with the shiny grey of the underside.

(b) Sub-Adult and First Year:

The overall plumage (see Plate 1B) could be described as non-descript, if that is not a contradiction in terms, at least in comparison to the male breeding dress. The underparts are pale greyish yellow, with an area of purer yellow between the legs and on the upper tail coverts and an area of darker more olivaceus yellow on the breast. The throat is a paler yellow. The beak is a uniform horn colour. The upper parts are dark olive with a yellow tinge but much duller than those of the adult male. The upper and underside are the same as the adult male's except that the yellow borders on the remiges are duller. The crown, lores, ear coverts and nape are a uniform dark olive. The feet are darker than those of the adult male.

The first year male is distinguished from the adult male by having a uniform brown iris. The subadult male is classified as such as soon as the iris colour becomes pale grey (5 - 7 months after fledging) or is yellow as it is later.

The plumage of the chick on fledging would be classified as a juvenile plumage for moult purposes (see section 5) but is identical to the first year plumage.

(c) Eclipse Male

The adult male during the height of summer (January to March) adopts an eclipse plumage which is half-way between the golden yellow of the adult male breeding plumage and the inconspicuous subadult male plumage. The general appearance is a blotched, patchy yellow, and the brightness of the plumage is lost. However, lack of information makes it uncertain to what extent the eclipse plumage forms a separate entity. In other words, it is not certain whether the male undergoes a complete body moult twice over, once from worn breeding plumage into eclipse body plumage and then a second prenuptial eclipse to breeding plumage body moult. Certainly in an adult male in moult, some of the new body feathers are bright breeding yellow. It is possible that the eclipse plumage is a partial body moult, the patchy plumage being produced by a mixture of new feathers and old ones which would lose their brightness as explained above 3. 3. a) when the outer yellow part of the feather is worn away.

Eclipse birds were found in the population in most of the later non-breeding months i. e. January to June. Birds in breeding plumage were recorded in every month except February and March, when <u>all</u> adult males were recorded as eclipse. This suggests that adult males indulge in a partial moult into an eclipse, and possibly the remainder of body moult is delayed through February to March and completed after March.

In the eclipse plumage, the dark black of the beak becomes intermediate to the pale horn of the subadult male.

Moreau (1960) says that P. capensis may be an anomalous case by assuming only a partial non-breeding dress as suggested above. He quotes McLachlan and Liversidge (1959) as his authority but in fact the latter do not suggest this but state that "most males plain in winter".

It is difficult to distinguish the adult eclipse plumage from the sub-adult eclipse and the sub-adult going into full breeding plumage. All these will have patchy yellow areas on the body. Therefore, any bird identified as eclipse could be any age from about 14 months old onwards.

(d) Female:

The appearance of the female is very much like that of sub-adult and first year males. The underparts are same pale yellow though the posterior end is slightly paler and the undertail coverts more whitish. The breast is the same darker yellow and the throat a slightly paler yellow than the immature male's. The beak is horn brown. The upperparts are indistinguishable from the sub-adult males except that the scallopped appearance of the feathers is less pronounced. The feet are identical in colour to the immature male's.

There is sufficient variation in plumage in females for the above slight differences from first-year males not be be of any use either as field or as in-the-hand sex guides.

The iris colour of females is characteristically deep chestnut brown. This is the most useful point of distinction from subadult and eclipse males. A small percentage of females have an uneven colour to the eye which is described as having "gold flecks". The flecks give a superficially pale appearance to the eye but can be recognised with close examination and experience.

The only method discovered for distinguishing females from first year males is the usually striking size differences (see under section 3 and 6).

It is noticeable that the females appear more drab in high summer than at the beginning of the breeding season when the yellowness of the plumage seems to intensify and brighten, though, of course, it is never comparable to that of the adult male. Mackworth-Praed and Grant (1949) found similar slight changes in the brightness of female ploceines in East Africa.

3.4 Physical Dimensions

Table 3 : 3 sets out the detailed measurements of a sample of Cape Weavers, the sex of which was confirmed by dissection. The large size of the samples for culmen length, wing-length and weight is due to these measurements being taken on all specimens. The measurements were all taken on dead specimens, in the usual manner - for example wing-length as maximum chord of the wing *in situ*. All the measurements were taken by myself or by helpers under my supervision so there is unlikely to be any individual variation in method.

	Adult Male	Subadult Male	Female
Body Length	179.8(5)	175.2(5)	157.0(5)
(Range)	177-184	172-181	154-163
Wing Span	284.6(5)	279.2(5)	254.0(5)
	280-290	272-284	247-260
Head Width	19.8(5)	19.4(5)	18.4(5)
	19.5-20.0	19.0-20.0	18.0-19.0
Tarsus	27.8(5)	26.9(5)	25.34(5)
	26.5-29	26.3-29	24-27.4
Middle Toe	23.7(5)	23.5(5)	20.94(5)
	22.5-25	21.5-25	20 - 22
Tail	64.0(5)	58.7(5)	53.3(5)
	63.3-65	55-64	52.4-55
Culmen Depth	11.5 (5)	11.3(5)	10.4(5)
	11.0-11.9	11.0-11.9	10.0-11.0
Culmen Width	10.5(5)	10.3(5)	9.8(5)
	10.0-11.0	9.9-11.0	9.4-10.6
Culmen Length	23.72 (40)	23.08 (40)	22.16(136)
	22-25	22-25	20-25
Wing Length	91.76(40)	89.12(40)	84.19(136)
	86-96	86-93	80-89
Weight	48.30(40)	43.0(40)	38.46(136)
	36-57	35-53	30-50

TABLE 3 : 3 Sexual dimorphism - detailed dimension of birds dissected for sex. Figures in brackets are sample sizes. Range is given below. All measurements are in mm. weight in gms.

The first point which emerges from the table is the extent of dimorphism in the species. For certain non-standard measurements, the differences should be treated with caution because the sample sizes are small. They do illustrate that in all dimensions the female is smaller than the male and that in all measurements the mean value for subadult males is smaller than for fully adult males. This suggests that the process of physical maturation is quite a long one since subadult males are all more than about seven months old and less than about 20. Full physical size would therefore not be achieved until more than 20 months age.

If the degree of dimorphism between adult males and females is quantified in terms of the difference as a percentage of the female measurement, it is found that the greatest difference is in weight at 25.6%, followed by overall body length at 14.5%. Other differences are wing-length 8.99% and tarsus 9.7%. Since dimorphism might result in the development of different diets (see Section 6), some attention was paid to the relative bill dimensions. The differences were found to vary between 7.04% for culmen length, to 10.5% for culmen depth. Again sample size may have an influence but it would seem safe to assume a difference of only 7%.

3.5 Guides to Sex

To establish the sex of the Cape Weaver on the live bird in the field, it is evident from the above discussion on plumage, that the chief difficulty lies in distinguishing males younger than seven months from females of any age. Table 3 : 3 shows that there is no overlap in the categories of body length and wing span, and only the extremes overlap in headwidth, tail length and culmen depth measurements. However, none of these depend on large sample sizes and in the whole population much greater overlap is likely to occur. Further for use in field studies, the first two would be difficult to record on live, struggling birds. Head width and culmen depth are both difficult measurements to carry out uniformly. For ease of use, culmen length, wing-length and weight rank best and the differences in these measurements were concentrated on. A total of 581 birds was dissected for sex. Almost all of these were weighed and most were measured for culmen length and wing length. Individual variation in weight was found to be quite high though there was not much mean variation during the year. The effects of maturation on weight increases tended to make weight vary over a considerable range in young males and females, the categories of chief interest (see Table 6 : 16 for details). Culmen length involves a very small difference (Table 3 : 3) of one or two millimetres which makes this category of little practical use under field conditions. It seems therefore that wing-length is the most useful guide to sex, although it is of only limited use when the outer primaries are being moulted.

As a guide to sex, the wing-length of 88 mm. was chosen as the dividing line between males and females, that is between all males not showing other male characteristics such as a pale eye, i. e. young males, and females. All birds with wing-lengths 88 mm or more were designated males and all birds of 87 mm. or less, females. Of 256 birds dissected and found to be females, 17 had wing lengths of 88 mm or more. The exact breakdown was 88 (12), 89 (2), 90 (2) and 91 (1). Using the 88 mm. guide, the error rate is thus 6.64% for females being identified as males.

Although it was a rule that all birds in the field with 88 + mm. were designated males, the reverse for 88mm birds was <u>not</u> always applied. If there were signs, such as soft plumage, fault bars in the primaries or swollen gapes, that a bird was recently fledged, but the wing-length was already 86 mm. or more, then the bird was described as a first-year male. It was found that of 30 birds classified as first-year males on this basis, the diagnosis proved correct in all cases. Two mistakes uncovered by retrapping, both occurred before the above procedure was established. The original records have all subsequently been corrected according to the above scheme.

Included in the data, there will still be a number of males their post-juvenile moult and no longer recognisable as recently fledged. Some of these will have wing-lengths of 87 mm or less and therefore will be incorrectly classified as females. An estimate of the number involved can be gauged by the number of subadult males which have wing-lengths of less than 88 mm. Wing-length will not change appreciably between first-year and subadult males. A check of the the dissected birds shows 11/87 subadult males in this category - 12.8%. For first-year males to be classified female, they must have lost all signs of having recently fledged, have wing-lengths of less than 88 mm. and be sampled between the end of post-juvenile moult and before their iris colour begins to pale. As shown about 12.8% of the population will be in the right dimensional bracket and it seems a reasonable assumption that about half of these will be sampled at the difficult time i.e. 6.4% will be incorrectly classified. Compare this with the 6.64% of females incorrectly classified.

It is therefore concluded that about as many males as females will be incorrectly classified and that estimates of sex ratio based on direct findings will be accurate. This point becomes important in Section 7 below.

3.6 Comparative Dimensions of Age/Sex Classes

Table 3 : 4 gives the comparative dimensions of the age/sex classes. All the data were collected at the main study colony so the differences are directly comparable. The sample sizes in all cases except possible that of the eclipse males are very large. Although the ranges found are considerable, the standard deviation values are in most cases small, and indicate that most of the values fall close to the mean. It is noticeable that the standard deviation values for the first year birds are comparatively high which would be expected since the greatest growth and maturation occurs in these classes.

To establish the degree of sexual dimorphism in the whole population, the means of the three parameters of males and females were compared. In each case the smallest mean for the males was compared against the highest mean for the females. Except for culmen length where the mean for first year males is less than that of unspecified and adult females, the mean values for all the male age classes were statistically significant at the 99.9% level, $p < .001$. Such a clear difference is due to the large sample size and the comparatively small standard deviation. The culmen length of first-year males is significantly larger than that of first-year females, - $p < .001$. It is interesting to note that the mean weight of first-year males is also significantly heavier

	Adult Male	Eclipse Male	Subadult Male	First-Year Male	Unsp. Female	Ad. Female	First-Year Female
CULMEN	23.27(193)	23.16(19)	22.61 (471)	21.19 (153)	21.39 (557)	21.70 (156)	19.83 (126)
RANGE	21.26	22.25	19.26	14.24	18.25	18.25	14.22
ST. DEV.	0.920	0.898	0.982	1.436	0.839	1.068	1.392
WING LENGTH	91.54(246)	91.72(36)	89.58(577)	89.26 (418)	84.74 (930)	84.29 (164)	83.13 (201)
RANGE	87.98	85.96	84.98	82.96	79.91	80.88	64.91
ST. DEV.	3.344	2.445	1.912	2.770	1.628	1.590	2.851
WEIGHT	50.31(269)	48.42 (36)	47.87 (603)	47.57 (417)	40.78 (937)	40.84 (190)	38.81 (197)
RANGE	41.64	38.54	35.59	35.53	30.66	33.59	21.50
ST. DEV.	44.45	3.706	3.668	4.358	3.227	3.853	3.871

TABLE 3 : 4 Physical Dimensions of the Cape Weaver population. All records taken at the main study colony. Measurements in mm., weight in gms. Sample size is given in brackets.

than even that of adult females. This suggest that the young males rapidly increase their body weights above the female mean after fledging. In fact many of the chicks weigh more than the mean female weight before they have even left the nest, a phenomenon quite common in birds.

Within the sex groups, it should first be pointed out that there is no difference between unspecified females and adult females. Except very soon after fledging, the age of females could not be established with any certainty.

If the mean weights within the sexes are compared, it is established that adult males weigh significantly more than eclipse males ($t = 2.8$ $p < .01$). This would be expected since the eclipse males will be moulting, and also males are only found in eclipse in the non-breeding season when food might be short. As pointed out in Section 6, the difference is so small that it could be largely due to the eclipse male being minus a few feathers. The weight of all body feathers is however only about 3 gms., so a food factor is likely to be involved as well. The difference in mean weight between subadult and first year birds is not significant ($t = 1.15$) but both these categories are significantly different from adult males ($p \quad .01$). Similarly the mean weight of first year females is significantly different from adult females ($t = 6.67$, $p < .001$).

3.7 Discussion

Two questions are posed by the information supplied above. The first concerns the presence of plumage dimorphism in the Cape Weaver; why the male has bright plumage during the breeding season and a dull plumage for at least part of the non-breeding season. The problem of deferred maturity is also relevant but will be discussed below (Section 8). The second question concerns the significance of size dimorphism in the species.

The presence of a non-breeding plumage or eclipse plumage (the terms are used synonymously here) is widespread in the Ploceidae (Moreau 1960, Mackworth-Praed and Grant 1949) and is characteristic of those species which are open-country birds. These weaver species are also usually polygynous, so there is a correlation between the mating system and the plumage type. But since non-breeding plumage occurs in many passerines and non-passerines which have a normal monogamous pair-bond, it would seem that other factors other than type of pair-bond must at least initially be involved. Skutch (1940) found that in humid afforested Central America, dull non-breeding plumage was almost unknown. He contrasted this to North America where many species have a non-breeding dress and where perhaps the greatest difference between breeding and non-breeding dress is shown by long distance migrants.

Harrison (1964) states that there are two explanations of eclipse plumages. One suggests that the standard plumage is a dull one adapted to a generally cryptic situation while the nuptial dress has been subsequently developed for breeding purposes. The alternative is that bright plumage is developed for breeding purposes and the eclipse plumage serves a specific anti-predator function. The difference is perhaps marginal, a question of order, except that the first theory offers only a vague function for the dull plumage. At the same time, one can accept Skutch's point as a general one to all birds i.e. that there is a relationship between the presence of a non-breeding dress and open country habitat, regardless of the type of mating system. Compared with forests, open-country is characterised by a more uniform appearance and a tendency for there to be large stands of similar vegetation. Presumably this necessitates a greater development of crypsis than in the forest where the denseness of the vegetation means that visibility is restricted to small distances. Perhaps the result is that the savannah species tend to adopt the same type of crypsis so that there is a tendency for birds in cryptic plumage all to look the same. This in turn will necessitate the development of seasonal secondary sexual characters for species-recognition to ensure that the correct species is selected.

The above may well apply generally to the development of a seasonal bright plumage. Returning to weavers, we find that Crook (1964) proposes that the contrast between male and female plumages is caused by the necessity for the female to have protective colouration since she does all the rearing of the brood. The male is suggested to have bright plumage to assist him in the severe competition for females. The "cryptic" plumage is then adopted in the off-season as an anti-predator measure. Lack (1968) also supports the idea of the advantage of crypsis to the male, and suggests that in the breeding season, the male may suffer heavier mortality than the female because of his bright plumage. Wynne-Edwards (1962) offers a further explanation for crypsis in ploceids. He suggests that the uniformity of the non-breeding plumage of many savannah ploceids, making them "notorious for their visual similarity" is an adaptation to their forming a closely integrated complex to exploit similar foods.

In the Cape Weaver, an impression gained was that to the human predator, the bright breeding dress of adult males was very difficult to see in the field especially in trees. Lack mentions a similar difficulty for brightly coloured monogamous forest weavers. While attempting to shoot Cape Weavers for specimens, I found it very difficult to see the birds. Their presence was usually given away by their calls. Quantitative information on mortality will be given in a subsequent section.

There seems to be little doubt that in polygnous species, the bright plumage of the male assists in the acquisition of mates. Experiments on Red-Winged blackbirds (Smith 1972) where the red epaulets of the male were painted out showed the importance of breeding plumage. It seems certain that the same applies to the Cape Weaver. The conclusion is that the breeding plumage does serve a function, but the fact that it is lost after the season, suggests that the non-breeding plumage is also functional.

Craig (pers. comm.) suggested the protective function of cryptic male plumage operated in the Red Bishop - that if adult male plumage was retained in the non-breeding season, the males would appear very conspicuous and would be singled out of the flock by any predator.

If this was the case in the Cape Weaver, one would expect the non-breeding plumage to be present in <u>all males</u> continuously from the moment the breeding season ended until just before the new breeding season starts. However, as shown above this is not the case and all males are only in eclipse plumage for two months of the year. In the Red Bishop, my impression is that the eclipse plumage is maintained for the maximum period from the end of the breeding season until shortly before the next breeding season.

The male plumage in the Cape Weaver is closely related to territorial behaviour and aggression. It is essential to a male for the obtaining and defence of a breeding territory. It is suggested that the main function of non-breeding dress is the removal of aggressive signals (i. e. bright male plumage) from foraging flocks where the efficiency of the flock depends on its operation as a unit. If males were in full breeding plumage, territorial aggression would be continually released, preventing the efficient feeding of the individual. It is suggested that the cryptic effect of the plumage has been largely overstressed though it need not be entirely absent. It should be noted that my explanation is related to that of Wynne-Edwards (loc. cit.) but the latter was referring to multi-species flocks of ploceids.

If my hypothesis is correct, it might well be asked why it is that male Cape Weavers are not all in non-breeding plumage for the duration of the non-breeding season. It is proposed that this is due either to food only being sufficiently short to necessitate flocking for those two months, February and March, or that only during this time is the type of food eaten mainly that which is best searched for by a flock. (for further discussion see Section 6). On the other hand, if the chief selection pressure was predation, this would be expected to be cryptic for the full duration of this season.

In conclusion, there seems to be no reason why flocking considerations should not be the primary selection pressures in the development of non-breeding plumage in birds in general rather than anti-predator pressures. In certain circumstances, such as the development of winter white plumage in the Ptarmigan Lagopus mutus predation is probably more important.
But in seed-eaters generally, and in such groups as the charadriiform waders, it is proposed that flocking is the main factor involved in the development of a dull non-aggressive winter plumage.

The contrast between the Cape Weaver and the Red Bishop is of interest, the former having a relative short period in non-breeding dress. It is suggested that this is because the Red Bishop is much more dependent on grain as its main source of food, than the Cape Weaver which has a much greater variety of food types (see Section 6). If this is the case, it will necessitate the Bishop remaining in flocks and therefore retaining the dull plumage for a much longer period.
It could also be argued that the black and red plumage of the Red Bishop is much more conspicuous than the Cape Weaver's, and that this would tend to attract the attention of predators. But the weaver in bright plumage is only more difficult to see in trees. When feeding in flocks in the open, the contrast between the male and female weaver would only be marginally less than in the Red Bishop.

The above has presented ideas on the presence of non-breeding plumage in the Cape Weaver and in birds generally. At the same time there is no dispute as to the function of breeding plumage. In polygynous species, the competition for mates will be extra-high and tend to produce even greater contrasts in the plumage of males compared to the females.

On the question of size dimorphism, there are two accepted explanations, one that it has evolved in order to reduce competition for food and the other that it is a result of competition for mates. Larger males will be higher up in a social or territorial hierarchy and therefore more able to obtain mates. The question of competition for food is dealt with in Section 6. In a polygnous species, the competition for mates will be very much greater than in monogynous ones. The selection pressure for larger size as well as for brighter plumage will be correspondingly longer. The difference in size will be counteracted by other ecological pressures.- The fact that dimorphism exists in the Cape Weaver is therefore to be expected as a result of competition of mates within the polygnous system. Whether or not larger mates in fact succeeded in obtaining more mates, within the level of individual variation, will be discussed in a subsequent section.

SECTION 4 - BREEDING SEASON

4.1 Introduction

The considerable range of distribution of the Cape Weaver (See Section 2), over more than 2400 km, makes the species a good one for the study of breeding seasons. Over this range, the climatic system almost reverses, changing from a winter rainfall system (peak rainfall June/July) in the south-western Cape, to a summer rainfall one in the east and north (peak rainfall December/January). The climate within each area varies considerably from year to year with large differences in rainfall and the occasional anomaly in maximum/minimum temperatures.

Detailed breeding data were obtained from three main colonies in the Cape, separated by some 20 miles from each other. Occasional data were collected from several other colonies in this area. Data from the same and remaining parts of the species range were available from the Nest Record Cards (NRC) of the S.A. Ornithological Society (S.A.O.S.)

Only one short note on the species' breeding ' Early breeding in the Cape Weaver' (Rowan 1953) has been published apart from the details given in avifauna hand-books and check-lists. None of this information has been found to be very accurate, as indicated below.

4.2 Study Area

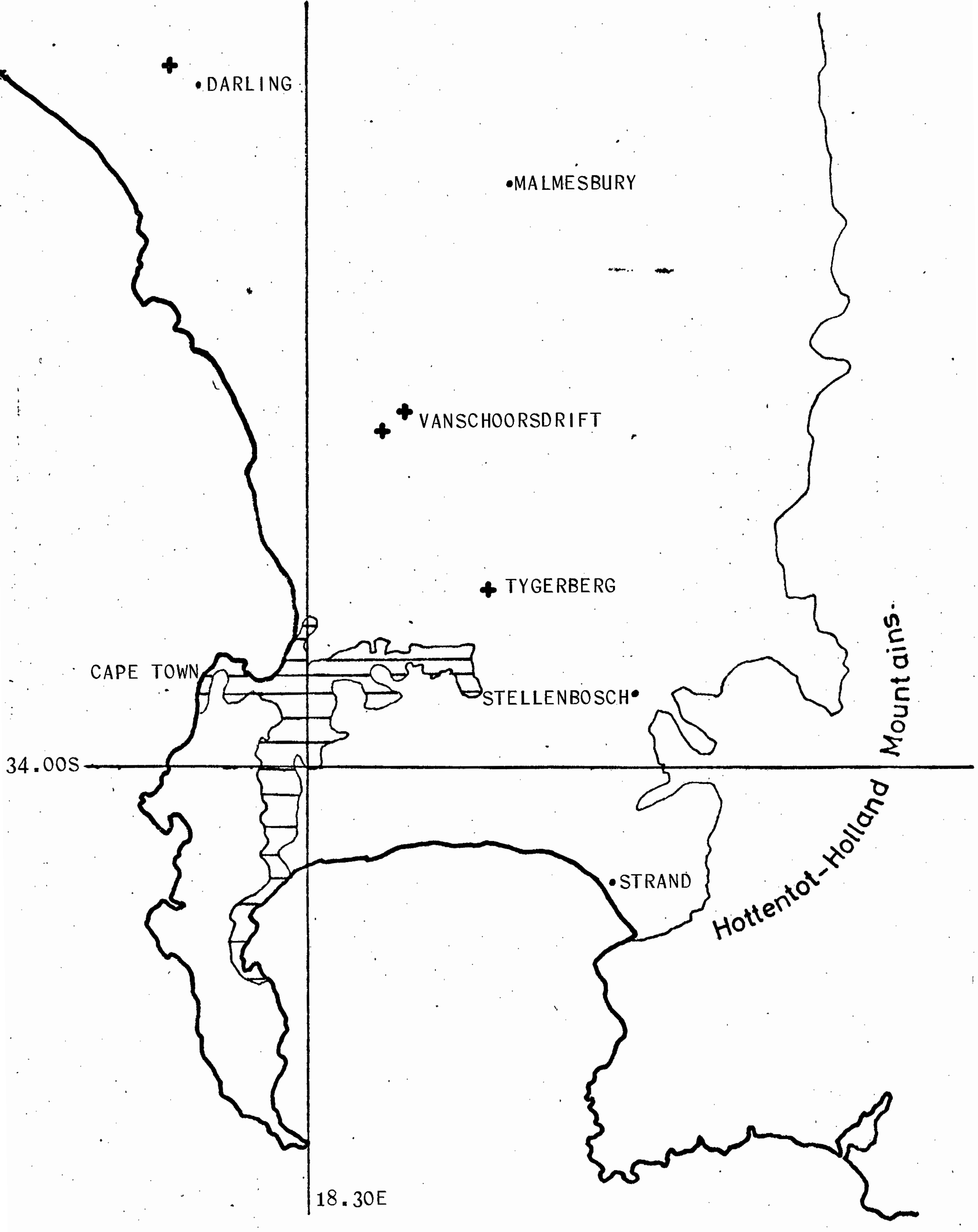
Observations on the timing of breeding and related studies were carried out chiefly in the broad coastal belt from Clanwilliam southwards between the Atlantic and the mountains of the Hottentot Hollands (see Map 4 : 1). The great majority of observations was made in a rectangle between Darling and Malmesbury, south to the Strand and Somerset West. High intensity studies were carried out at the Tygerberg colony, near Kraaifontein.

The whole study area falls within the winter rainfall area, although the quantity of precipitation decreases to the north.

The area is highly and intensly cultivated and generally affected by the presence of man. Irrigation is widely practised and most farms have numerous small dams for collecting run-off precipitation.

According to Siegfried (1969), the Stellenbosch magisterial district has 73% of the land under cultivation (mostly vineyards and orchards). Only 2% is built on and 25% is uncultivated. The Malmesbury district probably has a higher percentage under cultivation as large areas are given over to monocultures of cereal crops.

Over the rest of the Cape Weaver's range, the effect of man is also considerable but probably not as total as in the south-western Cape. In the study area, censuses have shown (Winterbottom pers. comm.) that the species is one of the five most common. Throughout its range, there is a definite association with and benefit from man's agricultural



MAP.4:1 – The Study Area – showing the location of the main study colonies (+) in the winter rainfall area between the Atlantic and the Hottentot-Holland Mountains.

practices. Colonies are often found in trees on dry land near houses, and almost every dam with strategic reeds or trees has a colony of weavers. Where there is more indigenous bush remaining, as in the Eastern Cape, the impression given is that the species is less common, occurs in smaller flocks and breeds in smaller colonies. At the other extreme the species does not seem to benefit from the excessive human activity of urbanisation and becomes less common as such areas spread.

It should therefore be remembered that the study was carried out in probably the most extensively man-modified area in southern Africa outside urban areas. This may well affect both the results and the conclusions in terms of the evolutionary pressures.

4.3 Method

Cape Weaver colonies were found in two main sites, reeds or trees. Both sites presented problems for the effective study of breeding activities. Reed colonies were normally examined by walking amongst the reeds in chest-high waders, but many colonies were in water too deep to wade. One such colony was inspected in two consecutive years using an inflatable rubber boat, but this method was too complicated to be used on a regular basis.

Colonies in trees were examined using an extra-long ladder which gave an effective reach of seven metres but nests were often built up to heights of 20 - 35 m. above ground. In any large tree colony, the chances of every nest being within reach were small.

The examination of the nests, provided they were in reach and despite the retort shape of the nest, could usually be achieved by thrusting two fingers up the entrance. The length of the entrance tube varied from nest to nest but it is flexible compared with the solid structure of the main body of the nest. In other nests the lip of the nest chamber was built unusually high, making access difficult but with a little force, which might bend the entrance tube but not damage the nest, the nest contents could always be determined.

Because of the nest-shape, the extraction of eggs for marking proved to be too difficult. No data could therefore be collected on egg-replacement or precise incubation times. The counting of the eggs was easily achieved by feeling the clutch. The counting of the chicks was more difficult especially in newly hatched birds and, as was often the case, where there was pronounced size differences between the chicks. In such cases, the chicks were pulled gently out of the nest by their heads, for counting.

In the main study areas, nests were marked either as soon as they were built (first three seasons) or as soon as the first egg was laid. Black plastic sticky tape on which numbers were painted, was used and wound round the reed stems above the nest. The territory-holding males occasionally attacked the tags attempting to tear them to pieces with the same movements used to dismantle old nests. The painted numbers were occasionally pecked at and the paint peeled off. Both actions resulted in a small percentage of the tags being lost but by following a set path through the colony, missing numbers could almost always be determined, and replacement tags fitted. For a straight breeding study, placing the tags below the nest (see Woodall 1971 for Euplectes orix) would reduce the tag loss but for this study, behavioural observations were also made requiring the easy visibility from a distance, of nest numbers.

4.4 Results - Tygerberg Colony

This colony was in reeds in a disused farm dam. All the nests were accessible. The frequency with which this colony was inspected varied from year to year according to whether breeding studies were given priority (as in 1970) or observations on behaviour (1969, 1971). Table 4 : 2 shows that the mean frequency of inspection was once every 5.4 days. The number of nests with active (i. e. not addled) eggs was used as an index of breeding activity in the colony. The breeding data in terms of this index for the Tygerberg study colony are given in Table 4 : 3. In Table 4 : 4, the number of nests containing chicks is given. Those nests containing eggs and chicks where the last eggs of the clutch had not yet hatched, were counted as "nests with eggs". Nests which were subsequently shown by the failure of hatching, to contain addled eggs, were discarded from the totals from the date at which they should have hatched onwards.

Fig 4 : 5 presents the Table 4 : 3 in graphic form, and shows the fluctuations in the breeding season. As can be seen, the first three seasons were broadly very similar and the end of the period of "eggs present" in all four seasons is restricted to a period of not more than two weeks.

Year	Number of Inspections	Number of days during which nests with eggs were present	Inspection Frequency
1968	10	82	8.2
1969	16	99	6.1
1970	29	106	3.6
1971	21	124	5.9
			Mean 5.4

TABLE 4 : 2 Frequency of inspection of breeding rate at the Tygerberg colony.

MONTH	YEAR	DATE																														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
	1968																															
JULY	1969																															
	1970																															
	1971														1				1									15			20	
	1968																															
AUG.	1969																						9						20			
	1970															1			3		5				7		9		14			13
	1971				25					43	47		47							70						16	10					
	1968				37						40										17		22									
SEPT.	1969				29	32						28						29			38				40						41	
	1970		12		13			13						13					13			14				22				20		
	1971	5							10						20																	
	1968									32									47					40								39
OCT.	1969									51												60										36
	1970	20				20				27				32			32			31			30				26					
	1971	28					25									16						33										
	1968																12				8											
NOV.	1969					23												8			4					1						
	1970			18						13				10						8				2								
	1971	22		20						14																						
	1968																															
DEC.	1969																															
	1970																															
	1971																															

Table 4:3 The number of nests with eggs by date during 1968/71 at the Tygerberg colony

DAYS

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
	1968																															
JULY	1969																															
	1970																															
	1971																															
	1968																															
AUG.	1969																												1			
	1970																										1		1			2
	1971				3					10	15		19							20						15	7					
	1968				19						29									21							22					
SEPT.	1969				9	10						19					22				23				24						22	
	1970		4		4			8		10					11				11			9				12				15		
	1971	4							3																							
	1968									20									28					32								44
OCT.	1969									29					32							38										41
	1970		14			17				18				17			16						24				26					
	1971	21					25									29						26										
NOV	1968																41				29											
NOV.	1969					44												27			20					4						
	1970			23						19				14						13				4								
	1971	28		24						24														10								
	1968																															
DEC.	1969																															
	1970																															
	1971																															

Table 4:4 The number of nests with chicks by date during 1968/71 at the Tygerberg colony

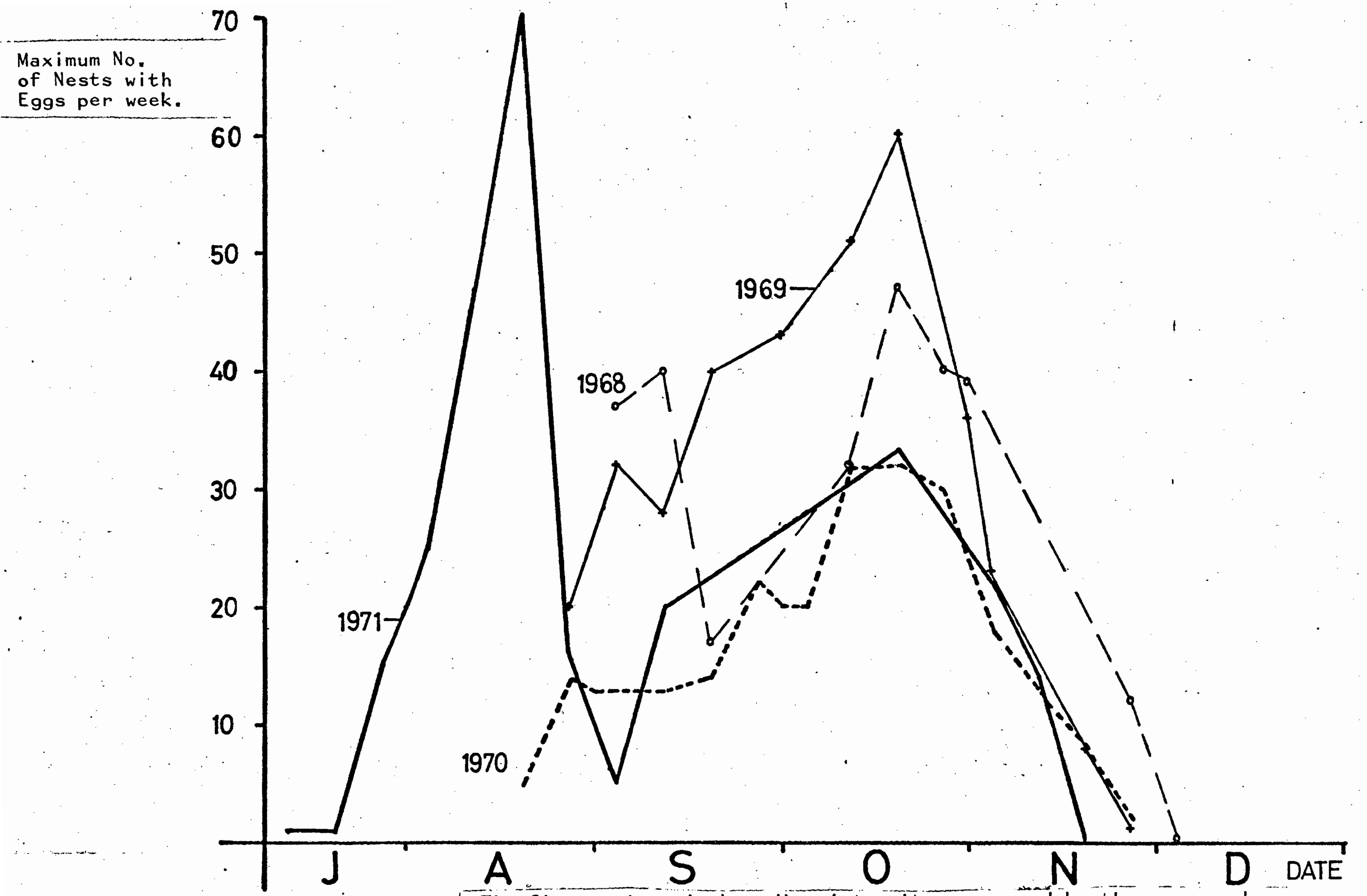


FIG.4:5 – The fluctuations in breeding intensity, measured by the max. number of nests with eggs recorded each week at the Tygerberg Colony in the four seasons 1968/71.

The earlier parts of the season, show some major differences; the early breeding in 1971 is particularly striking. These differences pose questions as to the control of breeding season in the Cape Weaver. For further discussion, see below.

4.5 Other colonies in the study area

In the 1971 season, two other colonies were studied during the whole season, the Vanschoorsdrift colony and Mosterts colony. Both were in reeds, the former in a narrow tributary in the broad flood area of a small river; the latter in a small dam surrounded on all sides by a large expanse of cereal crops. The two colonies were separated by about 3 km. and lay 20 km due north of the Tygerberg study colony. The frequency of inspections was about twice a month.

Caution should be used with the details of the Vanschoorsdrift colony since this colony was the main collecting area for chicks for sex ratio dissection. During the season, 150 chicks of all ages were removed from the colony and killed. It is not known exactly what effect this had on the colony's development. It may have caused a premature ending to the breeding season. Chick removal certainly did not affect the start of breeding nor the main egg-laying peak with the result that these data are a useful contribution to the whole breeding picture.

In 1968, data were collected from a series of tree colonies along the Muddy River north of Darling. The difficulty in reaching nests easily precluded frequent visits and so the data are scanty.

4.6 Results - other colonies

The results are given in Table 4 : 6. In addition to the data on the number of nests with eggs, the percentage of egg-nests per total occupied nests (i. e. total with chicks or eggs) has also been tabulated. The percentage figure gives a better impression of the progress of the colony, particularly where observations are widely spaced.

The Vanschoorsdrift results compared to Tygerberg shown graphically in Fig. 4 . 7, indicate that breeding started in the former one week before the latter in 1971 despite only 20 km separating the two colonies. The Vanschoorsdrift colony did not show a late season burst like that of Tygerberg, but this may have been an artefact of the chick removals.

The development of Mostert's colony closely parallelled that of Vanschoorsdrift as far as the main breeding burst was concerned but thereafter the colony ceased to operate at all. The Darling data were collected only for 1968 and so a strict comparison is not valid. It seems likely that the breeding season 45 km further north, may be an additional week ahead.

4.7 Data from Nest Record Cards

By courtesy of the South African Ornithological Society all the nest record cards on the Cape Weaver over the whole of its range in South Africa, were scrutinised. The number of cards containing useful information was not high because a good number merely recorded that birds were building.

EKS	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3
E/N+C VANSCHOORS-			20/0	-	32/20	-	-	94/31	-	67/38	-	59/41	36/42	31/41	-	22/54	-	3/19	-	-	-
N+E DRIFT 1971			100	-	64	-	-	75	-	64	-	59	51	43	-	29		14			
N+E TYGERBERG '71						100	89	71	77	50	55	33	-	-	57	-	63	-	44	36	
E/N+C MOSTERTS COLONY '71			1/0	-	2/1	-	-	7/4	-	1/0	-	1/0	0	-	-	-	-	-	-	-	-
E/N+C DARLING '68		4/0	9/3	4/2	-	-	-	6/4	-	-	-	-	2/2								

Table 4:6 Breeding data comparison between four colonies in the study area. The number of nests with eggs and number with chicks are given as N+E/N+C and the % of N+E in the two main colonies is tabulated.

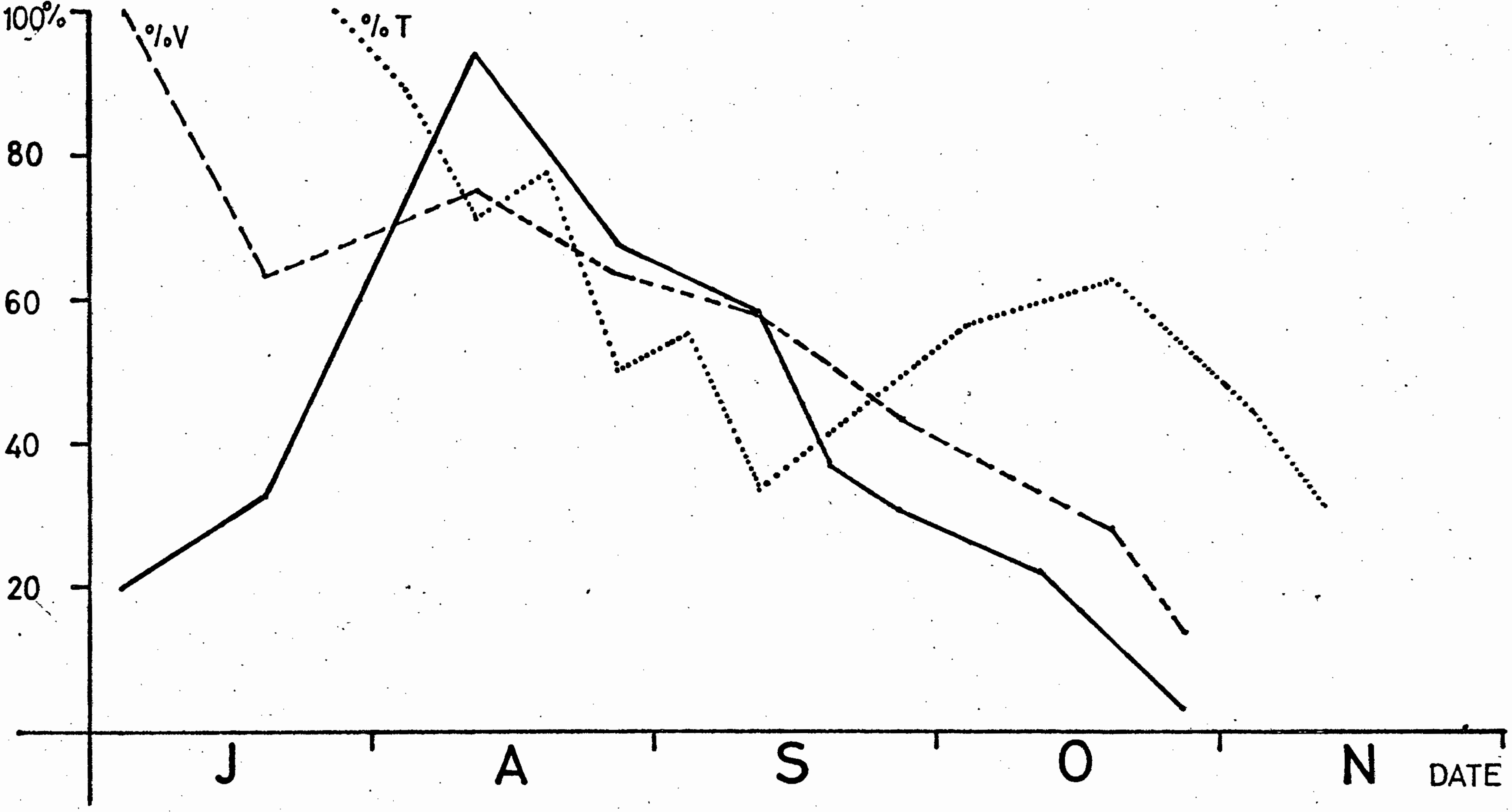


FIG. 4:7

A comparison of breeding intensity at the Van Schoorsdrift and Tygerberg colonies.

- - - - - - % of active nests which contained eggs at Van S. by date

······ % of active nests which contained eggs at Tygerberg by date

——— Actual number of nests with eggs at Van S. by date.

In the western Cape, Cape Weavers have been recorded building during every month of the year. Usually in the off-season, such activity is carried out by young males carrying out incipient nest building. In Spring adult males or males coming into plumage may build nests, particularly if the weather warms up for a few days, but the nests are never occupied.

For example, in 1970 at Tygerberg, the outer shell of the first nest was completed on June 22nd but the first egg was not laid until August 15th, seven weeks later. Twenty or thirty other shells were built during this period and the males displayed beneath the nests, especially on warm days.

Records of birds building are, therefore, no sure sign that breeding has actually begun.

4.8 Results:

The data from the nest record cards are summarised in Table 4.8. Each vertical bar indicates a record of breeding directly observed or deduced from the begging calls of chicks or the presence of broken egg shells beneath nests. Where several records have been made on the same day, the bars have not been duplicated. I have added in my own records taken from colonies other than the Tygerberg study colony.

The distribution of records is not very uniform except for the Cape where good coverage occurs other than in the extreme northern parts and a gap in the information for most of the area between Port Elizabeth and Cape Town. As would be expected the data from the Transvaal is concentrated around

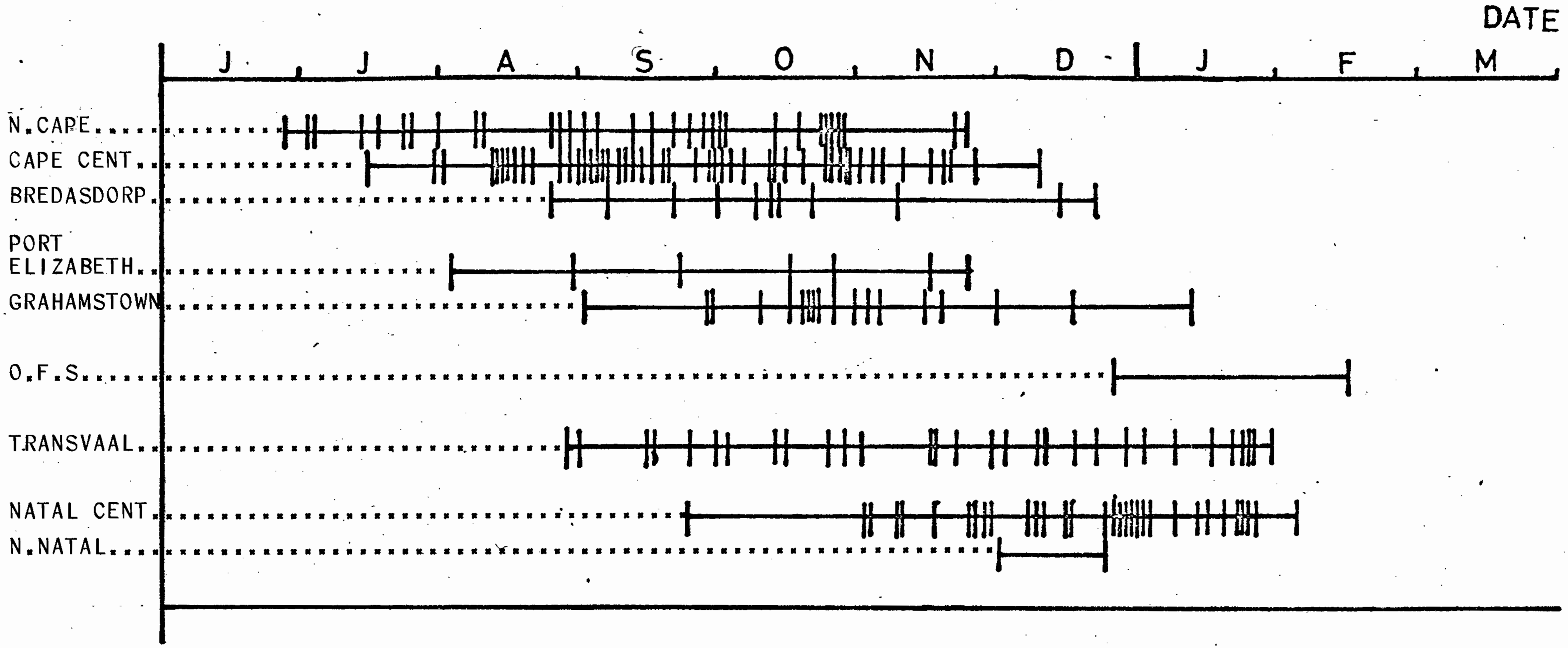


Table 4:8

Breeding Records of the Cape Weaver in South Africa - information chiefly from nest record cards. Each vertical line is one record of active breeding; each horizontal line spans the extreme dates for each area.

population centres, mainly Johannesburg while that for Natal is chiefly in the Pietermaritzburg area stretching towards the high country on the edge of Lesotho, where nests have been recorded up to about 3000 m.a.s.l. The records for the O.F.S. are very scanty being derived only from Ficksburg on the western slopes of Lesotho. Detailed study of the breeding outside the area would probably give a wider spread of the breeding dates just as it has done in the western Cape. There seems to be a tendency only to look for nests when they are supposed to be there.

Despite these weaknesses in the data, it is clear that the breeding season differes in the extremities of the Cape Weaver's range and that there is a gradation from one extremity to the other.

4.9 Gonad Activity - Method

Birds were collected mostly by using mist-nets at breeding colonies or roosts. Some birds were shot. Specimens were dissected for sex and the length of the gonad was measured *in situ* to the nearest mm.

In males, the length of the left testis only was measured. According to Marshall (1961), the left testis is usually the larger of the two. It was felt that possible differences in size between the testes were likely to be relatively small compared to seasonal size changes. Therefore to measure the left testis only was a good and convenient approximation. Liversidge (1970) found that of the various parameters he used for *Pycnonotus* spp., length was the best indication of testis condition. For the Cape Weaver, therefore, the routine measurement taken was the testis length, though the extremes of diameter were also noted.

In females, the length of the ovary and the diameter of the largest follicle were the measurements taken.

4.10 Gonad Activity - Results

The results of dissections of 505 Cape Weavers are given in Table 4 : 9. As can be seen, all the samples were taken within the S. W. Cape study area except for two from the eastern Cape, at Mossel Bay (34.11S; 22.08E) and Port Alfred (33.26S; 26.55E). The data for the males has been separated in Adult/Eclipse birds and Subadult/First Year birds, since in the early breeding season the difference in testis size between breeding adults and non-breeding young birds is very marked. A mean value for all males would obscure the trends.

Although testis length was the standard sex condition measurement for males, note was also taken of diameter so that an approximate testis volume change could be estimated. The maximum testis length recorded was 13 mm. and the maximum diameter 5 mm. The minimum figures for adult males were 2 x 1 respectively. The volume of the testis is calculated by : $4/3 \pi l \left(\frac{d}{2}\right)^2$ where l = length; d = diameter (after Liversidge 1970). The maximum volume was therefore 338.8 mm^3 and the minimum 2.08 mm^3, giving a maximum change of 163 times.

Table 4:9 GONAD SIZE - Length mm.; figures in brackets are sample sizes.

Date	Adult/Eclipse	Imm./1st Year		Locality
	♂	♂	♀	
08.07.68	10.0 (3)	2.5 (15)	7.6 (21)	S.W.Cape
(26.07.68	7.5 (4)	3.2 (11)	7.8 (24)	Mossel Bay)
20.08.68	3.3 (3)	-	7.7 (17)	S.W.Cape
12.09.68	12.0 (1)	2.6 (5)	10.8 (21)	"
(22.01.69	3.0 (1)	2.4 (7)	4.8 (18)	Port Alfred)
03.04.69	3.7 (4)	1.7 (4)	6.2 (4)	S.W.Cape
24.04.69	3.8 (6)	3.5 (2)	6.0 (1)	"
29.04.69	6.3 (7)	2.5 (2)	7.5 (2)	"
29.09.69	11.2 (11)	4.0 (2)	9.0 (14)	"
10.01.70	3.5 (2)	1.5 (16)	4.8 (38)	"
20.02.70	3.3 (6)	1.0 (2)	6.4 (5)	"
15.03.70	2.6 (5)	1.2 (8)	5.3 (7)	"
01.05.70	2.8 (5)	2.0 (1)	6.5 (2)	"
03.06.70	10.0 (1)	2.0 (1)	7.5 (2)	"
27.06.70	10.0 (3)	-	8.2 (5)	"
20.07.70	8.7 (3)	2.0 (4)	7.3 (6)	"
06.08.70	10.9 (13)	2.0 (5)	8.7 (3)	"
02.10.70	10.5 (10)	1.5 (6)	7.9 (9)	"
10.11.70	10.0 (5)	5.5 (4)	8.7 (4)	"
26.04.72	-	1.0 (5)	6.7 (10)	"
10.05.72	-	1.4 (5)	3.7 (4)	"
01.06.72	-	2.2 (12)	6.6 (22)	"
20.10.72	-	2.42 (7)	4.5 (4)	"
25.01.73	3.4 (12)	2.3 (10)	4.5 (23)	"
Totals: 24	(105)	(134)	(266)	

The mean length of an adult males testis in the breeding season taken from Table 4.9 was about 10.5 mm, and the mean non-breeding length, about 2 mm, giving volumes, respectively, of 274mm^3 and 8.3 mm^3, a change of 33 times.

The mean length of the ovary during the breeding season was 9.2 mm. The maximum size recorded was 24 mm. in a case where the ovary was dominated by a single large oocyte of 24 mm. This measurement is equivalent to an almost completely formed egg. McLachlan and Liversidge (1959) give the egg size as 24.8 x 16.5 mm.

The seasonal changes in the testis and ovary lengths are illustrated in Figs. 4.10, 4.11 and 4.12. The contrast between the three graphs is striking. Fig. 4.10 shows that the mean ovary length increases slowly from about the end of April onwards. Sample size variation and long gaps in some of the data produces some odd results as in the data for 1972, but the trend of a steady increase remains clear. Marshall (loc. cit) points out that female gametogenetic development lags behind that of the male until the final swift oocyte development. The measurements of the largest follicle in the ovary given in Table 4.13 show that little variation or startling increase was found. In general the ovaries of breeding females differed from out-of-season ones by having a 'bunch-of-grapes' appearance as opposed to an unstructured one. The individual follicles seldom measured more than one mm. and were not measured until they did. On only 13 occasions out of 266 females dissected were follicle measurements of more than 3 mm made. The probable explanation is that, as indicated by Marshall,

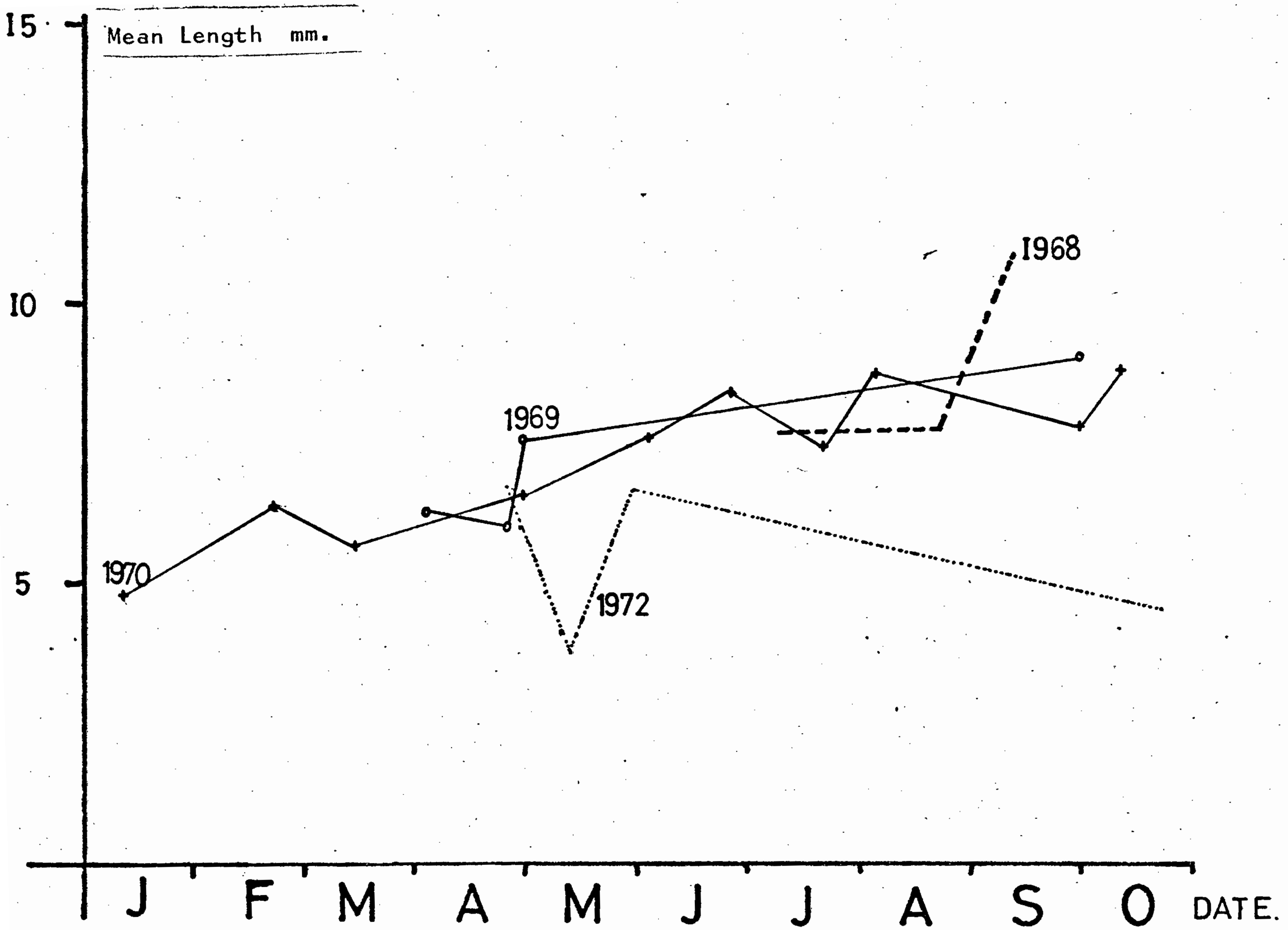


FIG.4:10 The change in mean length of the ovary in the four seasons 1968/71

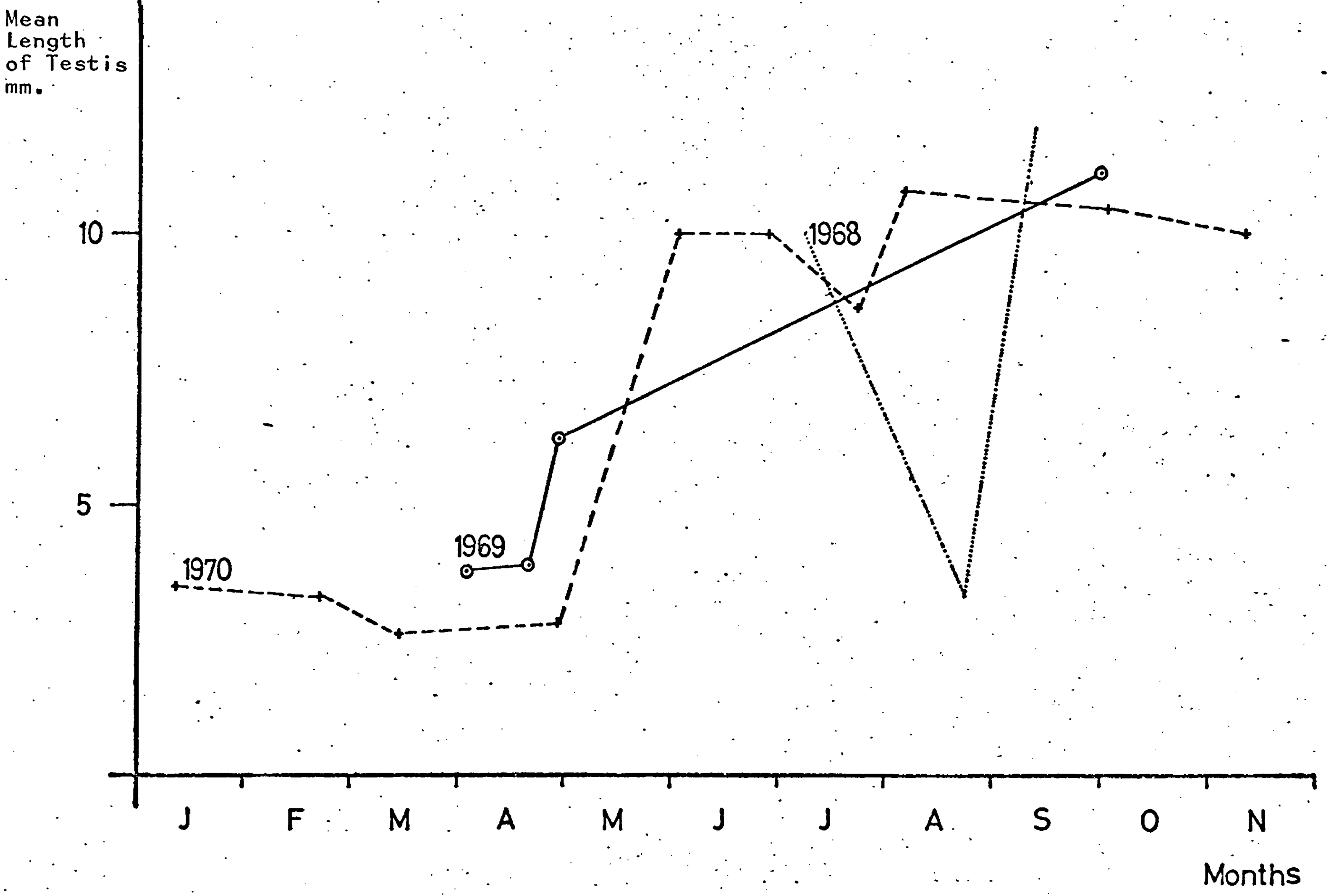


FIG.4:11 The change in mean length of testis with date for Adult/Eclipse male Cape Weavers.

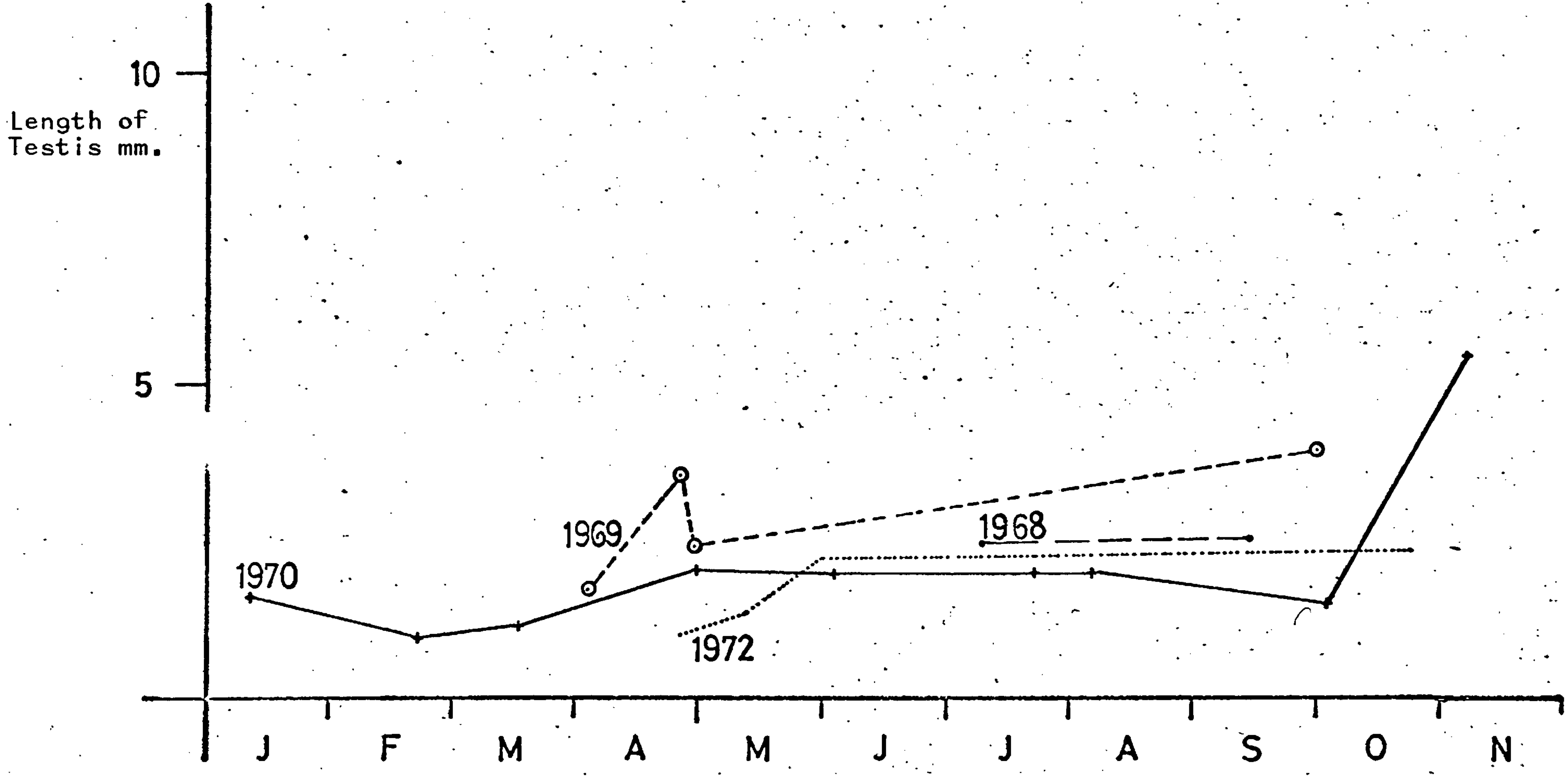


FIG.4:12 The change in Mean length of testis with date for Subadult/1st Year male Cape Weavers.

Date	Diameter of Mean largest Follicle (Sample Size)
31.8.68	5.25 (4)
6.9.68	7.88 (9)
12.9.68	6.0 (4)
29.9.69	3.0 (13)
26.7.70	2.0 (1)
6.8.70	2.3 (3)
2.10.70	2.6 (8)
10.11.70	2.0 (4)
7.1.71	2.0 (1)
14.6.72	2.0 (1)
20.10.72	3.0 (1)
Totals - 11	(45)

TABLE 4.13 Mean Diameter of Largest Follicle against date.

the oocyte maturation is very fast and therefore the chances of a specimen being found in such a stage is small.
The sudden high figure for 1968 in Fig 4 : 10 is probably caused by such a chance.

By contrast Fig 4 : 11 shows a rapid increase in testis length in adult males from the end of April reaching a peak between six weeks and two months later.
As stated above, this period covers an increase of about 30 times. No data is available for late November and December but a fairly rapid decrease in size must occur during this period to bring the testis down to the January size. From the data, the sample size of which is not large, it would appear that minimum testis size occurs in March.

Further differences are shown in Fig 4. 12. for subadult /first year birds (i. e. birds 3 - 22 months old). During the year, there is virtually no increase in testis size at all. A slight increase is shown in the 1969 results between two widely separated collecting dates. In 1970 a sharp increase occurs but very late in the season. Both results would seem to fit in well with the idea that some individuals in this age class come into partial adult plumage early in their second year at about 14 months old, i. e. late in their first breeding season after hatching. It is suggested concominantly that some first year males are sexually mature late in the season even if unable in the wild to defend territories and secure mates (see below Section 12).

4.11 Clutch-size and Incubation

Also arising out of the above studies on breeding season, data were collected on clutch-size and incubation. The information on clutch-size is presented in Table 14 : 4. Two important points emerge from these figures. First the mean clutch of the Cape Weaver is 2.73. This fits with the general comments of Lack (1968) on ploceid clutch-sizes, where polygynous species tend to have larger clutches than monogamous species. According to Lack's general theory of clutch-size, this presumably means that polygynous species can potentially raise more offspring. This seems likely to be related to their food supply, which is thought to be scattered and locally superabundant (see Section 6). In good years, polygynous species will be capable of raising more offspring than do monogamous forest species. In bad years, they may raise fewer. There are however no data on breeding success of forest monogamous weavers.

The second point in Table 4.14 is that there seems a clear trend of smaller clutches in the early season and in the late season, and larger clutches in the mid-season. Such a phenomenon has been observed in a number of species (e.g. Perrins 1970 - Parus major). To what extent the clutch-size is the result of food conditions operating at early and late parts of the breeding season and to what extent according to the conditions applying to the feeding of the chicks, will not be discussed here. It suffices to say that in the Cape Weaver, there will be more chance of successfully raising early and late broods if they are small.

		JUL.	AUG.	SEP.	OCT.	NOV.
1968	C2	-	-	25	18	3
	C3	-	-	18	34	1
	C4	-	-	4	3	-
	C5	-	-	-	-	-
	MEAN	-	-	2.55	2.72	2.25
1969	C2	-	9	8	15	3
	C3	-	22	30	31	1
	C4	-	6	6	12	-
	C5	-	-	-	2	-
	MEAN	-	2.91	2.95	3.01	2.25
1970	C2	-	7	11	12	5
	C3	-	7	19	28	6
	C4	-	-	2	5	1
	C5	-	-	-	1	-
	MEAN	-	3.14	2.71	2.89	2.66
1971	C2	12	39	6	9	10
	C3	5	35	8	38	11
	C4	-	-	1	7	-
	C5	-	-	-	-	-
	MEAN	2.29	2.47	2.66	2.99	2.52
ALL YEARS	C2	12	55	50	54	21
	C3	5	57	75	131	19
	C4	-	6	13	27	1
	C5	-	-	-	3	-
	MEAN	2.29	2.58	2.73	2.90	2.51

Table 4:14 The variation of clutch-size per month between 1968 and 1971 in the S.W.Cape. Mean clutch-size for all records is 2.73

Another adaptation to the large clutch of polygynous species, in the Cape Weaver is that incubation begins with the first egg. The hatching of the chicks will therefore be staggered and at least early in the fledging period, there will be a considerable size range in the chicks. Such size disparity was often very striking during the routine nest checks. In certain cases, it may have been accentuated by sexual dimorphism in the species (for further discussion, see Section 7). This incubation pattern will result in size differences in the chicks which in turn will mean that in times of poor food availability, the smallest chick will often die. As a result the remainder of the brood will have greater chances of survival. In good food conditions, obviously the whole brood would be expected to fledge successfully. The above would seem therefore to be an adaptation to a fluctuating food source.

4.12 Discussion

One of the more recent expositions of the factors controlling breeding seasons is that by Immelmann (1971). This author follows Baker (1938) in dividing these factors into "ultimate" and "proximate" ones. From the above description of the breeding seasons of the Cape Weaver, it should be possible to identify the ultimate and proximate factors responsible where the detailed information is available.

4.13 Food

It is generally accepted that the most important factor controlling bird breeding seasons is the availability of food both during the whole breeding season and, as Immelman points out, in the critical period after the end of the season, when a large number of inexperienced fledglings are searching for food. There is very little data on insect population fluctuations in South Africa. Siegfried (1969) in his study of the Cattle Egret Ardeola ibis also in the S. W. Cape, attempted to assess these fluctuations from drag-net collections through pasture land. His results are shown in Fig. 4 : 19. It can be seen that the main peak of insect abundance is given as April/May and the lowest levels in the July to September period. A second peak occurs in November. These findings are surprising both in terms of my subjective impression and in terms of both the egret and weaver breeding seasons. They could, as Siegfried says, be due to artefacts of the sampling method. My impression was that the peak time of insect abundance specifically of insect larvae coincides with spring growth, flower blooming and rising temperatures characteristic of the August to October period. However, if Siegfried's assessment is correct (for further discussion, see Section 6), the only obvious relation with the Cape Weaver's breeding season is that the second November peak would coincide with the maximum fledgling population.

4. 14 Habitat

In the Cape Weaver, certain aspects of the nesting habitat have an ultimate influence on its breeding season, according to Immelman's classification. In the S. W. Cape about half the colonies observed were situated in trees. The remainder were placed in various types of reed usually Typha or Arundo spp. Observations indicate that, of the alternative habitats,

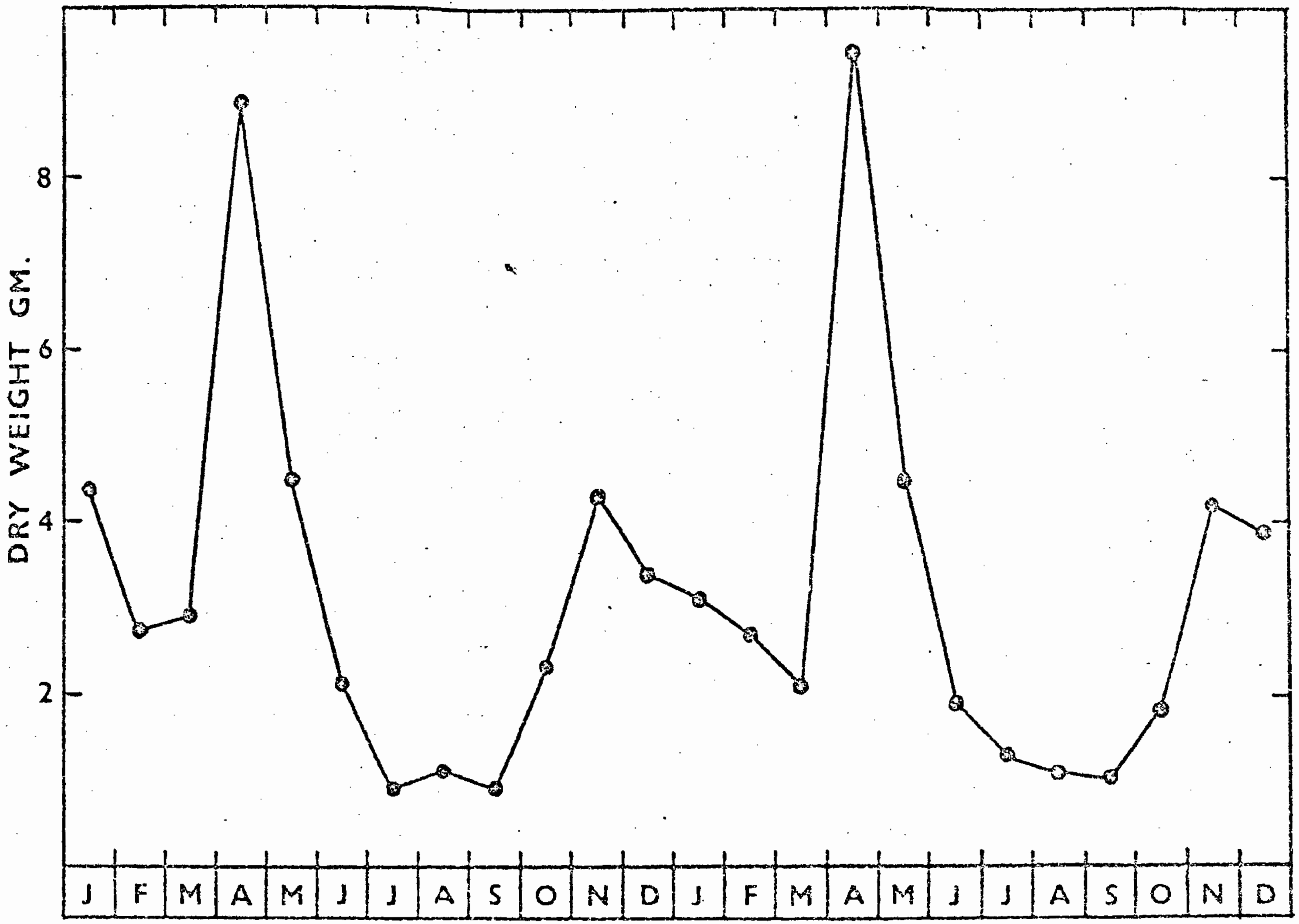


FIG. 4:19 Average weight (dry) of the total invertebrate catch in the monthly drag-net samples. (After Siegfried 1969)

the reeds are preferred. Vernon (pers. comm.) observed a colony in trees to be abandoned in favour of reeds when heavy rains flooded the reed area. This indicates that the species has evolved a response to water at the breeding site. In the majority of sites, trees are selected which hang over water, and reeds are never used unless standing in water. Immelmann (1967) suggested that the tendency for other ploceids to breed in trees over roofs was due to the birds responding to shiny corrugated iron roofs as if they represented the reflection of a watery surface. This conjecture seems unlikely and it seemed that the mean factor influencing nest-site choice was the presence of a gap beneath the nests, rather than any reflecting surface.

In the S. W. Cape, since the bulk of the rains falls before the breeding season starts, the presence or absence of water is probably not so important in influencing the start of breeding, but rather in affecting the choice of the site.

However, an artificial situation developed at Tygerberg in 1969 and enabled the response to the presence of water to be tested experimentally.

4.15 Tygerberg Experiment

In 1969, the Tygerberg dam was completely dry. By early August, breeding was taking place in most areasof the S. W. Cape. In the immediate vicinity (50 metres) of the Tygerberg dam, a colony had developed in some *Eucalyptus* trees.

The dam was then filled artificially and the following sequence of events occurred:-

6 August 1969	Dam completely dry.
7 -	Piping fitted; pumping started 1700 hrs.
8 -	Pumping continued all day.
9 -	First birds seen landing on reeds in dam.
10 -	First nest constructed
11 -	Pumping stopped.
12 -	ca. 10 nests constructed
13 -	first egg laid (back-dated)
14 -	Nests 1 - 15 marked

This experiment illustrates the very rapid response of the Cape Weaver to this habitat factor, the first egg being produced within six days of the habitat becoming suitable. In areas other than the S. W. Cape, perhaps in the Pietermaritzburg area where Vernon made his observation, where rainfall can be more irregular and local, this factor may be an important one affecting the start of breeding. However in view of the facility for the species to breed in trees as well as reeds, this is doubtful. It was not known where the Tygerberg breeders came from i. e. whether they had been breeding elsewhere and deserted other sites or if the tendency to breed in the reeds is sufficiently strong among certain individuals for them not to breed unless the reed habitat is available.

Another habitat factor which does not appear to be important for the Cape Weaver season, is the presence of suitable grass for nest building material. Collias and Collias (1964) suggested that this factor was important to central African ploceids. In the S. W. Cape, however, fresh grass is available from the first winter rains in May onwards, well before the breeding season begins.

4.16 Proximate factors - Photoperiod

One of the most important of the proximate factors affecting breeding is climate, encompassing photoperiod, temperature and rainfall. All data on these factors given below derive from Schulze (1965) or by courtesy of the Meteorological Office at D. F. Malan airport near Cape Town.

Rowan (1953) suggested that the Cape Weaver may be unusual in that its "breeding programme is well advanced" when day-length is still decreasing. The solstice is, of course, 21 June and there is no positive evidence of weavers actually laying before the end of June. Certainly as shown above testiticular recrudescence begins well before the winter solstice, in May, and would therefore appear to be unaffected by photoperiod. As far as egg-laying is concerned, since none has been proved to occur before the solstice, photoperiod may be a more important influence on female condition. As stated earlier, the building of nests in every month of the year by males has tended to confuse the picture and give the impression that birds are "nesting" earlier than in fact is the case.

It is generally accepted that photoperiod can affect the onset of breeding condition (Lofts and Murton 1968), although in many cases insufficient attention has been paid to the food regime during experimentation (Ward 1972). But the close proximity of the earliest records of the Cape Weaver's breeding to the winter solstice suggests that day-length is not an important factor in the S. W. Cape. There the number of hours of day-light at the winter solstice is 9 hrs 54 minutes (Table 4 : 15) and at the peak abundance of nestlings (at Tygerberg - end of October), day-length is 13 hours 24 minutes, still 61 minutes behind the maximum day-length recorded at the summer equinox (14 hours 25 minutes).

Compared to the northerly parts of the Cape Weaver's range, the S. W. Cape has a greater annual day-length change - 4 hrs. 31 mins. - than the Transvaal - 3 hrs 13 mins. The importance of day-length should therefore be greater in the Cape. That it is not, indicates that other proximate factors are more important. It is interesting to note that Kluyver (1952) came to the same conclusion that photoperiod was not an important factor influencing the onset of laying in the Great Tit Parus major.

4.17 Temperature and Rainfall

In northern temperate regions, temperature has long been thought to be a major influence on the start of the breeding season. Kluyver (1952) showed that the onset of laying was determined four days prior to the laying of the first egg and this "determinant date" was strongly influenced by the warmth sum of the previous four weeks.

Efforts to correlate temperature with the onset of breeding in South Africa have been singularly unsuccessful e.g. Rowan (1966) Siegfried (1969) and Liversidge (1970). The difficulty is to devise a scheme which applies to the timing of the breeding season for species with wide distributions.

DAY LENGTH - hours/minutes

DATE	CAPE TOWN	JO'BURG	DURBAN	DATE	CAPE TOWN	JO'BURG	DURBAN
JAN. 1	14.22	13.44	14.02	JULY 2	9.57	10.32	10.15
8	14.17	13.41	13.59	9	10.00	10.35	10.19
15	14.10	13.36	13.52	16	10.06	10.40	10.24
22	14.00	13.20	13.44	23	10.15	10.46	10.31
29	13.51	13.20	13.35	30	10.24	10.52	10.38
FEB. 2	13.38	13.12	13.24	AUG. 6	10.34	11.01	10.48
12	13.24	13.02	13.14	13	10.47	11.10	10.59
19	13.09	12.50	13.01	20	11.00	11.18	11.10
26	12.56	12.42	12.48	27	11.12	11.28	11.22
MAR. 5	12.41	12.32	12.37	SEP. 3	11.30	11.37	11.35
12	12.28	12.21	12.25	10	11.40	11.48	11.45
19	12.14	12.10	12.12	17	11.57	11.58	11.58
26	11.57	12.00	11.58	24	12.15	12.10	12.12
APR. 2	11.42	11.49	11.45	OCT. 1	12.30	12.21	12.25
9	11.29	11.39	11.35	8	12.41	12.32	12.33
16	11.14	11.28	11.22	15	12.53	12.40	12.47
23	11.01	11.18	11.10	22	13.09	12.50	12.59
30	10.49	11.10	10.59	29	13.24	13.02	13.11
MAY. 7	10.35	11.01	10.48	NOV. 5	13.34	13.10	13.22
14	10.24	10.52	10.38	12	13.47	13.20	13.33
21	10.15	10.46	10.31	19	13.58	13.28	13.43
28	10.08	10.40	10.24	26	14.07	13.36	13.50
JUN. 4	10.01	10.35	10.19	DEC. 3	14.15	13.43	13.57
11	9.57	10.32	10.15	10	14.21	13.46	14.01
18	9.54	10.31	10.13	17	14.24	13.47	14.04
25	9.54	10.31	10.14	24	14.25	13.44	14.05
				31	14.22	13.41	14.02

TABLE 4.15

Fig 4 : 16 shows the variation in temperature for the four seasons of study at the Tygerberg colony. There is no obvious correlation between Fig 4 : 16 and Fig 4 : 5, but certain parts of the maximum/minimum values in Fig 4 : 16 do stand out. For example, the high peak of temperature in the last week of July in 1970, the triple peaks of warmth at two-weekly intervals from early July 1971 and the sudden plunge in temperature in 1971 in the last week (w 4) of August/wl September. If temperature was the sole proximate factor stimulating the onset of breeding, relatively early seasons would be expected in 1970 and 1971 and later ones in 1968, 1969. Fig 4 : 5 shows this not to be the case, the 1971 season being early and the 1970 season a month later. The data for the start of 1968 and 1969 cannot be relied on because the former colony was only discovered when it was under way and the latter was affected by the absence of water in the colony dam. If the rainfall systems of 1970 and 1971 seasons shown in Figs 4. 17 and 4.18 are compared, it can be seen that in 1970 the rainfall was relatively high in June and July and there was a heavy peak during weeks three and four (W3 and W4) in July.

It is suggested that heavy rainfall during the early part of the season has an inhibitory effect on breeding in the S. W. Cape. During rainfall, observations on behaviour gave the impression that normal activity was curtailed, display generally stopped and birds sat around with ruffled feathers. Rainfall was usually accompanied by a drop in temperature. Rising temperatures on the other hand seem to stimulate the onset of breeding. It is suggested that early breeding in 1971 was due to 1) the abnormally low rainfall in June and 2) the increase in temperature mainly in W2 July. I suggest that an early

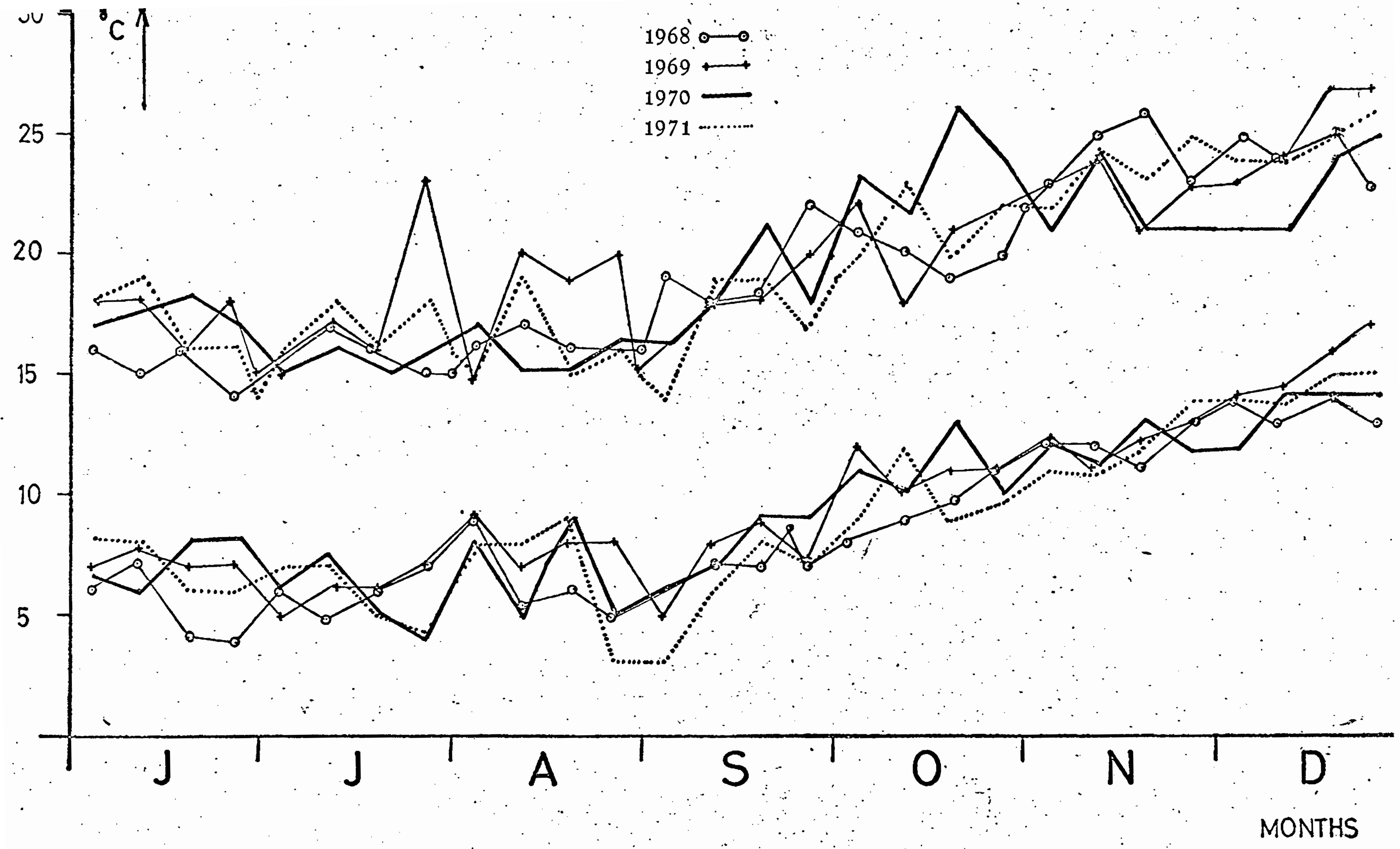


FIG.4:16. Maximum/Minimum Temperatures °C - weekly means to the nearest degree.

FIG. 4:17 MEAN MONTHLY RAINFALL

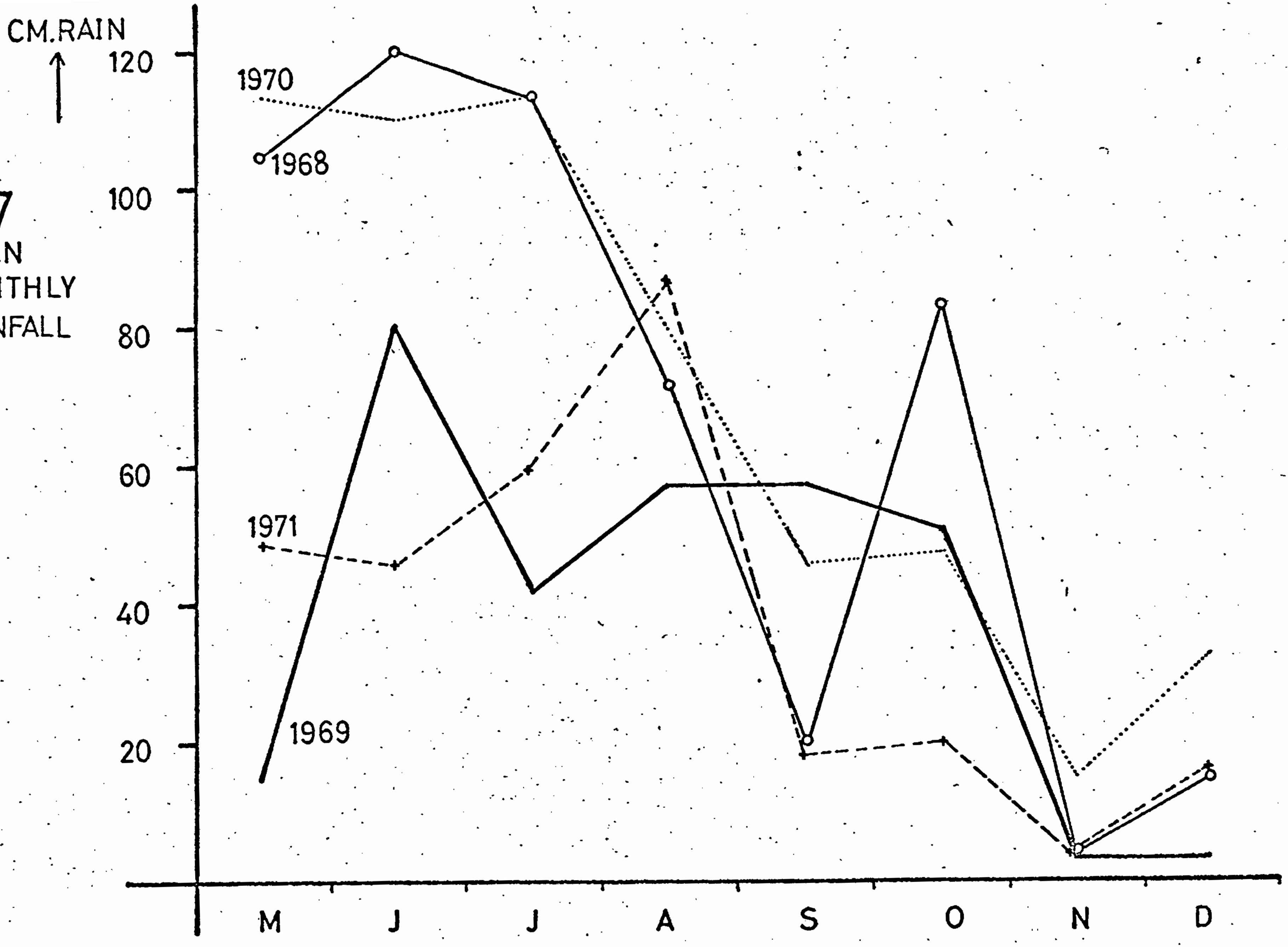
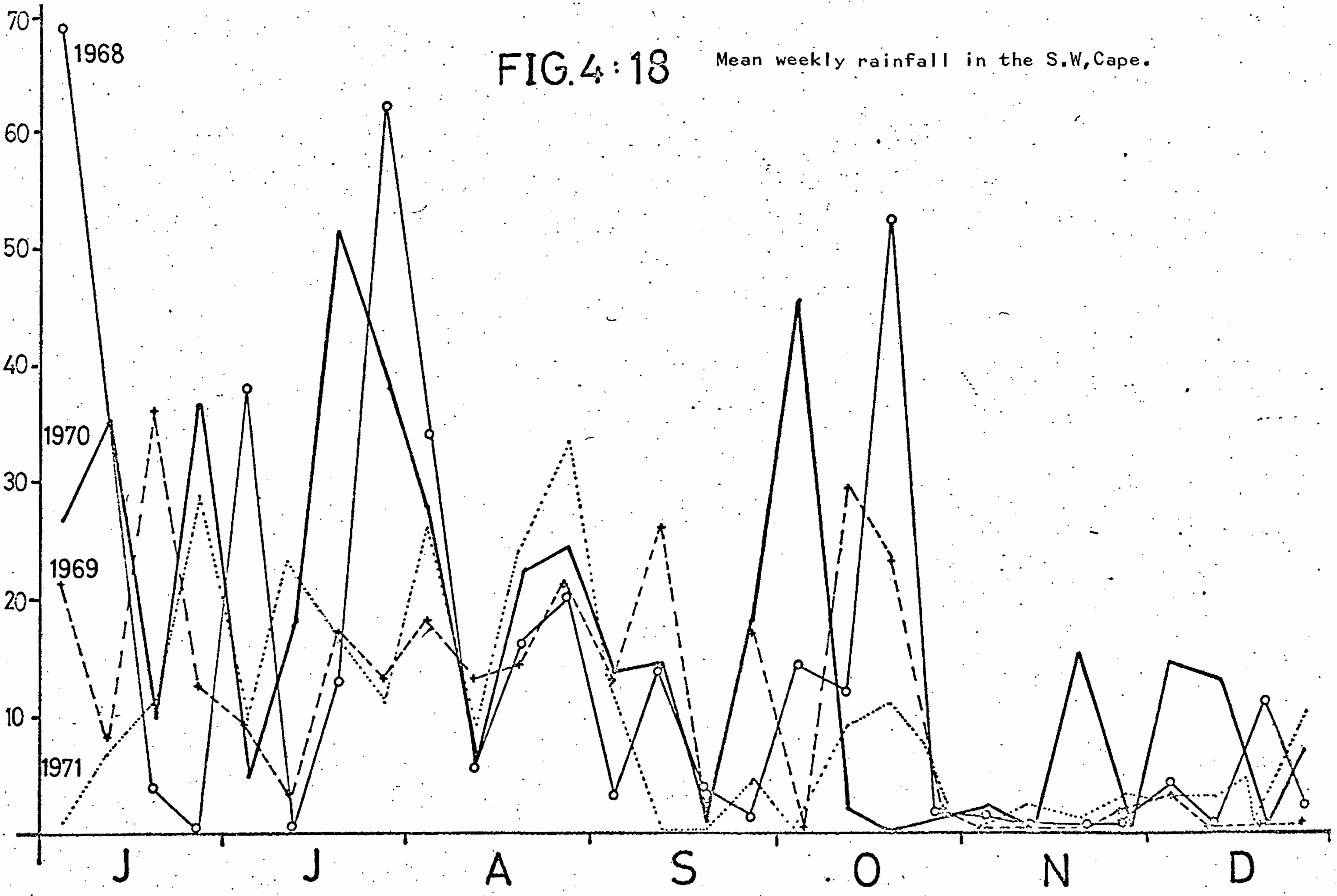


FIG.4:18 Mean weekly rainfall in the S.W,Cape.



season can be predicted on this basis. It is noteworthy that Rowan (1953) in discussing the early season in that year pointed out that April and May were abnormally wet months having twice the normal rainfall. June was unusually dry with half the normal rainfall. Rowan suggested that the abnormal rainfall in April influenced early breeding in July. Data from Kluyver (loc. cit.) and the fact that some weavers are still moulting in April and May makes such a long-term precise forecast seem unlikely. It seems much more likely that 1953 was like 1971 and that a relatively dry June and rising temperature were the proximate causes of early breeding.

The deleterious effect of adverse temperature and rainfall conditions was shown in the 1971 breeding disaster at Tygerberg. The reduction in numbers of nests with eggs was seen in Fig. 4.5 to fall from 70 in W.3 August to 15 in W4 to 5 in W1 September, and this drop can be directly related to heavy rainfall in W3, W4 August and W1 September. The pace of breeding only picked up again as the rainfall ceased and temperatures rose again in W2 September.

It is also interesting to note that the precipitous fall of breeding at Tygerberg was not paralleled by the Vanschoorsdrift colony (Fig 4 : 7). It is suggested that that is due to the more advanced stage of the latter with the result that most of the eggs of the W2 August peak were hatched by the time the cold spell struck. In Vanschoorsdrift, the number of dead chicks increased markedly but it seems that the female weavers are less prone to desert chicks than to desert eggs in the event of bad weather. The phenomenon is well known in passerines in response to disturbance, eggs being readily deserted, and bad weather may be analogous. After the bad weather, the colony gradually reduced activity but as explained above, this may have been due to the artificial removal of chicks. In the smaller colony nearby Mostert's colony, the cold period had the effect of apparently causing the abandonment of the colony altogether. This may be an indication of another function of large colony size - the resistance to environmental hazards.

4.18 Other Areas in South Africa

The general conclusion of the above is that in the S. W. Cape, rainfall is sufficiently regular for the start of the season to be orientated towards the absence of rain after the main body of the rain has fallen, with a concomitant rise in temperature. However consideration has now to be given to the factors affecting the breeding season in the rest of the species' range. The above discussion has concentrated chiefly on the detailed effects of the environment on the main study colony. It has already been pointed out that in 1971, the only year when adequate comparative data was collected, the difference in start of breeding between two colonies separated by only 20 km was about one month. The rainfall data in Figs 4 : 17 and 4 : 18 have been taken from D. F. Malan airport which lies 14 km South East of the study colony at Kraaifontein. No detailed data is available for Kraaifontein except on a monthly basis. Table 4 : 20 shows that the mean rainfall at Kraaifontein is 69 mm less than D. F. Malan's. It also shows that Kraaifontein starts to dry up earlier and July and August are prominently dryer there. It is suggested that this earlier drying up may be responsible for the differences. The maximum daily temperature also starts to increase earlier to the north of

RAINFALL - A Comparison : Kraaifontein vs. D.F.Malan

MEASUREMENTS IN mm/24hrs. ENDING 0800.

Mean monthly rainfall 1926/60

Month	J	F	M	A	M	J	J	A	S	O	N	D	Total
Kraaifontein	9.0	14.5	12.5	47.8	76.4	88.4	81.9	67.6	46.5	33.0	18.9	9.6	506.1
Days with Rain	2	2	3	6	9	9	9	9	7	5	3	2	66
D.F.Malan	8.6	15.2	13.8	66.0	93.6	85.3	100.3	79.9	47.4	33.9	21.4	8.8	575.1
Days	3	4	4	8	12	10	12	12	10	7	4	3	89
Difference in Rainfall	1.6+	-0.6	-1.3	-18.5	-17.2	13.1	-18.4	-12.3	-0.9	-0.9	-2.5	+0.8	-69.0

Mean Rainfall at Kraaifontein 1931/60 = 514.8mm (-60.3)
Opinion is that Tygerberg Range would not affect weather at Kraaifontein by causing precipitation there but rainfall at Kraaifontein is generally slightly less than at D.F.Malan.

Tygerberg colony is 13.6km. from airport control tower.

Table 4:20

Cape Town, while at night temperatures fall lower. The early drying and the earlier incidence of warm days would seem the most likely causes of the early breeding.

However, the very fact that a month's difference can occur between two such adjacent colonies, suggest that only a detailed survey in any given region will give clues as to the factors influencing the start of breeding. The water level experiment at Tygerberg indicated the importance of the right conditions in a potential or previous colony before breeding can start. Such phenonema are likely to be purely local but have a marked effect on breeding.

The data for Bredasdorp, though scanty, indicate that Cape Weaver breeding may be about one month behind the S. W. Cape. Table 3 shows the fluctuation in mean monthly temperature. It can be seen that the mean maximum does not reach 17.0° C until a month after the S. W. Cape. The rainfall system for Bredasdorp is the same in distribution as that of the S. W. Cape except that it is generally lower.

The differences in breeding season for the Cape Weaver in Port Elizabeth and Grahamstown are probably instructive, if the breeding data can be relied on. Port Elizabeth has a very evenly distributed rainfall, some falling every month while Grahamstown lies on the edge of the summer rainfall zone. Liversidge (pers. comm.) has suggested that breeding can take place in Port Elizabeth in February and March, but he may have been misled by the nest-building activities of subadult males, and was unable to prove the presence of eggs. The data to hand indicates that Port Elizabeth birds start to breed about one month before the inland areas. The superfluity of rainfall at the coast suggests that temperature may have a more important influence, so that on a mean annual basis, August - the temperature rising from 19.5 to 19.9 degrees, would seem to be the logical starting point, as supported by Table 4 : 8.

In Grahamstown, the main rainfall begins to fall in September and this coincides with the start of breeding.

The Transvaal has a stricter summer rainfall regime than Grahamstown and the breeding season is almost identical. It is noticeable that the mean temperatures in the Transvaal undergo a big jump of 3.1° C between July and August. Rainfall in the area occurs mostly in thundershowers as opposed to the rain-days on the coast (Schulze loc. cit.). It is suggested that after the temperature rise in August, the Cape Weaver will start breeding as soon as the first rainfall begins. i.e. the system seems to be the reverse of the coastal region, where breeding starts after the rain has mostly stopped and then the temperature rises. The breeding data in the Transvaal is insufficiently detailed to test this hypothesis but it is in agreement with the start of breeding in the area in late August/early September despite the temperature rise in early August. The problem in the Transvaal is to explain why the breeding stops at the end of January when the rainfall is still far from finished and the mean daily temperature is more or less constant. On the available data, particularly the absence of information on food fluctuations, it is not possible even to speculate on the factors influencing the end of breeding.

4.19 Conclusion

After Immelmann (1971), it is accepted that the chief ultimate factor influencing the timing of the breeding season in the Cape Weaver is food, though little supporting evidence is presented. The condition of the habitat, especially standing water, is also an important ultimate factor in the species. Evidence is given which indicates that the proximate factors influencing the precise start of the breeding season vary over the full range of distribution. In the S. W. Cape, reduced rain and rising temperatures appear to be important, while in the Transvaal the start of the rains is more significant and temperature less so.

SECTION 5 - MOULT

5.1. Introduction

The importance of moult in the annual energy cycle of most birds is generally considered axiomatic. The reasons for that importance are usually given as the physiological strain and the necessity of fitting this energy-requiring process into a time of food abundance. Yet not many detailed ecological studies have been carried out and most have been restricted to the comparative extremes of climate of northern temperate regions.

In southern Africa, not a single study has been published and only one (Liversidge 1970 - unpublished thesis) has appeared on the moult of resident passerines in the region. Brooke (1966) records data on the onset of prenuptial moult (body moult only) in Euplectes species. Elsewhere in the southern hemisphere and the equatorial region some studies have been carried out notably: Moreau et al. 1947, Miller 1961, Keast 1966 and Ward 1969. These indicate that there are considerable differences in the moult duration and season in these regions compared with the north.

It was, therefore, necessary to study moult in the Cape Weaver to establish how important moult was in the annual cycle in terms of duration, rate and energy-requirements. Within the special theme of the work, it was possible that moult might influence mortality rate, as was found in Europe (Newton 1966) where there was an apparent correlation between time of moult, age and mortality. Such correlations, particularly if they were correlated also to sex, could affect the social structure and the mating system of the Cape Weaver.

5.2 Method

Since one aspect of the proposed moult study was to pick up possible sex differences, it seemed likely at the outset that large samples would be necessary. It was, therefore, decided to restrict the large scale quantitative collection of data to the primary moult only. Such a restriction has been considered a fair assumption in other general studies on moult (e.g. Newton, Keast, Miller (loci. cit.) and in analysis of the importance of moult (Evans 1966), on the grounds that primary moult just about spans the full duration of the total body moult. Some non-quantitative data were collected on the sequence of the moult of the feather tracts other than the primaries.

Samples of the Cape Weavers were taken in the course of normal ringing procedures by capturing birds in mist-nets usually as the birds came to roost.

The numerical scoring system for moult follows that used by Ashmole (1962) and Newton except that the actual point system is moved on one point from the latter's score, i.e.

Old Feather	1
Feather missing or in small pin stage	2
Feather in large pin or brush stage	3
Feather brush to half-grown	4
Feather half to three-quarters grown	5
Feather three-quarters to full grown	6

The additional point was used since it allows computerisation. A computer reads zero and blank as the same. Therefore no distinction would be made between a bird not examined for moult and one with no moult unless the above scoring is used.

Only one wing, usually the right, was examined for most of the moult records. Thus a freshly moulted bird with nine new primaries would have a moult score of 54, and a bird with only old primaries would have a score of nine.

To check that there was not much variation in moult between the two wings of a given bird, a sample of 11 birds was examined on both sides. The results were given in Table 5 : 1. As can be seen in 60% of the cases the primary moult of the left wing was identical to that of the right. The greatest difference found was only equivalent to growth of half a feather. It is concluded that it is a fair assumption to examine only one wing of the Cape Weaver in studies of its primary moult.

The number and distribution of the feather tracts of the Cape Weaver are similar to those of most other passerines. The nomenclature used to describe them follows Dwight(1900).

Right Wing	Left Wing	Score Difference
18	17	1
19	19	0
37	37	0
10	10	0
27	27	0
17	17	0
42	43	1
22	22	0
13	10	3
14	13	1
53	53	0

TABLE 5.1

Difference in Moult Score for Primaries of Left and Right Wings of the same bird.

RESULTS

5.3 The Moult Cycle

Since only primary moult data were collected in quantity, the outline of the moult cycle given below is a generalised one. In the whole population there is likely to be some variation on this outline.

The Cape weaver chick on hatching is naked except for a very fine covering of natal down. The juvenile plumage begins to develope at about four days old and displaces the down during this post-natal moult. The juvenile feathers continue growing until shortly after fledging. The quality of the feathers is noticeably thinner and lighter than those of adult birds. In some juveniles, fault bars in the feathers are clearly visible.

From two weeks to about one month after fledging a Post-juvenile moult of all feathers occurs. Only one pullus was recaptured in moult (see Table 5.14). The second recapture gives a moult rate of 0.37 (see below). If this rate is worked back, the start of moult is calculated to be on about 26th November or 25 days after ringing as a pullus. Assuming fledging within about three days, this would give a time lapse of three weeks between fledging and the start of primary moult.

In fully grown Cape Weavers, the main moult is, as in most passerines, a post-nuptial moult of all feathers. This moult occurs once a year after breeding during the period October to March.

5.4 Post-nuptial Moult Sequence

Remiges

There are nine primaries, six secondaries and three tertials in the Cape Weaver's wing. Moult begins with the first primary which is the innermost or proximal primary. The primary moult occurs in descendent order from the innermost feather to the outermost. The number of primaries growing at one time varies from individual to individual. Table 5.2 shows the degree of variation in a sample of 167 birds. More than half (56.3%) were found to have two primaries in moult at the same time, and 33.5% had two primaries growing simultaneously.

The first secondary is only shed after the third primary is fully grown. The relationship between primary and secondary moult is shown in Fig. 5.3. The data are scanty towards the end of secondary moult, but the impression gained was that in most birds, the last one or two secondaries were still unmoulted by the time the primary moult had been completed. There does seem to be some indication from the slender data of an increase in speed of the last three secondaries, compared with the first three, but this appears not to be very marked.

The moult of the tertials occurs out of sequence with the secondaries. It seems to start at any time from the moult of

No. of Primaries in moult	No. of birds	% sample
1	56	33.5
2	94	56.3
3	16	9.6
4	1	.6

Mean 1.77 primaries moulting : Sample 167 birds

TABLE 5.2 Number of primaries in moult at the same time, for birds having a moult score of 48 or less

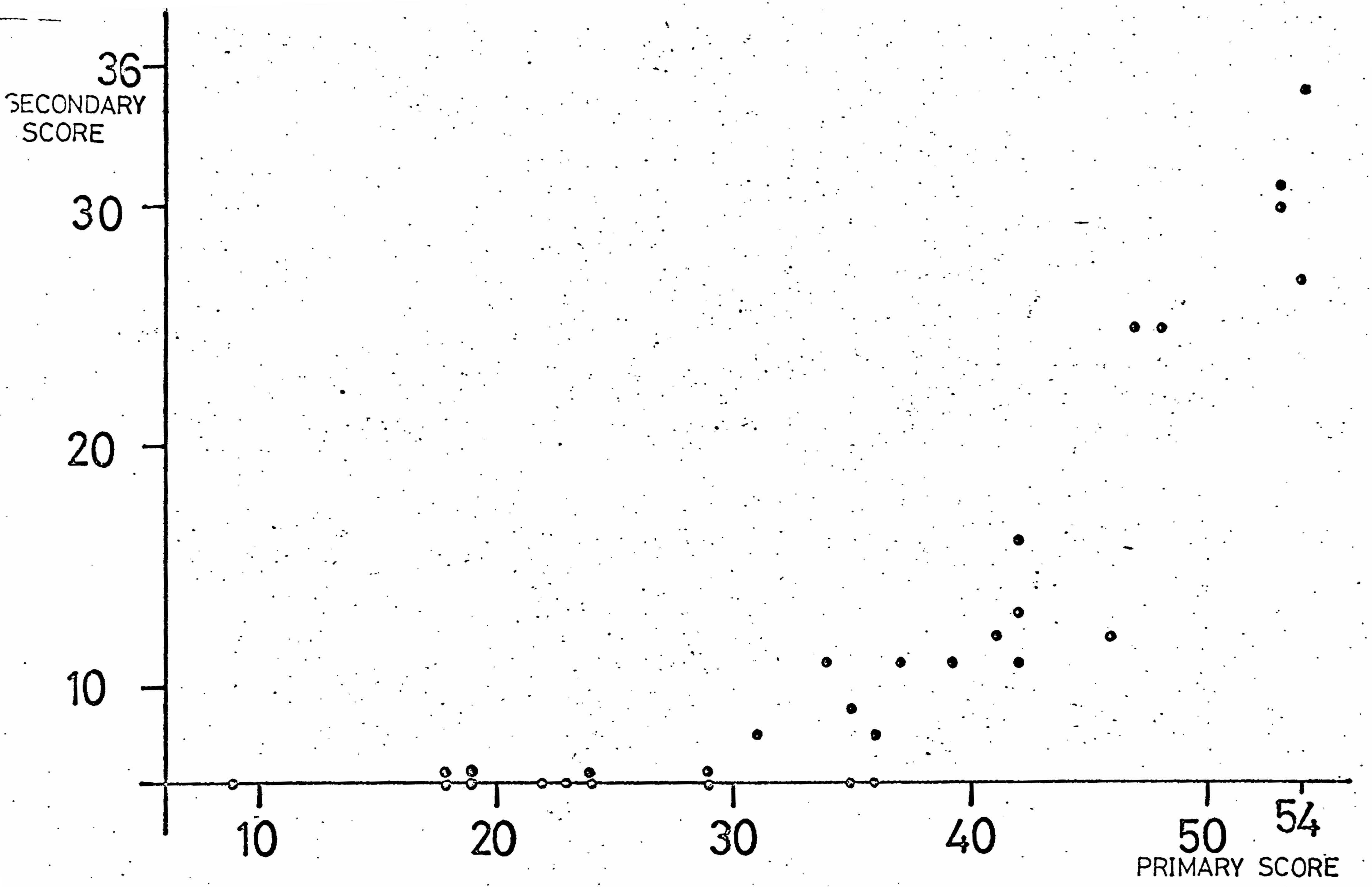


FIG.5:3 The relationship between primary and secondary moult.

the fifth primary to the moult of the eighth primary. There is also some variation as to which tertial is moulted first. In some it is the first tertial, in others it is the second. In some of the birds examined, all three tertials were in various stages of growth. In others the first two were growing and still others the first and third were growing while the central one had yet to be shed. The moult of the tertials is complete before the secondaries, usually when the secondaries still have one or two feathers left to moult. In two cases the tertials were full grown before the primaries (primary score 47 and 48 respectively).

Rectrices:

The moult of the tail feathers was very irregular. In the small sample examined, see Table 5.4, the only order to the moult sequence appeared to be that moult of the rectrices started with the inner pair. In most cases, the inner pair moulted together. Yet in two birds with advanced moult, one of the inner pair was not full grown, indicating that one of the innermost rectrices was the last to moult. Once the first pair of rectrices has been dropped, there seems to be no regularity in the moult at all. Table 5.4 shows that the number of feathers moulting in the two halves of the tail may differ by as much as three feathers. Even where the moult score is not very different, this does not mean that the same feathers are involved. The score can differ by as much as eight points, or the equivalent of about one and a half feathers. Table 5 : 4 also shows that up to seven feathers can be moulting at any time in the tail. Generally four feathers moulting, two in each half, was the condition most commonly encountered.

Left Tail	No. of feathers moulting	Right Tail	No. of feathers moulting	Score Difference
7	1	7	1	0
7	1	7	1	0
7	1	7	1	0
15	2	22	5	7
7	1	8	1	1
35	1	36	0	1
14	2	12	2	2
22	4	14	3	8
7	1	7	1	0
9	1	9	1	0
13	1	20	3	7
8	1	8	1	0
35	1	36	0	1

TABLE 5.4. Comparison of Moult in the left and right sides of the Rectrices. A score of 36 indicates 'moult complete'.

In relation to primary moult, the tail moult was found to start at any time from the moult of the first primary to that of the eighth. Tail moult was at most only half complete when primary moult was complete and therefore would presumably continue for a number of weeks after this point.

Body Moult

Body moult begins very soon after the start of primary moult. It appears to begin in the plumage of the upper parts and under parts. The median coverts are moulted early in the moult cycle and are one of the first areas to be completed. The moult of the head feathers seems to vary more from individual to individual. In some it is completed while the rest of the moult is still continuing and in others it continues after the end of the moult of the primaries.

Both the head, upperparts and underparts can show very heavy simultaneous moult with large sections of the feather tracts growing at one time.

From the data available, it is not certain exactly how long the body moult lasts. It seems probable that the bulk of the body feathers is replaced while the remiges are being moulted. At the same time it is certain that some body moult continues after the primary moult is complete. It is possible that body moult is complete by the time the tail moult is finished, but as stated this may be a number of weeks after the end of primary moult.

Since males are seen in adult plumage in all months except for February and March (see section 3.3c) the gap between completing body moult and undergoing a prenuptial body moult must be quite short.

5.5 The Moulting Season - the Primary Moult Approximation

After Ward (1969), the moulting season is defined as the season during which any birds in the population are in moult. Excluded are those which are moulting to replace feathers lost through injury. The approximation that primary moult is a good indication of the duration of total body moult is also followed, but with reservations indicated below.

It is indicated above, Section 5 : 4, that in the Cape Weaver, secondary moult is still partly incomplete when primary moult is finished. Although the bulk of body moult is over, some body moult also continues after primary moult is finished and furthermore adult males indulge in a prenuptial body moult.

A similar situation exists in other species but its extent is usually not stated. For example Ward loc. cit. states that it is 'normal' for the rest of the plumages to have been renewed by this time, but 'sometimes' one or two secondaries and tertials still remain to be renewed. No mention is made of body moult. The species referred to is Pycnonotus goiavier. Evans loc. cit. states that primary moult covers the whole moult period although in a 'few' birds, the innermost secondary has not completed growth.

No mention of body moult is made at all. Newton loc. cit. mentions that in Bullfinches Pyrrhula pyrrhula, secondary moult continued in 50% of the birds examined for a few days after the end of primary moult. No specific mention is made of body moult in relation to primary score. But his Table 3 shows that over 60% were still moulting the ventral tract and over 80%, the thigh tract during the last primary moult stage (score 80-90 out of max. 90). In his Table 11, the mean primary score at the completion of ventral body moult was 85 and for thigh moult 86.

It seems, therefore, that some moult does continue after the end of primary moult.

As stated moult is generally considered to be a physiological strain. If it is measured in terms of primary moult, the relative importance of the primary feathers in relation to the other feathers should be assessed.

Table 5.5 gives the wet and dry weights of the primary feathers and the remainder of the body feathers i.e. the rectrices, secondaries and all the body feathers. In the sample taken, the highest value found for the dry weight of the primaries as a percentage of the total feather weight was 13.2%, the mean

Age/Sex	Wet Weight of Primaries	Dry Weight of Primaries	Wet Weight of Body Feathers	Dry Weight of Body Feathers	Weight of Primaries as % of total dry feather-weight
Adult Male	0.50	0.36	3.04	2.50	12.6
Female	0.29	0.19	3.51	2.80	6.4
Female	0.40	0.37	3.14	2.73	11.9
1 Year Male	0.31	0.15	3.63	1.71	8.1
1 Year Male	0.36	0.20	2.36	1.71	10.5
1 Year Male	0.25	0.14	2.72	1.38	9.2
1 Year Male	0.39	0.24	2.49	1.57	13.2
Mean	.36	0.24	2.98	2.06	10.3

TABLE 5.5. The Comparative weight (gms.) of primary feathers and the remaining body feathers of a sample of 1 Adult Male, 4 First Year Males and 2 Females.

being 10.3%. A similar value of 10% was found by Newton for the Bullfinch. In the latter the heaviest group of feathers was those of the ventral tract at 7.36 g., and the dorsal tract at 4.90 g. Since the percentage weight of the primaries is the same in both the Cape Weaver and the Bullfinch, it seems likely that proportionately the ventral and dorsal tracts would also be the heaviest and therefore the most energy-requiring in the Cape Weaver.

The primaries are therefore not a good indication of the physiological strain of the moult season especially as the duration of their moult does not totally cover the important body moult. In the Cape Weaver, as stated, no details of the exact end of body moult were taken but the impression gained was that the bulk of the moult did take place during primary moult. The use of the latter is, therefore, a convenience since it allows easy quantification and comparison with other species. For greater accuracy however, it would have been preferable to study primary moult together with the moult of the two major body tracts, the ventral and the dorsal. This conclusion would seem to apply to studies of primary moult in all passerines.

5.6 The Moulting Season - Duration

Data on the moulting season was collected in the normal way and records of 1646 birds examined, are summarised in Table 5 : 6 with the exception of one locality, Port Alfred, all the localities fall within the broad study area of the South-Western Cape.

Of the birds samples, 663 were found to be in moult.

Date	Locality	No. of Birds Examined	No. of Birds in Moult	% Moulting
11.12.68	Tygerberg	71	15	21.1
21.1.69	Port Alfred	41	31	75.6
4.11.69	Tygerberg	47	11	23.4
20.11.69	Tygerberg	75	24	32.0
26.11.69	Tygerberg	43	21	46.5
4.12.69	Tygerberg	15	11	73.3
9.1.70	Firgrove	35	28	80.0
12.1.70	Firgrove	47	45	95.7
13.2.70	Firgrove	4	4	100.0
1.3.70	Stellenbosch	9	1	11.1
15.3.70	Stellenbosch	18	5	27.2
6.11.70	Tygerberg	17	1	5.8
10.11.70	Darling	13	3	23.0
16.11.70	Tygerberg	48	13	27.0
3.12.70	Tygerberg	45	14	31.1
10.12.70	Tygerberg	15	10	66.6
7.1.71	Fauré	27	6	22.2
22.1.71	Tygerberg	2	2	100.0
17.5.71	Tygerberg	7	0	0
23.5.71	Tygerberg	27	0	0
10.9.71	Tygerberg	25	0	0
1.11.71	Tygerberg	38	16	42.1
2.12.71	Tygerberg	43	22	51.2
15.12.71	Tygerberg	54	30	55.5
28.1.72	Tygerberg	80	77	96.2
4.2.72	Tygerberg	72	70	97.2
16.2.72	Tygerberg	52	37	71.1

Date	Locality	No. of Birds Examined	No. of Birds in Moult	% Moulting
25.2.72	Tygerberg	61	32	52.4
15.3.72	Tygerberg	63	34	54.0
24.3.72	Tygerberg	84	15	17.8
29.3.72	Tygerberg	40	9	22.5
13.4.72	Tygerberg	60	6	10.0
26.4.72	Tygerberg	68	4	5.9
10.5.72	Tygerberg	70	1	1.4
6.9.72	Tygerberg	94	0	0
4.10.72	Tygerberg	56	7	12.5
25.10.72	Tygerberg	55	15	27.3
25.1.73	Firgrove	45	43	95.3
	Totals:	1646	663	

TABLE 5 : 6 Moult in the Cape Weaver population.
Number of birds examined and percentage of birds in moult in trapped samples.

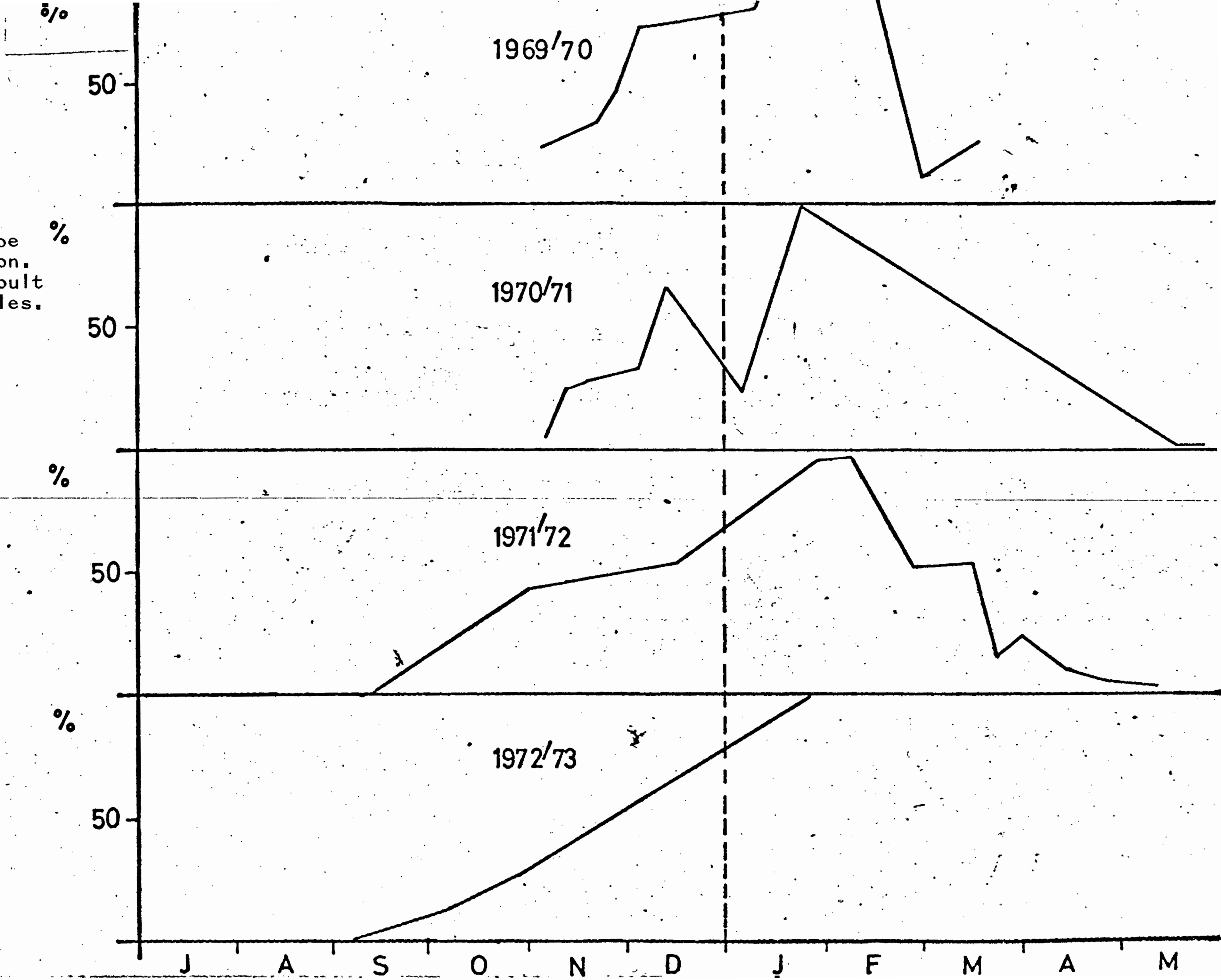
The moult season is depicted in Fig 5 : 7. The bulk of the data was collected in 1971/72 but the other three seasons have been included for some comparative purposes. Some of the sample sizes are small, but most give a good indication of the proportion of the population in moult.

It can be seen that moult begins in the population in late October - early November and continues through until the latter half of April, a total season of about six months. The peak period when virtually the whole population is at some stage of moult is late January/early February.

The pattern of moult from one year to the next seems from Fig. 5 : 7 to be fairly constant. The start of moult in the four seasons is shown to occur within about two weeks of the same date. But the percentage of birds moulting in 1971/72 is rather high for the first record that season. 1971/72 was the one year in the study period where there was a burst of very early breeding (see Section 4 : Fig. 4 : 1). This would agree with the logical correlation between breeding and moulting seasons. Above (Section 5 : 3) it was estimated from one record in the field that chicks begin moult within about 21 days of fledging. Studies carried out in an aviary on hand-reared birds gave a minimum period of 18 days and a maximum period of about 40 days. However under aviary conditions, it is difficult to judge the equivalent day of natural fledging and the food regime is obviously different. An average time elapse would seem to be about three to four weeks after fledging. An early breeding season as in 1971/72 would therefore result in an early start to the moulting season. The lack of variation in Fig 5 : 7 is therefore due to lack of data for the early part of the season.

FIG. 5:7

Moult in the Cape Weaver population. % of birds in moult in trapped samples.



The end of the moult season as deduced from the 1971/72 season is mid-April. The data is insufficient in the other seasons to allow comparisons to be made.

5.7 The Duration of Moult per Age/Sex Classes

Little has been reported in respect of different moult regimes in different age/sex classes. Newton (1966) pointed out in passing that different age/sex classes began moult 'on average' on different dates but he did not comment on the extent or significance of this phenomenon. Other workers divide their data according to age, into adult and juvenile classes (e.g. Ward 1969) but not according to sex.

Table 5 : 8 presents the Cape Weaver data according to four age/sex classes. The 'mature' males have been lumped since the adult and eclipse birds are stages of the same age group and distinguishing immature birds from eclipse birds at this stage of the season is sometimes difficult. The female categories are a little unsatisfactory since first-year birds can only be distinguished from adults for a few weeks after fledging while the gape is still swollen and bright. Towards the end of moult season, first year birds were often separated on the grounds that, relative to the majority, they showed retarded moult. Hence there tended to be selection of the data on moult characteristics, and conclusions drawn should be strictly tentative.

The data given in Table 5 : 8 are the mean moult scores of all those birds actively in moult from the date on which moult was first observed in the population. A total of 950 observations is given. This figure is larger than that of Table 5 : 6

1971/1972 SEASON

Record No.	Date	Ad/Eclip/Imm. Males	1Y Male	Ad/Unsp. Female	1Y Female
1	1.11.71	15.3 (3)	9.0 (1)	15.4 (8)	9.5 (2)
2	12.11.71	18.3 (3)	24.0 (1)	12.0 (1)	-
3	20.11.71	25.2 (8)	15.0 (4)	13.4 (11)	9.0 (1)
4	28.11.71	-	24.5 (4)	11.8 (6)	9.0 (1)
5	2.12.71	26.2 (6)	22.2 (6)	18.2 (10)	21.7 (4)
6	15.12.71	32.8 (8)	21.3 (18)	23.7 (8)	10.2 (8)
7	30.12.71	40.0 (4)	48.5 (4)	29.0 (2)	22.8 (9)
8	13.1.72	42.5 (11)	30.7 (4)	26.0 (2)	24.0 (2)
9	28.1.72	51.1 (16)	37.2 (23)	37.6 (31)	28.6 (5)
10	4.2.72	51.1 (12)	41.5 (28)	38.9 (28)	-
11	16.2.72	52.9 (10)	45.2 (20)	48.3 (20)	-
12	25.2.72	52.8 (12)	49.0 (23)	51.0 (17)	34.0 (1)
13	15.3.72	53.4 (5)	51.0 (30)	51.7 (24)	-
14	24.3.72	53.9 (15)	53.4 (33)	53.6 (40)	-
15	29.3.72	54.0 (11)	53.3 (11)	53.5 (2)	-
16	13.4.72		53.9 (23)	53.9 (21)	-
17	26.4.72		53.2 (14)	53.9 (28)	52.0 (1)

1972/1973 SEASON

1	4.10.72	9.5 (9)	12.4 (9)	-	-
2	20.10.72	14.2 (9)	13.1 (13)	12.2 (13)	
3	28.10.72	12.0 (1)	-		
4	25.1.73	52.4 (11)	39.2 (9)	41.3 (23)	

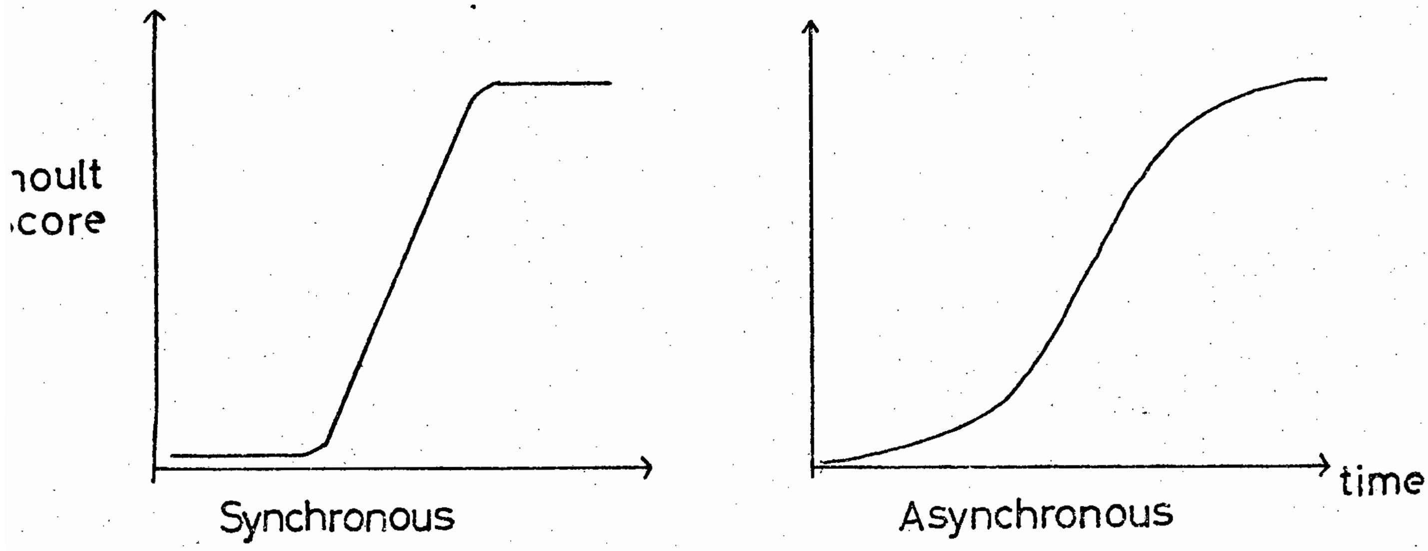
TABLE 5 : 8

Mean moult scores of sex/age groups per date during the period 1968/73. Data collected from the S. W. Cape except for data collected on 22.1.69. (Port Alfred*) Total number of records 950.
Sample sizes are given in brackets.

because it includes all the data taken from specimens and some additional data supplied by other ringers. The figures in brackets are the sample sizes.

Figs 5 : 9 and 5 : 10 give the data in graphic format for the 1969/70 and 1971/72 seasons. The data for the other seasons is too scanty to show any trends. Fig. 5 : 9 shows a close parallel between older males and the female group. But the data is very scattered and does not allow close examination. Only in 1971/72 are the sample sizes large enough and the sample dates frequent enough for this treatment.
Fig 5 : 10 shows that there is considerable variation in mean moult score early in the season. This is likely to be a facet of sample size, just as is the sudden jump in moult score in first-year males. But for the most part the sample size is more than adequate .

The general shape of the graph seems to be latterly sigmoid. This tendency was mentioned by Evans and Newton for northern temperate passerines. A sigmoid shape for moult score would be expected when the whole population is considered. The degree of sigmoidness would depend on the degree of synchrony in the moulting population. Shown below are theoretical graphs for highly synchronised populations and comparatively asynchronous ones.



Synchronous

Asynchronous

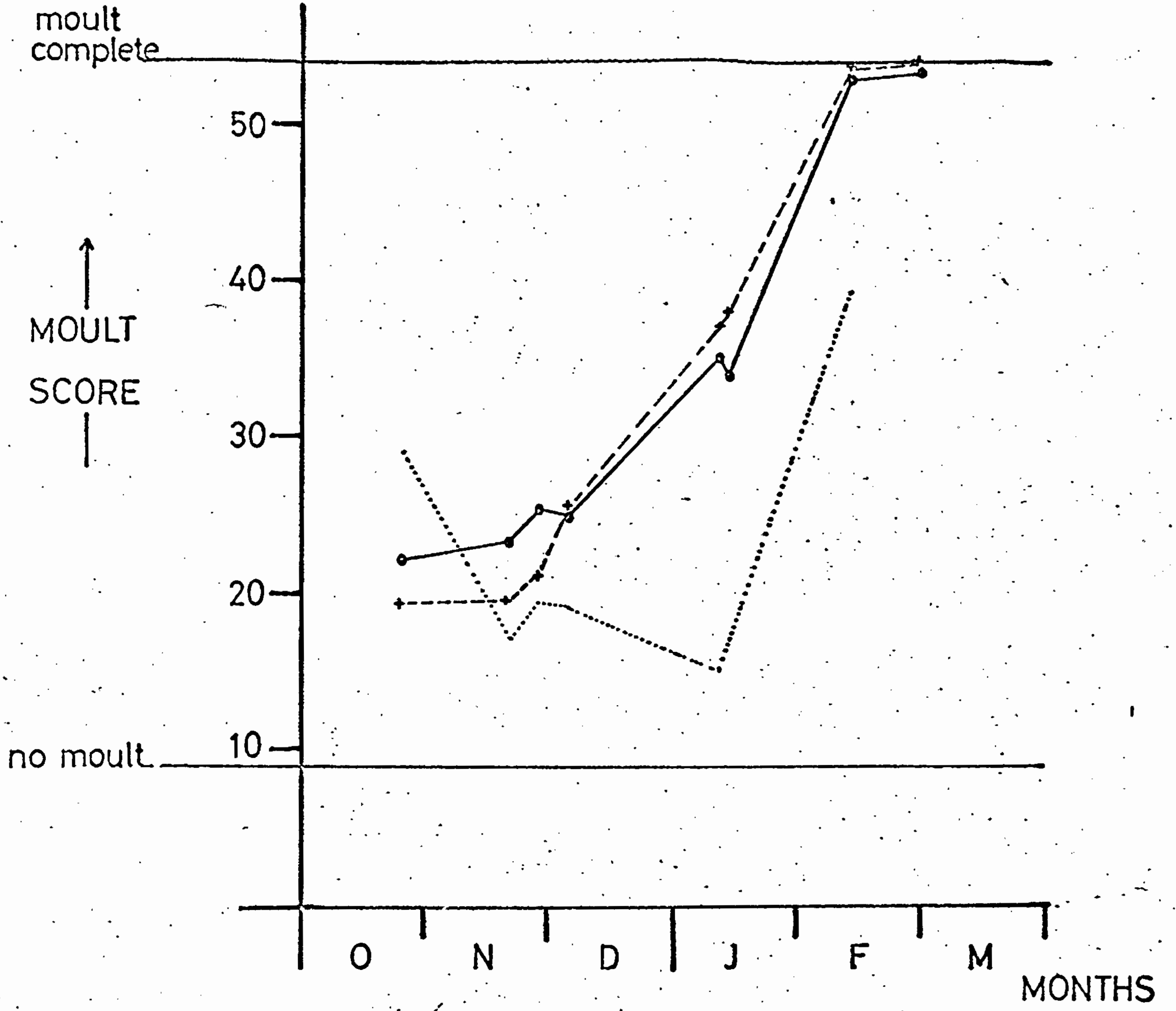


FIG.5:9 Mean moult scores of sex/age groups per date during the period 1969/70. Data collected in S.W.Cape except for records 5 & 6 from Port Alfred, E.Cape.

Ad./Eclip./Subad.♂♂...o——●

1Y♂♂ ....+----+

Ad./Unsp.♀♀ ....·········

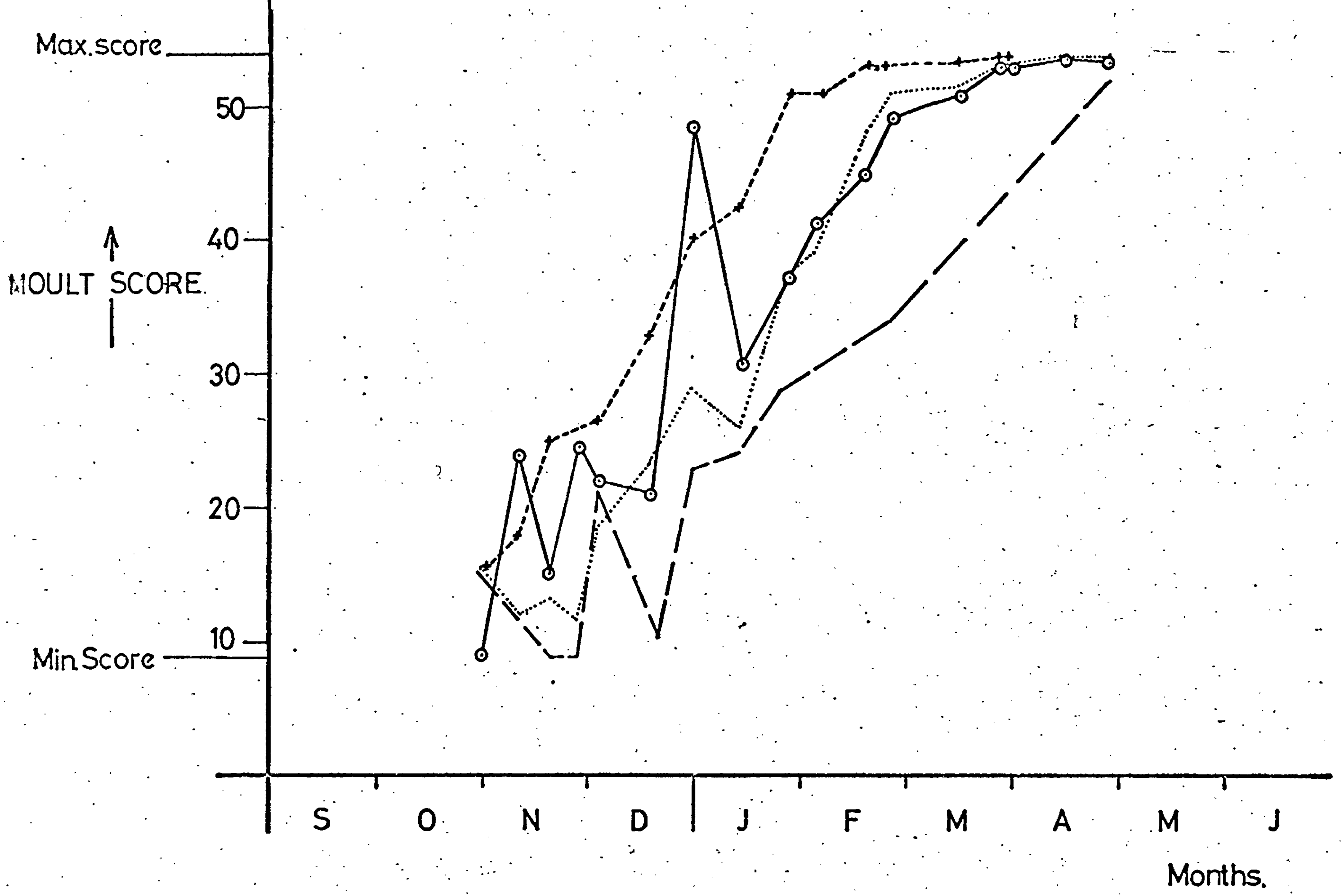


FIG.5:10 — Mean Moult Scores for different age/sex classes in the 1971/72 season.

+----+ Ad/Eclip/Subad.♂♂

o——o 1Y ♂♂

.... Ad/Unsp.♀♀

— — — 1Y♀♀

The type of curve will depend on how the data is selected. If only birds in moult i.e. having a moult score > 9 and < 54 are included, then the sigmoidal aspect will be reduced and the tendency towards a straight line increased. If, however, the population is considered as a whole, the build-up in moult score will be slow, the mean score being low, depending on how synchronised moult is in the population. For example in Fig. 5 : 7, it takes an average three months before 50% of the population is in moult.

In presenting the data in Fig. 5 : 10, only positive moult values have been included (with three exceptions) i.e. values of >9, at the beginning of the moulting season. At the end, the value is a mean of the whole population, hence the slow progression to the maximum value. The latter method has also been used by Evans and Newton. The standard practice is then to calculate the regression line values for the data and finally to test for linearity.

Evans and Newton remark, separately, that it is fortuitous that they found no departure from linearity. But in view of the above, it seems that this was, at least in the latter case, due to a) not considering the population as a whole at the start of the moult and b) to there being sufficient synchrony in the population at the end of moult not to upset the linearity.

Following these two authors, the data in Fig 5 : 10 was calculated for regression lines according to:-

$$Y = bx + a \quad \text{where} \quad \Sigma y = aN + b\Sigma x$$

$$\text{and} \quad xy = a\Sigma x + b\Sigma x^2$$

The correlation coefficient between the regression values of the mean moult scores and the actual mean moult scores was calculated from:-

$$r = \frac{N\Sigma xy - (\Sigma x)(\Sigma y)}{\sqrt{N\Sigma x^2 - (\Sigma x)^2 (N\Sigma y^2 - (\Sigma y)^2}}$$

and the significance level of the correlation from:-

$$t = \frac{r\sqrt{N-2}}{\sqrt{1-r^2}}$$

The values of these calculations are given in Table 5 : 11 and the regression lines for the four classes are shown in Fig. 5 : 12. The calculated regression lines are all significantly close to linearity $p < .001$ in all four cases. As shown above, this is likely to be a product of the method of selecting the data.

From the regression lines, further information can be deduced namely 1) the relative rates of moult of the age classes 2) the relative timing of moult of the age classes 3) the relative duration of moult in the age classes. The regression lines can also be a measure of the actual values within each age class where there is a reasonably high degree of synchrony with each class.

The relative rates of moult as given by the slopes of the regression line were tested to see if they were significantly different according to the relationship:-

$$t = \frac{b_1 - b_2}{S\sqrt{\frac{1}{\Sigma x_1(x - \bar{x}_1)^2} + \frac{1}{\Sigma x_2(x - \bar{x}_2)^2}}}$$

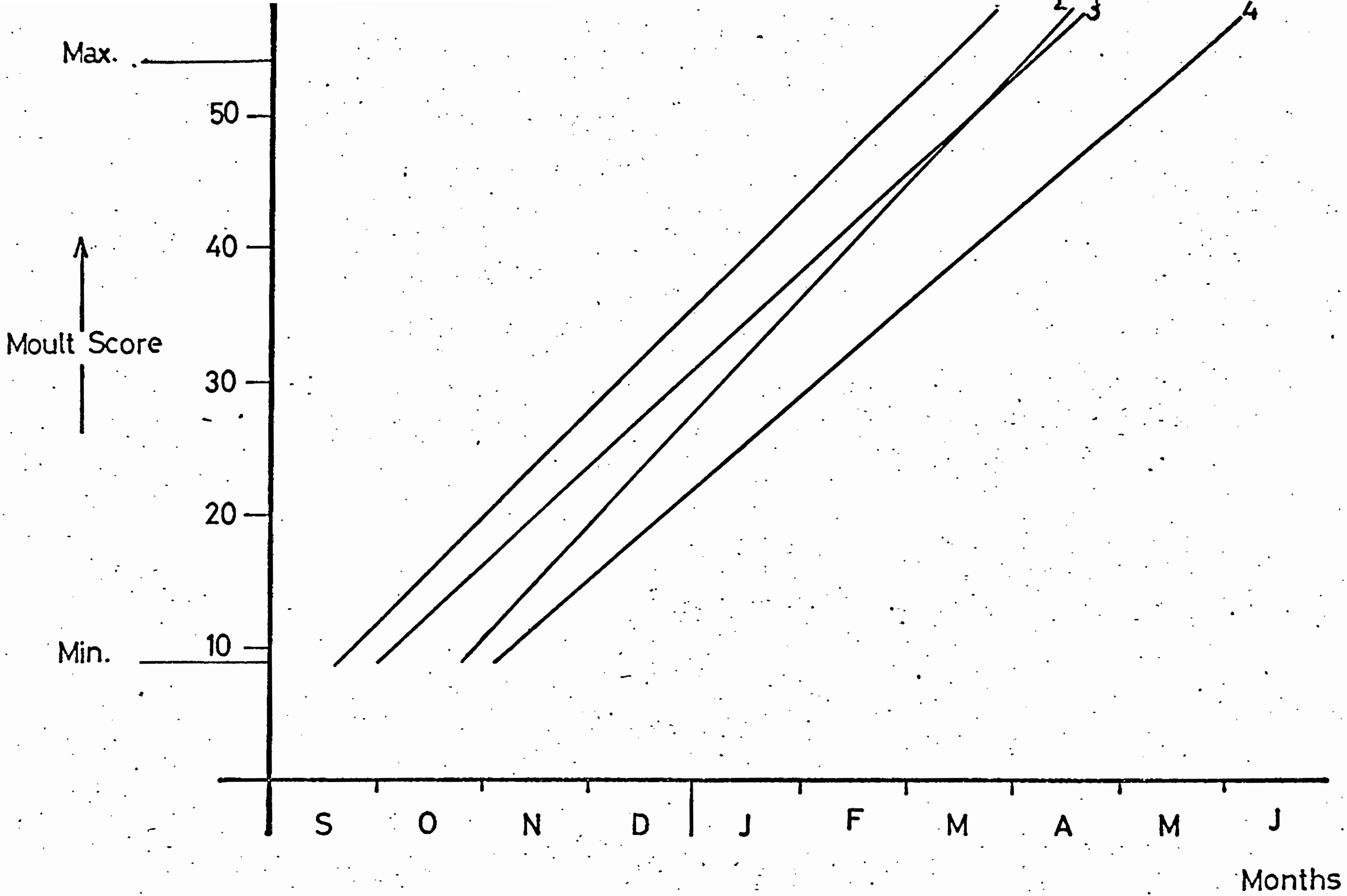


FIG. 5:12 Regression lines of mean moult scores of age/sex categories:-
1 - Ad/Eclip/Subad ♂
2 - Ad/Unsp. ♀
3 - 1Y♂
4 - 1Y♀

The values given for difference in the slopes or the different rates of moult of the age/sex classes were found to be not significant. To the eye, the regression lines in Fig 5 : 12 can be seen to have very similar slopes, but at the same time there is some spacing of the timing of the lines.

The data was then tested using the relationship for the difference between non-independent samples (Croxton and Cowden 1955), the non-independence arising from samples being taken in pairs on the same data. The t values for the significance of the difference of the samples are given in Table 5 : 13. These values show that the timing of moult in the "older" males group was significantly earlier than any of other classes ($p < .001$) The difference between the older and younger groups was significant for both sexes ($p < .001$). But the timing of moult in young males was not significant from that of older females ($p > 0.05$).

The duration of moult in the four classes as shown by the regression lines was not significantly different for the first three classes (about 5 months or 150 days) but was longer in the first year females (about 6 months or 180 days). However, as explained above, this difference may not be a real one.

Apart from comparative purposes, the regression lines also indicate values within each class. The rates of moult for the classes can be seen in Table 5 : 11 to vary between 0.23 and 0.29 moult score points per day. As stated above, the duration of the moulting season in the different classes varies between five and six months.

Age/Sex Class	Ad./Eclip./Subad Male	1Y Male	Ad/Unsp. Female	1Y Female
Regression Equation	$y = 0.27x + 19.54$	$y = 0.25x + 15.7$	$y = 0.29x + 9.85$	$y = 0.23x + 7.75$
Correlation & Coefficient	0.95	0.92	0.85	0.82
t value	10.40	8.90	6.21	4.77
Significance	$p = < .001$	$p = < .001$	$p = < .001$	$p = < .001$
Rate of Moult	0.27	0.25	0.29	0.23

TABLE 5.11. Regression Line data for the moult scores of the four age/sex classes.

In addition to the information given above, the same data can also be estimated by retrapping birds in moult.
For details see below.

Class Pairs Regression Line Values		t value	P value
Ad/eclip/subad M:	1Y M	20.12	$p = < .001$
"	Ad/Unsp F	31.30	$p = < .001$
1 Y M	"	1.94	$p = < .05$
"	1 Y F	6.60	$p = > .001$
Ad. F	"	6.29	$p = < .001$

TABLE 5: 13 Results of the Test of Difference between non-independent samples - the Regression Line Values of different Age/sex Classes.

5.8 Duration and Rate of Moult - Retrap Information

Only 14 birds were retrapped twice while they were in moult. Records were obtained from an additional five captive hand-reared birds, giving a total of 19 individuals, the details of which are shown in Table 5 : 14. The rate of moult varies between 0.63 to 0.05 points per day. The mean for the wild birds is 0.42 points/day. The mean for captive birds is 0.29 which indicates that stress, food, or some other factor may be slowing down the moult of birds under these conditions (see Section 3.2a).). The contrast between the moult rates of captive and wild birds are shown graphically in Fig 5 : 15. It shows that in the wild there is considerable variation in the moult regardless of the length of time between retrapping. The rates of moult of the captive birds are all comparatively similar. The captive birds, three males and two females, were all on the same diet and this may explain the similarity in their rates of moult.

For wild birds above the mean duration of moult is 107 days or 3.5 months. It is at once noticeable that these figures differ considerably from those calculated from the regression lines, where the mean rate was 0.26 and duration 173 days. It seems likely that the retrap method will give the more accurate result since it is a direct measurement. Its main source of error is that the speed of moult may vary in the individual at different stages in the moult. Newton found that the rate in Bullfinches tended to be fastest in the middle and slowest at the beginning and the end of the process. If the relative rates given in Table 5 : 1 are examined, there seems no evidence of this, but the sample is small.

	Dates	Age/sex	Moult Score	Time Elapsed Days	Points Increase	Rate of Moult /day
1.	4.2.72	1 Y M	41			
	25.2.72		52	21	11	0.52
2.	4.2.72	F	46			
			51	12	5	0.42
3.	1.11.71	Pull	N/M			
	4.2.72		35			
	24.3.72		53	49	18	0.37
4.	15.12.71	1 Y M	14			
	16.2.72		44	63	30	0.48
5.	28.1.72	F	25			
			29	7	4	0.57
6.	4.2.72	1YM	29			
			34	8	5	0.63
7.	13.1.72	1YM	33			
			48	62	15	0.24
8.	13.1.72	Ad.M	37			
			48	22	11	0.50
9.	4.2.72	1YM	30			
			34	12	4	0.33
10.	2.12.71	1YM	10			
			39	57	29	0.51
11.	1.11.71	Imm.M	18			
	16.2.72		51	46	33	0.43
12.	25.2.72	1YM	40			
			53	48	13	0.27
13.	28.1.72	1YM	48			
			49	19	1	0.05
14.	4.3.73	1YM	31			
			53	66	22	0.32

	Dates	Age/Sex	Moult Score	Time Elapsed Days	Points Increase	Rate of Moult /day
15.	22.12.70	1YM	32			
	22.1.71		41	31	9	0.29
16.	- ditto -	1YF	34			
			45	31	9	0.29
17.	- ditto -	1YM	39			
			50	31	11	0.35
18.	- ditto -	1YF	34	31	14	0.45
			48			
19.	- ditto -	1YM	22	31	12	0.39
			34			

TABLE 5 : 14 The Rate of Moult as deduced from retrapping birds in moult. Data for records 1 - 13 are from the 1971/72 season; 14, from 1972/73 and 15 - 19 are from experimental aviary birds.

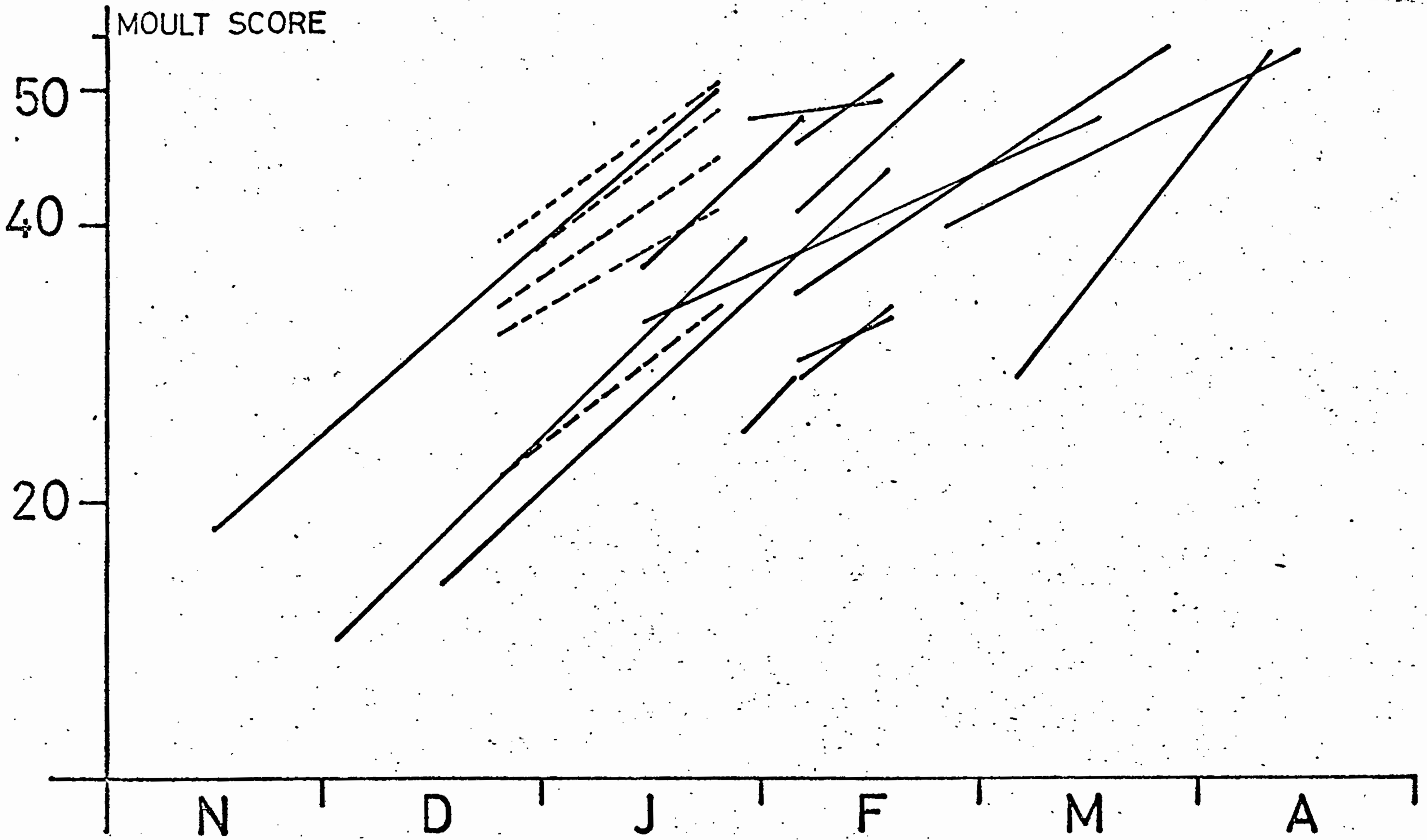


Table 5:15 The rate of moult score increase for birds retrapped in moult

—— 1971/72 wild birds

------- 1970/71 aviary birds

Furthermore only three of the retrap moult rates fall within the range of the regression values (0.23 to 0.29). This suggests that the difference between the rates calculated from the regression lines and those found by retrapping are real. It seems likely that this difference is due to one of several reasons. The curve produced as the mean moult score approaches maximum in Fig 5 : 10 will tend to decrease the slope of the regression line. According to the figures, this tendency was insufficient to invalidate the linearity of the regression line. The effect can also be produced by relatively few late moulters. A second factor producing the difference could be that by taking the regression values of mean moult scores, rather than the individual scores themselves, the effect of individual variation is reduced and the effect of each mean given equal status regardless of sample size. If, however, taking the older male group as an example the last four mean moult scores are excluded to reduce the tailing-off effect, the regression calculation gives a slope or rate of moult of 0.33 instead of 0.27. This is closer to the wild-moult rate mean, and suggests that the rate of moult in the central part of the graph of Fig. 5 : 10 is similar to the rates found from retrap rates. By chance, this section of the graph is also represented by larger sample sizes. The difference between the regression and retrap rates is therefore likely to be due mainly to the tailing off effect rather than to any false assumptions in the regression calculations.

5.9 Discussion

The above constitutes the first comparatively detailed study of moult in a resident passerine in Southern Africa, where quantitative data on aspects of the primary moult is given.

The questions then posed are how do the results compare with other less detailed studies in the area (as stated - in fact only one - Liversidge 1970) and what comparisons can be drawn with studies conducted elsewhere. Finally how important is moult in the annual cycle of the Cape Weaver.

Liversidge gives very little quantitative data. His study on Pycnonotus capensis was carried out in the Eastern Cape in an intermediate rainfall area. The bulk of the rainfall follows the pattern of the S. W. Cape, but there is an occasional burst of rainfall in March which sometimes causes a late burst of breeding (See his Fig. 20). The moulting season presents a very odd picture where apparently at one point 100% of the specimens collected were simultaneously showing moult and had completed fresh plumage. Clearly a mistake has been made.

As presented, Liversidge's information lacks too much in quantification to allow proper comparisons to be drawn. His Fig. 13 shows that 100% of the birds examined in six months of the year showed some moult. No distinction is made between the different body area. It is possible that the bulbul primary moult is quite seasonal but that the body moult is very prolonged. It is also not clear if there is a prenuptial moult in the bulbul and whether this could account for the length of moult. If the data in Fig. 13 are taken, then the minimum duration of moult in the bulbul is over six months, and that is for each individual bird, since all were recorded in moult for this period. The longest duration on record is that for Pycnonotus goiavier (Ward 1969) at 17 weeks, yet Liversidge's data suggests a minimum of 26 weeks for P. capensis. Clearly the method used or the presentation of the data has led to error. Liversidge states that the long duration may by due to individual variation but if 100% of all birds examined are in moult over a six month period this can be taken as a minimum individual figure.

In the Cape Weaver, the mean duration of primary moult was 107 days or about 15 weeks. Although the retrap data gives rates of 0.05 to 0.63 moult scores per day, the likelihood of the rate of moult being different at different stages, makes the mean a reasonable figure to take. The extremely low figure of 0.05 was found on a bird which increased its score by one point over 19 days. In view of the comments in Section 5 : 5, and the fact that primary moult does not quite cover full moult, then the true duration of moult in the individual bird is likely to be about 15 - 17 weeks. This duration is quite a bit longer than that in northern temperate zones where rates of 10 - 12 weeks were found in some Fringillidae (Newton 1968). Comparable rates were, however, found in warmer regions in the Southern U.S.A. - 15 weeks in House Finch - (Michener and Michener 1940) and of course, in Pycnonotus goiavier in the tropics.

The wide spread in the start of moult coupled to the comparatively long individual duration gives a total moulting season of about six months. This compares with the eight months of the Pycnonotus goiavier season and the continuous moulting season of the Pycnonotus capensis. It seems that the apparently continuous season for the latter may be due to data for a number of years being lumped together. With some variation in year to year in the breeding season, especially the occasional burst of breeding in March, a result would be produced which would be somewhat misleading. If Liversidge's data was split into years, probably much greater seasonality would be shown.

One point of interest that does come out of the Pycnonotus capensis data, is the apparent simultaneous occurrence of moult and breeding. Although Liversidge does not go into the extent of his evidence - the number of observations of the phenomenon - to what extent breeding birds were in moult - the incidence of arrested moult etc., it seems clear that the coincidence did occasionally arise. In the Cape Weaver, observations at the Tygerberg colony showed that some birds, particularly males, showed signs of having started moult while they were still breeding. However, this was only observed very late in the season usually as the last chicks were being fed. In these circumstances, these seems little significance in the partial overlap, except that at the end of the season there is some "urgency" to the start of the moult.

The incidence of Cape Weaver males in moult with well-developed testes was very low. Table 5 : 16 gives the details for 59 specimens of which only three had testes of five mm. length or more, the longest being six mm. In full breeding conditions, testes length is ten mm. Comparison of Fig 5 : 7 with 4 : 5 shows that breeding and moult overlap by about three months, as it does in P. goiavier . However, the evidence of the testes size and moult, indicates that birds that are breeding are not those moulting i. e. in individuals, the two events are mutually exclusive. In the Cape Weaver, there must be a large population of subadult non-breeding males and presumably other males which are unsuccessful in obtaining mates. As shown in Fig. 5 : 10, the older males start

Moult Score	Mean Testis Size	Range	Sample
9	1.57	1 - 3	7
11	5.00	5	1
12	4.00	2 - 6	2
15	2.00	2	2
17	2.00	2	1
19	2.00	2	1
20	1.00	1	1
22	3.00	3	1
24	2.00	2	1
27	2.00	2	1
29	4.00	2 - 6	2
32	2.00	2	1
33	2.20	2 - 3	5
39	2.25	2 - 3	4
40	2.00	2	1
42	2.00	2	1
43	3.00	3	1
45	2.00	2	2
46	2.00	2	1
50	3.00	3	2
51	3.00	3	3
52	3.66	3 - 4	4
53	2.82	1 - 4	11
54	2.83	1 - 4	6
			59

TABLE 5 : 16 Relationship between testis length and moult score.

moulting before any of the other age/sex groups, and this early start was found to be statistically significant.

The moult cycle of the Cape Weaver was found to be standard to that of most passerines except that probably a more significant part of moult continues after primary moult is complete.
The Cape Bulbul cycle given, has some oddities such as body moult not starting until primary moult is complete.
In P. goiavier , body moult started first of all regions, a clear week before primary moult began.

Compared to studies on resident passerines in northern temperate regions, the Cape Weaver has a slower rate of moult, 0.42 in the weaver to 1.3 in the Bullfinch (Newton 1966) and a longer moulting season, six months to four months. Neither Ward nor Liversidge commented on the possible causation.

It is suggested that one of the main reasons for these differences, is that in Southern Temperate regions, the food regime is much less severe than in the north. It seems likely that in the north, the food fluctuations are more marked with high peaks of superabundance in summer and lower troughs in the winter. In some non-passerines, such as parrots, pigeons and doves, especially in the tropics, prolonged or almost continuous moult occurs which usually overlaps with the breeding season (Payne, R. 1972) Payne states that such overlapping is indicative of the energetic compatibility of moulting and breeding. This suggests that prolonged moult is a "strategy" developed to spread the effects over a long period of available but not superabundant food.

It seems that in the Cape Weaver, there is enough food to allow some birds to be moulting during six months of the year, to be breeding for an overlapping further six months, leaving only a short period from mid-April until the end of June when neither activity is going on. Unfortunately direct evidence on the availability of food was not obtained but further discussion of this point will be found below under the indirect evidence of weight fluctuations and food studies.

The important difference found in the Cape Weaver is the more marked difference in the timing of start of moult in the different age/sex classes. This difference cannot for reasons already explained be deduced from the regression lines. But if a rough estimate is made from the "straight" part of the moult scores in Fig 5 : 10, it can be seen that older males start about three weeks earlier than older females. However, it is likely that this difference is not so much caused by environmental differences between the north and south, but by the polygnous pair-bond system in the Cape Weaver as opposed to the monogamous one in the Bullfinch.

It is suggested that the males which start moulting early are either adult males which fail to obtain females, or young males, the polygynous system producing a large population of unmated males. If truly polygnous species were found in the north temperate zone, a similar difference in the start of moult might well be found.

The fact the age/sex classes did differ in this respect but not apparently in the rate of moult suggests that moult may have an important effect on the social structure in the Cape Weaver.

Since some males are able to moult during a presumably better time of year than females, it must mean that there will be at least a slight selection pressure in favour of males at this time of year. But the males favoured are likely to be the non-breeding males. Whether this advantage to some males is sufficient to affect the sex ratio is debatable and will be discussed below. It may be that at the time of year in which moult takes place, the food situation is sufficiently favourable not to have any effect and that it is only in the two month "off-season" that there is a real pressure on survival. If there was any selection pressure on females, then one would expect the female rate of moult to be relatively faster, but this is not the case. It is clear that these possibilities should be kept in mind in the examination of the ecological parameters discussed below.

SECTION 6. - FOOD, FEEDING RATES AND WEIGHT FLUCTUATIONS

6.1 Introduction

As mentioned under Section 1 : 1, in the Ploceinae, the mating systems (Crook 1964), and plumage types (Moreau 1960) have been correlated with various ecological parameters, one of which is diet. The odd thing about these studies and that of Lack (1968) is that no mention is made of how these food classifications are decided upon. But Crook remarks at one point that all Ploceinae which have been adequately studied have been found to feed their young on insects, often together with seeds. Presumably the adults are also feeding themselves on insects at this time. One concludes therefore that the food classifications are based on what the birds feed on in the non-breeding season. For example, one of the other common ploceines in the study area Euplectes orix is defined as seed-eating while at least initially, it feeds its chicks on insects (usually larvae - pers. obs.) In the non-breeding season, the impression gained was that it was exclusively seed-eating, roosting birds arriving in the evening with a milk of crushed seeds/grain dribbling down their beaks. The Cape Weaver falls into the uncommon classification group of mixed feeders, which were pointed out by Lack (See Section 1 : 1) to be of special interest. Detailed analysis of the food of most weavers would probably place more of them in this bracket complicating the classification. (See Rowan 1971).

In the three papers initially cited, the food habit of the Cape Weaver is referred to as "mixed insect/seeds including nectar". This information is all second-hand being gleaned from Skead (1947). Two other papers have also contributed to the knowledge of the bird's food, namely Oatley and Skead (1972) and Rowan (loc. cit). Their information will be included below.

Interest in the food of the Cape Weaver stemmed from the necessity to re-examine its classification as a mixed feeder in relation to its social system. It was hoped that some indication of the relative importance of insects and seeds at different times of the year particularly at the onset of breeding would be produced. An attempt was also made to gauge any differences in the diets of males and females which would reflect on possible competition or sexual dimorphism. However, the food study was not one of the main lines of research and therefore the sample size is small for conclusive information.

6.2 Method

The food of the Cape Weaver was assessed by three methods i) examination of stomachs and crops of specimens collected (ii) observation of birds feeding and (iii) observation of food being brought to the chicks.

Specimens were collected usually by mist-netting birds coming in to roost at dusk. Birds were killed within an hour of being caught either by squeezing the thorax or by chloroforming. The bodies were then deep-frozen until they were dissected. Some specimens were collected by shooting at various times of the day, either while they were feeding or while they were present at their breeding colonies. Chicks were collected from nests.

Only incidental observations were made of food while birds were feeding. It tended to be the unusual, such as weavers feeding on aloes, which caught the eye and was recorded.

During observations of feeding rates to chicks at different stages in the season a note was kept of the type of food being brought in. Obviously such observations depend on the food being large and identifiable at some distance (usually five metres) and there would tend to be a bias in this direction.

6.3 Analysis

It was decided at the outset that in this food study, it was the relative abundance of insects and seeds in the constituent diet which was of interest and not the energetics of food consumption. No attempt was made to determine the amount of food eaten or required per day by the weaver. The information sought was the insect/seed ratio in relation to its polygnous classifications to sex differences if any and to diet changes during the year.

A total of 279 birds from a few days old to fully mature were collected. An additional 35 were collected but were found to have empty stomachs and empty crops. All the birds were dissected and the crop and stomach contents examined. A representative sample of the stomachs of 103 full-grown birds and 15 pulli were preserved in 70% alcohol for examination.

The remainder, 119 full-grown and 42 pulli were examined superficially. The apparent proportion of insects to vegetable matter was assessed and major items of diet were noted. In a review of the methods and problems of detailed analyses of bird foods Hartley (1948) implied that any study should incorporate several different methods of analysis. Any consistency in the results, would then suggest an approach to the real situation. He also pointed out that exact details should be given so that comparisons between food studies on different species could be made.

Accordingly in the detailed analysis of the preserved Cape Weaver stomachs and crops, the following procedure was adopted:-

1) All contents were assessed "as found". No attempt was made to extrapolate back to the original size of the food items.
2) All food items which could be recognised separately were given symbols and used as a reference collection.
3) At the end of the study, the reference collection was identified where possible. The insects were identified to order and in some instances to sub-order. The vegetable matter was identified where possible to species.
4) After Hartley, two methods of analysis were used, numeric and volumetric. The numerical analysis was made according to the reference collection i.e. if the item was "piece of coleopteran elytron", then the number of pieces was counted. No attempt was made to assess

the number of individual coleopterans represented by the pieces because the high degree of fragmentation would have made this very difficult. The volumetric analysis was conducted by water displacement in a graduated cylinder in the standard manner. Volume was assessed down to 0.05 ml. and all smaller items classified as <0.05 ml.

6.4 Results - Diet

Of the 118 samples examined in detail, only ten consisted of both crop and stomach contents, the remainder only of stomach contents. The complete range of diet found in the species is given in Table 6 : 1. Additional published information has been incorporated in the table.

It is interesting to note the range of coleopteran sub-orders represented in the diet and the inclusion of families which are normally considered noxious such as the Coccinellidae. The vegetable diet significantly contains many items of exotic food such as *Acacia cyclops* and *Hordeum vulgare.* The impression given in the literature is that nectar-feeding is a frequent phenomenon in the weaver. Although quantitative information is lacking, it is felt that its importance has been exaggerated because of its conspicuousness It would also be of interest to know how often birds apparently feeding on aloe nectar are in fact searching for beetles attracted by the nectar. It is sometimes obvious that it *is* nectar which is being consumed, since the bird tilts its head back in the drinking position, but one wonders how often this corroborative evidence has been obtained.

ANIMAL DIET

ARTHROPODA

INSECTA

Isoptera	Hodotermitidae	(Harvest Termite)	Imago
Orthoptera		(Grasshoppers)	Imago
Coleoptera	Unsp.		Larva/Imago
	Carabidae	(Ground Beetles)	Imago
	Coccinellidae	(Lady Birds)	Imago
	Scarabidae	(Scarab-beetles)	Imago
	Elateridae	(Click-beetles)	Imago
Lepidoptera		(Butterflies)	Larva/Imago
Diptera	Tabanidae	(Horseflies)	Imago
Hymenoptera	Apidae	(Solitary Bees)	Imago
Formicoidea		(Ants)	Imago
Unidentified Insect		D1	Imago
- Ditto -		B	Mouthparts
- Ditto -		G	Larva
ARACHNIDA		Unsp.	Full Grown

VEGETABLE DIET

Acacia cyclops	Rooikrans Aril/ Seed	+	Aloe ferox nectar
Ehrharta spp.	Grass Seed	+	Agave spp. nectar
Hordeum vulgare	Barley Grains	+	Aloe aborescens nectar
Zeya mays	Maize Grains	+	Schotia brachypetal nectar
Ficus spp.	Seed	+	Aloe candelabrum nectar

	Grass Seed unsp.	H	+	Aloe spectabilis	Nectar
	Brown oral seed unsp.	X	v	Apricot	Fruit
	Translucent seeds	P		Grape Vines	Fruit
	Unidentified vegetative matter	I/J/Q/T/V		Miscellaneous assumed vegetables	O
*	Pine cone seeds	Seed		Other Items	
	Leguminosae (Vegetable Pea)	Seed		Eggshell	
	Lycium campanulatum (Solaceae)	Fruit		Feathers (Probably artefacts)	
	Grevillea robusta (Silver Oak)	Nectar		Grit	

TABLE 6 : 1 Diet of the Cape Weaver. Alphabetical symbols refer to reference collection of items. * Skead (1947); + Oatley & Skead 91972); v Rowan (1971).

Also listed are three other items of "food". Eggshell, an important source of calcium for growing chicks, was the only item of any nutritional significance. The feathers were probably artefacts introduced during dissection. Some birds particularly grebes (Simmons 1964) are known to eat feathers, but the habit seems unlikely for weavers. The presence of grit is characteristic of seed-eating birds, as opposed to fruit-eaters, which do not generally have stomach grit. The grit is used to assist in the grinding up of hard seeds for digestive purposes.

6. 5 Dietary Composition

If all the numeric and volumetric data for the 118 samples are lumped together, the relative percentages of insect, vegetable and other items are seen to be:

	Volumetric	Numeric	Combined
Vegetable	48. 7	41. 7	45. 2
Insect	39. 3	44. 5	41. 9
Other	12. 0	13. 8	12. 9

This would seem to indicate that the Cape Weaver is a mixed feeder with insects and vegetable matter being taken roughly equally. However, as explained above (Section 6 : 1), any such assessment should be made during the non-breeding season and should not include food fed to chicks which are insectivorous in all ploceines. Table 6 : 2 shows the distribution of sampling dates for the detailed analyses. For the assessment, the pulli data and the September-November data is excluded. The percentages are given below.

	Male	Female	Pullus
21.6.68		2	
5.7.68	1		
4.6.70		1	
27.6.70	1	2	
17.7.70	1		
19.7.70		1	
26.7.70	1		
2.10.70	2	1	
10.11.70	3	2	8
7.1.70	1	1	
15.9.71			6
26.9.71			1
26.4.72	2	4	
14.6.72	2	4	
27.6.72	1	3	
18.5.72	1		
20.10.72	7	3	
10.5.72	5	4	
25.1.73	21	22	
	49	50	14

								Breeding Season			
45	-	-	6	10	16	4	-	(7)	13	5 +(8)	-
J	F	M	A	M	J	J	A	S	0	N	D

TABLE 6 : 2 Distribution of samples of stomach and crop contents per date, and month. Data in brackets in the per month table refer to the pulli.

It can be seen that the results produced by the two methods differ considerably. This is a result of the possible inaccuracies of the numeric method. Two samples boost the number of insect items by over a third. The samples contained counts of ca. 100 pieces of insect mouthparts in each. If these two records are deleted, the relative numerical method percentages become:-

54.1 (553), 37.1 (379) and 8.8 (90)

The high numerical figure for insects is also due to an apparent tendency for the insects particularly the coleopterans to be fragmented, whereas most of the vegetable items remained intact. An exception was the fragmentation of <u>Zeya mays</u>. Skead (1947) noted the tendency for the birds to use their beaks like knives and to gnaw at maize grains. In the numeric method used above, there would also tend to be a bias in favour of insects. In the volumetric analysis, the bias will favour vegetable matter since the soft parts and soft bodies of insects will not be evident. Certain vegetable foods such as nectar would also not be detectable in stomach contents. The same would apply to fruit juices of for example, the grape. A further point that is likely to affect the result is the distribution of samples through the year. One of the largest samples was taken in January (see Table 6 : 2) which being in the dry season is likely to be a time of insect paucity. Possible fluctuations of this sort will be investigated further (see below).

The conclusion from the above is that the Cape Weaver is predominantly a vegetarian in the non-breeding season.

	Volumetric Analysis			Numerical Analysis		
Food Item	Volume Present ml.	% Vol. of Vegetable Diet	% Vol. of Total Diet	Number Present	% No. of Vegetable Diet	% No. of Total Diet
Hordeum vulgare	20.5	33.85	23.79	365	23.44	12.0
Miscellaneous Veg.	11.3	18.66	13.11	-	-	-
Acacia cyclops/arils	9.45	15.60	10.96	120	7.70	3.94
Zeya mays	5.85	9.66	6.78	246	15.79	8.08
Ficus spp.	5.75	9.49	6.67	524	33.65	17.23
Unidentified veg.	2.9	4.78	3.36	141	9.05	4.63
Ehrharta spp.	2.1	3.46	2.43	78	5.0	2.56
Translucent seeds	1.0	1.65	1.16	10	0.64	0.32
Brown oval seeds	0.9	1.48	1.04	40	2.56	1.31
A. cyclops seeds	.7	1.15	0.81	15	.96	.49
Grass seed	.1	0.16	0.11	18	1.15	.59

Continued/......

		% Vol. of Insect Diet			% No. of Insect Diet	
Food Item	Volume Present ml.	% Vol. of Vegetable Diet	% Vol of Total Diet	Number Present	% No. of Vegetable Diet	% No. of Total Diet
Lepidoptera Ad/L	8.3	32.39	9.63	109	7.34	3.58
Coleoptera Ad/L	5.82	22.71	6.75	620	41.77	20.38
Insect Mouthparts	5.65	22.05	6.55	710	47.84	23.34
Insect caterpillar	2.4	9.36	2.78	6	0.40	0.19
Tabanidae	1.0	3.90	1.16	6	0.4	0.19
Diptera unsp.	1.0	3.90	1.16	8	0.53	0.26
Insect unident.	0.55	2.14	0.63	11	0.74	0.36
Scarabidae	0.3	1.17	0.34	4	0.26	0.13
Orthoptera	0.3	1.17	0.34	4	0.26	0.13
Isoptera	0.2	0.78	0.23	4	0.26	0.13
Hymenoptera	0.1	0.39	0.11	2	0.13	0.06

TABLE 6 : 3. Dietary Composition showing the relative importance of different items in the total diet or in the insect/vegetarian class. The data given summarises the detailed analysis of the stomachs/crops of all full-grown birds in <u>and</u> out of the breeding season.

However, it seems likely that insects still constitute at least a third of the diet and therefore it is justifiably classified as a mixed feeder. The fact that it is mainly vegetarian agrees well with the suggested factors which influence the incidence of polygamy. This point is discussed elsewhere.

6.6 Dietary Composition - Relative Importance

An assessment was also made of the relative importance of the different items in the diet. The data for all the stomachs/ crops of full-grown birds which were analysed in detail including those taken during the breeding season (hence the larger figures) are given in Table 6 : 3. The chick data are not included.

The importance of the different items is expressed in the table as a percentage first of the vegetable and insect diet separately and then as a percentage of the total diet, by volume and by number. Other items are excluded as being of no food value the eggshell being consumed by chicks only.

According to the figures, it seems that the Cape Weavers diet is not very varied. Three items alone constitute 68% by volume of the vegetable diet and four items, 86% by volume of the insect diet. But within both these percentages, there are general items, namely "miscellaneous vegetable" and "insect mouthparts", both of which could cover a large number of species. Since none of the insect items is identified to species, a number of different species could be involved. Also the food found in the analysed stomachs does not cover the complete range shown in Table 6 : 1.

The extent to which the Cape Weaver exploits exotic plant food is also evident from the figures, with three out of the top four vegetable items being exotic. The use made by the Cape Weaver of Acacia cyclops arils has been recorded elsewhere (Middlemiss 1960). According to Roux (1961), A.cyclops was systematically planted throughout the S. W. Cape from about 1845 onwards. Siegfried (1969) remarks that settled agriculture in the area only got under way at the turn of the 19th century. It would therefore seem likely that the two grains and A. cyclops have only been available for the last 150 years. Certainly the figures show that full use is made of them today and are another example of the involvement of the Cape Weaver with man-made influences on the environment. It may be that this involvement is partly responsible for the apparent lack of variety in the species diet.

Another means of assessing the importance of different items in the diet is by their occurrence in all the samples. The percentage occurrence of those items occurring in 10% or more of the 103 stomachs analysed in detail is given in Table 6 : 4. This gives a slightly different picture to that of Table 6 : 3. Particularly noticeable is the high incidence of the coleopteran larvae/adults, occurring in 32% of all samples. In both tables, it is felt that the Ficus spp. seeds figure disproportionately large, since this food item only appeared in almost all the stomachs taken in the large sample of 25.1.73 and in no other sampling date. Table 6 : 4 does show that insects form a significant proportion of the diet in terms of frequency of occurrence, even if it is less obvious in terms of volume and number.

Food Item	% Occurrence
Miscellaneous vegetable items	41.7
Coleopteran larva/adults	32.0
Barley grain	31.1
Insect mouthparts	28.2
Ficus seeds	21.3
Acacia cyclops arils	12.6
Lepidopteran larva/adults	11.6
Ehrharta grass seeds	10.7
Zeya mays grain	10.7

Table 6 : 4 Importance of food items as a percentage occurrence in all full-grown bird stomachs.

6.7 Seasonal Variation in Diet

The variation in the relative proportion of insects to vegetable matter was estimated by three different methods. First the 119 stomachs which were examined superficially were scored for insect or vegetable content. Stomachs containing only one or other type were given four points, equal proportions two each and intermediate levels, 3 : 1. The scores for the samples per month are given in Table 6 : 5. It is interesting to note that for all the samples the percentage vegetable matter is 59.8% which compares closely with the equivalent figure (excluding other items) of 64% for the detailed analyses. This indicates that the superficial assessment may at least approximate to reality.

The change in percentage of vegetable items during the year from Table 6 : 5 shows considerable fluctuation. Some of this may be due to sample size e.g. 0% in April, 57% in February. Nevertheless the percentage vegetable matter is surprisingly high in October, which is mid-breeding season, and also in spring when a switch to an insect diet might be expected.

The second and third methods derive from the detailed stomach analyses and are presented in Table 6 : 6.
The percentage of vegetable items per month from the volume and number of the food items are given. To make comparison of the three sets of percentages easier, they are all plotted out in Fig. 6 : 7. Although there is an extra difference in the value for April (0% and 96%) the remaining figures are more or less comparable.

Date	Sample Size	Insects	Vegetable	% Vegetable
Jan.	15	-	64	100
Feb.	4	6	8	57
Mar.	10	6	14	70
Apr.	2	8	-	0
June	6	20	4	17
July	7	8	20	71
Aug.	21	27	57	68
Sept.	27	61	42	41
Oct.	23	26	67	72
Nov.	10	30	10	25
	Total	192	286	
	%	40.2	59.8	

TABLE 6 : 5 Relative proportion of insects/vegetable matter found by superficial examination of 119 stomachs. For further explanation see text. Data for all years has been lumped.

Date	Sample Size	Vol. of Insect Items	No. of Insect Items	Vol. of Veg. Items	No. of Veg. Items	% Vol. Veg.	% No. Veg.
Jan.	45	7.3	831	14.4	996	66.35	54.51
Apr.	6	0.1	4	4.1	72	97.61	94.73
May	10	1.0	50	0.3	17	23.07	25.37
June	16	2.97	146	16.3	205	84.58	58.40
July	4	1.0	3	2.3	19	69.69	86.36
Oct.	13	4.13	100	5.8	94	58.40	48.45
Nov.	5	5.1	40	1.4	21	21.53	34.42
	99						
Undated	4						
	103						

TABLE 6 : 6 Relative percentages of insect : vegetable items per month, from stomachs analysed in detail. Data for all years has been lumped.

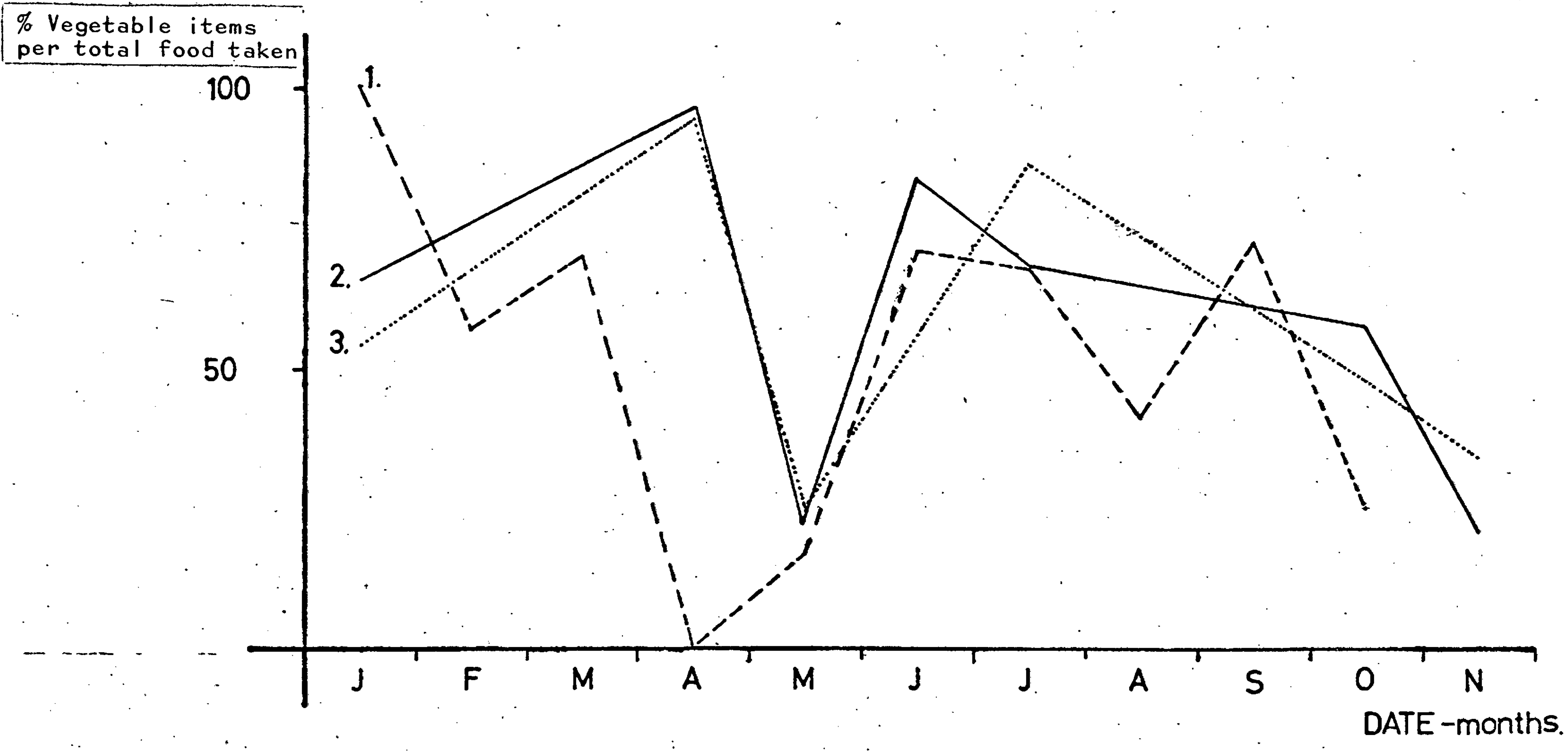


FIG.6:7 - Seasonal change in diet in percentage of vegetable items per total food taken as assessed by three methods:- 1. From 119 superficially analysed stomach contents. 2. From 103 detailed volumetric analyses. 3. From 103 detailed numeric analyses.

It is presumed that there are two factors influencing these figures i) the availability of food ii) the selection of food. Generally speaking a bird will eat the food in its diet which is the most readily available. But at certain times of the year, there will be a tendency to select certain sorts of food which may not necessarily be the most available. The apparent desirability of feeding insects to chicks is an obvious example.

The figures seem to show that vegetable items are important in the Cape Weaver's diet in the wet and cold (See Section 4) winter months, June to August. Only in August does this dependence become reduced. August is generally the start of the breeding season though this can vary by as much as a month in any given year. From August onwards there is an apparent fall off in the proportion of vegetable matter, reaching a minimum of about 30% in November. If this reduction represents the combined effects of selection and availability, it is interesting to note that the apparent insect maximum (other than April) falls at a time when the majority of the chicks are fledging. By January, the vegetable proportion is again high. The point that is most difficult to explain is the May figure where all three percentages are low. Whether this is due to a sudden increase in insect availability after the first autumnal rains is difficult to say. There may be a flush of insects or possibly an increase in insect activity making them more readily available, combined with a reduced availability of seeds through germination. The remarkable point is that these fluctuations closely follow those found by Siegfried (1969) (See Section 4. 15 and Fig 4 : 19). Siegfried found a peak of insect availability in April and May and a second lesser peak in November exactly as was found from

this study of the Cape Weaver stomachs (reflecting availability/ selection). As stated in Section 4 : 15, this seemed surprising and at that stage was thought to be a product of the sampling method. However, the correlation is close enough to indicate that this is a general situation. In terms of Kemp's (1969) study, an increase of availability so soon after rain seems unlikely unless as suggested here an increased insect activity increases availability through visibility. In terms of significance to the Cape Weaver, the April flush of insects may have importance in returning the protein condition of the bird back to normal after the possible debilitating effects of moult. But without further investigation, this point is speculative. The November peak as mentioned, would fit in well with Lack's theory that the hatching and fledging of the chicks and their survival is the most important single factor governing the timing of the breeding season.
It should be noted, too, that the April/May flush coincides with the increase in testis size of the adult male and may be involved with this (See Fig 4 : 11).

6.8 Sex Differences in Diet

Since the Cape Weaver is a physically dimorphic species (See Section 3), the sexes might be expected to have different diets at least to some degree. With a view to assessing any differences, a particularly large sample of birds was taken on one day in the non-breeding season. One sample on one day is not likely to be conclusive in respect of any differences. But it is likely to be a better indication than a number of small samples scattered throughout the year, when day-to-day differences may be misleading. The total sample taken on 25.1.73 was 43 birds or 21 males and 22 females.

For analysis purposes, the sample sizes were regarded as equal for each size. The stomach/crop contents were analysed volumetrically and numerically as before. The relative importance of each item was given as a percentage of the total food present in each sex separately. It should be pointed out that all age groups were included in each sex group.

The results are given in Table 6 : 8. The first point which emerges is that the range of food consumed by males and females is virtually identical with only three items being eaten by females but not by males. Two of these items are insignificant, but one, the Lepidoptera, at 12% by volume of the total female diet seems an important difference. Overall there is also a difference in the proportion of insect and vegetable items eaten. In males between 80.7% (volumetric) and 63.9% (numeric) of the food is vegetable. In females the figures are 58.5% - 38%. The difference is about 20% in each case.

In the actual items eaten, there is also a difference of emphasis. The females on the sampling day apparently eat twice as many coleopterans than the males and half the number of figs. The males eat twice as many insect mouthparts (=insects) than the females. In the less heavily eaten items, the chance factors are likely to be higher and the difference not real. For marginal differences, barley appears to be eaten slightly more by males than females.

The detailed analysis data for the remaining 60 stomachs collected over ten months and several different years was also examined for sex diet differences. The sample by chance consists of 28 males and 28 females, but the wide

	Males				Females			
	Vol. ml.	% Total Vol.	Number	% Total No.	Vol ml.	% Total Vol.	Number	% Total No.
Ficus spp.	3.15	26.9	333	43.5	1.7	18.2	185	22.2
Hordeum vulgare	3.0	25.6	62	8.1	2.0	21.5	22	2.6
Coleopteran elytran	1.4	11.96	158	20.6	.5	5.4	64	7.7
Insect Mouthpart	1.85	15.8	118	15.4	3.25	34.9	437	52.5
Miscellanous Veg.	1.8	15.4	-	-	.3	3.2	-	-
Zeya mays	1.1	9.4	77	10.1	.55	5.9	62	7.4
Acacia cyclops	0.2	1.7	10	1.3	.4	4.3	21	2.5
Lepidoptera	-	-	-	-	1.1	11.8	14	1.7
Oval Brown Seeds	-	-	-	-	.4	4.3	20	2.4
Ehrharta seeds	0.2	1.7	7	0.9	.1	1.1	4	.5
Unidentified Veg.	-	-	-	-	.05	-	3	.4

TABLE 6 : 8 Comparison of the Diet of Males and Females from specimens taken on 25.1.73 only

range of dates is likely to obscure any differences in diet. Nevertheless the data as presented in Table 6 : 9 shows several similarities to that of Table 6 : 8. The range of diet again shows that the male eats a smaller range of food than the female. There are nine items which are not shared, seven of which were found in female stomachs exclusively and two only in male ones. None of these items appears to be important in the diet except for Zeya mays reaching 10% in the females and zero in the males. The relative proportions of insect to vegetable matter are 72.2% and 42.7% for males and 64.5% and 43% for females. It seems unlikely that these differences are significant. In the relative proportion of different items, barley again appears to be eaten three times more by males than females. The only other item in which there is a marked difference is "unidentified vegetable matter" where the females are recorded as eating proportionately ten times more than males. But this category is too vague to be of any significance.

In conclusion, even within the limitations of the methods of investigation, the evidence particularly in Table 6 : 8 does seem to indicate a difference in proportional diet between male and female Cape Weavers. This finding is important to the social system in the species and possible implications are discussed in a subsequent section.

6.9 Diet of the Cape Weaver Chick

The diet of the chicks was assessed by the same methods described above (See Section 6.2). 15 stomachs were analysed in detail and a further 42 given superficial scrutiny. All the stomachs were collected in 1970 and 1971 on four different dates.

	Males				Females			
	Vol. ml.	% total vol.	Number	% Total No.	Vol. ml.	% total vol.	Number	% total no.
Ficus spp	-	-	-	-	-	-	-	-
Hordeum vulgare	11.3	39.9	167	28.0	4.3	13.3	60	8.1
Coleoptera	1.2	4.2	78	13.1	0.7	2.2	52	7.0
Insect Mouthparts	1.7	6.0	203	34.0	3.3	10.2	264	35.8
Misc. veg.	4.1	14.5	-	-	4.9	15.1	-	-
Zeya mays	-	-	-	-	2.9	8.9	77	10.4
Acacia cyclops	4.6	16.4	40	6.7	3.9	12.0	34	4.6
Lepidoptera	2.8	9.9	30	5.0	2.9	8.9	33	4.5
Oval Brown Seeds	-	-	-	-	-	-	-	-
Ehrharta seeds	-	-	-	-	0.7	2.2	15	2.0
Unidentified veg.	0.4	1.41	33	5.5	2.5	7.7	105	14.2
Translucent seeds	-	-	-	-	1.0	3.1	10	1.3
A. cyclops seeds	-	-	-	-	0.7	2.2	15	2.0
Grass seed	.05	-	15	2.5	.05	-	3	0.4
Insect larvae	0.9	3.2	2	.3	1.5	4.6	4	.5
Tabanidae	0.1	.3	1	.2	0.4	1.2	5	.7

Continued/....

Scarabidae	-	-	-	-	0.3	0.9	4	0.5
Diptera	-	-	-	-	0.3	0.9	1	.1
Unid. Insect	0.5	1.7	4	.7	.05	.1	7	.9
Hymenoptera	-	-	-	-	1.1	3.4	5	.7
Orthoptera	.03	.1	4	.7	-	-	-	-
Isoptera	.2	.1	4	.7	-	-	-	-
Coccinellidae								

TABLE 6 : 9 Comparison of diet of males and females from specimens collected throughout the year.

The results of the small sample of 15 are given in Table 6 : 10. If this is compared with previous data on adult stomachs, the dominance of insects as part of the food can at once be seen.

Vegetable matter makes up only 29% (volumetric) or 22.4% (numeric). Furthermore the category "miscellaneous vegetable matter" being identifiable and generally amorphous may well derive from the gut content of insects eaten particularly caterpillars. In which case the percentage of vegetable matter would decrease even further. Table 6 : 10 also shows the dominance of larvae in the diet where they constitute between 46% and 35% of the total diet. Eggshell and grit have not been included as nutritional items in calculating the different food proportions. The dietary importance of egg-shell as a calcium source is self-evident from the figures given. In the detailed analyses, eggshell occurred in nine out of 15 stomachs, in the superficial, in 12/42. One stomach contained only eggshell.

Another interesting point coming out of this brief study is the suggestion that the food fed to chicks changes during the breeding season. The data are however very scanty. Of 18 stomachs collected on 15.9.71, only 8 (44%) contained any grain or identifiable vegetable matter. Of four collected on 26.10.71 three (75%) contained grain or seeds. The difference in diet was also observed in the field where notes were made on birds bringing in beak fulls of obviously vegetable matter. Such changes in diet have been observed in other passerines in South Africa such as the Karoo Prinia _Prinia maculosa_ (Rowan and Broekhuysen). (1962). In Europe, changes have been recorded in the House Sparrow _Passer domesticus_ (Seel 1970) and the Great Tit _Parus major_ (Royama 1966). In these species

Food Item	Volume ml.	Number	% Total Volume	% Total Number
Lepidopteran larva	3.1	43	26.8	30.1
Insect larvae	2.3	7	19.9	4.9
Coccirellidae	1.0	5	8.7	3.5
Orthoptera	0.2	6	1.7	4.2
Carabidae	0.5	1	4.3	0.7
Unidentified Insects	0.6	8	5.2	5.6
Insect Mouthparts	0.4	37	3.5	25.9
Coleoptera unsp.	0.1	4	0.9	2.8
Misc. veg.	1.75	-	15.1	-
V/Q/T Unsp. Veg.	0.7	16	6.1	11.2
Hordeum vulgare	0.9	16	7.8	11.2
Eggshell	2.2	102	-	-
Grit	3.95	93	-	-

TABLE 6 : 10 Food of Cape Weaver chicks showing their relative dietary importance per volume and by number.

the type of food insect or vegetable, tends to remain the same but the actual items change. For example, dipteran flies are taken early in the sparrow's breeding season and become replaced by aphids later on (Seel loc. cit.). The sparrow was found to take a larger amount of grain later in the season, but non-insect food was still a significant proportion of the diet right through the season.

If the appearance of seed in the Cape Weaver chick's diet at this stage is real, it is surprising in view of the evidence from the analyses of the stomachs of full-grown birds. These showed an increase in the proportion of insects in October and November. This finding was supported by other studies (Siegfried 1969). Since the proportion of vegetable matter is predominant in full-grown birds early in the breeding season, this presumably means that parent-birds are actively selecting insect foods to feed their chicks. The occurrence of a peak of insects in the diet in October/November should mean that insects are more available during this period. However, it seems likely that by this stage the availability of larvae will be dropping off. The availability of grain on the other hand should be increasing. Grain crops are harvested from late October onwards. The decrease in easily visible insect larvae and the increase in grain availability may combine to give the impression recorded.

It seems therefore that the Cape Weaver and probably other polygynous species do not have any different mortality pressures from thos of other monogamous passeriens, especially those that are dimorphic or where the male does not breed until its second year. As stated in the introduction, Lack stated that if there was the least chance of young polygnous males obtaining mates, then they would still attempt to breed unless it was dangerous for them to do so. This suggests that because males do not attempt to breed, it is therefore dangerous. The danger aspect has been dealt with, but there is still the implication that males do not attempt to breed in their first season after fledging. In the Cape Weaver, this is certainly <u>not</u> so.

Young males are continually arriving throughout the day, moving through the colony, inspecting nests etcetera. But they are seldom given the chance to remain in the colony for any length of time. Almost always they are chased by resident territory-holding males from the moment they land in the colony. Towards the end of the season, the aggression of the males either decreases or the aggression of young males increases or both. Some young males manage to set up territories and build nests on the edge of the colony. None was observed even to build a nest anywhere but on the edge of the colony and none was observed even to attract a mate, although attempts were made to do so. On one or two occasions young males were observed to attempt to copulate with a female giving the precopulatory display to a resident adult male (see below Section 11). It was promptly chased from the scene. All these observations point to the fact that young male Cape Weavers <u>are</u> repeatedly trying to obtain mates in their first season.

This, of course, implies that it is not dangerous for them to do so which supports the general contentions given above. If this is the case then we are still faced with the problem of how deferred maturity evolved in the Cape Weaver and in polygynous species as a whole.

It is suggested that there are two possible reasons One is that the level of predation under which deferred maturity was evolved was far higher than it is today and so at the time when the plumage was evolved, it was dangerous for young males to have bright plumage and be inexperienced. More positive and more likely is that the one main difference between polygynous species and monogamous ones is, obviously, the mating system and as a consequence the competition for mates. I therefore agree with the first part of Lack's idea that it is the intensity of competition which has been the main selection pressure evolving deferred maturity. Even if the young male did attain full plumage he would not be able to compete against the marginally larger and heavier, and more experienced adult male (See Section 3). However unless there is some additional factor, one must accept that the young male would be more competitive if he did have full plumage. It is suggested that with such a premium on experience, it is to the young male's advantage to be able to visit regularly the colony and to attempt to build nests and defend a territory. Collias and Collias (1964, 1972) have shown in aviary studies how vital experience with nest building is for the young male. Birds deprived of nest-material in their first year often totally failed to build successful nests when provided with nest material later on.

If the young male Cape Weaver had full breeding plumage, it is suggested that this is such an aggression releaser, that he would at no stage be allowed to remain in the colony at all even towards the end of the season. By having a less aggressive subadult plumage, he can occasionally enter the colony and practise making nesta at least to some extent. This experience will be to his advantage in the following season. It should be pointed out that young males are also known to make "practice" nests well away from colonies. My impression was that these nests were made earlier in the season, and young males tended to move into the colonies later in the season, perhaps when adult male aggression is dropping off. This suggests that there is more to practice than just making nests; defence of territory and participation in the colony if only on the periphery, may also be important.

Since deferred maturity is known to occur, it is interesting to see the theoretical effect that this would have on sex ratio at a breeding colony. Given that males breed at about two years old and females at one year old, a scheme has been drawn up in Table 8 : 4, based on an original population of 50 adult males and 50 adult females. As can be seen, the system stabilises at a ratio of 3 : 1 in favour of females. The degree of polygyny present in the colony will be discussed further in Section 13 below.

6.10 Feeding Rates

Some attention was given to feeding rates of chicks at different times of the season especially with reference to the part played in feeding by the two sexes. According to Crook (1964), the task of raising the chicks in polygynous graminivorous weavers falls totally on the female. At the outset it was also intended to monitor possible feeding rate changes during the season to test whether early and late broods receive less food than chicks raised at the breeding peak. But there are many variables affecting feeding rates (see Moreau 1947, Royama, Seel (loci cit)) The more important are :- the size of the food being brought - the larger the food the more infrequent the feeding rate, but the quantity of food being brought need not be affected; the brood size - larger broods tend to be fed more often though not in proportion to their size - (Royama loc. cit). Although not mentioned by the above authors, there is also likely to be a diurnal variation, with feeding rates dropping off during the middle of the day. Such diurnal variation was found in the Orange-breasted Sunbird Anthobaphes violacea (Broekhuysen 1963). Finally the age of the brood affects the feeding rate which often does not reach its peak until four or five days after hatching. With all these variables to be taken into account, it would be difficult to establish seasonal changes in feeding rates. The following information was, however, obtained.

Observations on 375 feedings of Cape Weaver chicks were recorded during the study period. The time elapsed between feedings at one nest was the measure used to quantify the activity. The normal procedure followed was for several different nests to be observed simultaneously and for the time of each feeding, the food delivered if visible and the sex of the parent to be recorded. Mean feeding frequencies at different nests varied from once every 2.7 minutes (20 obs.) to once every 16.3 minutes (3 obs.). When all the data are lumped, no obvious relationship to brood size was found, the means being 8.8 mins. (B1), 7.8 (B2) and 9.3 (B3) between feedings. However, as explained, this is not surprising in view of the number of possible variables and the lack of standardisation in the observations.

Exactly 100 observations of male Cape Weavers feeding chicks were made. Of these 99 were recorded in November or later at the very end of the breeding season. One record on 25th September was also recorded.
All other observations of feeding involved the female only. These include the 300 actually timed and many more which were never specifically recorded. It seems therefore that the feeding of the chicks by the male is, almost without exception, an end-of-season phenomenon. The birds involved were all adult males in full breeding dress except for one male going into eclipse plumage which was observed feeding a chick. There were several males involved in the chick feeding so the behaviour was a general and not an exceptional one. It was observed both at Ellions colony and at the Tygerberg colony. Although in any given territory, there might be more than one nest with chicks, generally the male fed the chicks at one nest only. One male was once observed feeding chicks at two nests in his territory.

Usually the chicks were near fledging and at a stage where their begging calls were very loud and audible at about 100 m range. It is interesting to note that feeding by the male has been recorded in other polygynous species such as the Redwing Agelaius phoeniceus (Haigh 1968) and in the Bobolink Dolichonyx oryzivorus. (Martin 1971).
In the latter the male tended to help feed only the chicks of the first brood.

Table 6 : 11 gives the ratio of chick feeding visits by males and females at different nests. It can be seen that the ratio varies considerably but in many cases the contribution of the male is as large if not larger than the female's. In these records it was noticed that the male tended to feed the chicks in bursts.

Particularly loud begging by the chicks would appear to stimulate the male often into approaching the nest and looking in.
The male would then feed the chicks a number of times in rapid succession. The female would meanwhile continue feeding and both parents would often arrive simultaneously at the nest carrying food. The burst would last perhaps 30 minutes during which time up to ten or more feeding trips would be made by the male. He would then stop feeding while the female carried on.

The exact controlling mechanism of this behaviour presents problems. Why does the male not assist in feeding the chicks throughout the season? If it serves a function at the end of the season, why does it not do so earlier on? In related monogamous species such as Passer domesticus Seel (1970) found that the male took a considerable part in the feeding of

Date	Nest Number	No. of Male visits	No. of Female visits
4.11.70	N 13	11	10
	N 81	5	13
10.11.70	N 96	1	12
	N 127	4	2
	N 13	1	7
13.11.70	N 142	6	4
	N 127	1	10
19.11.69	-	19	14
		9	0
20.11.69	N 66	18	0

TABLE 6 : 11 : Ratio of chick feeding visits by Males and Females

every brood regardless of the period in the breeding season. The male sparrow tended to take a larger share at the beginning of each brood and a smaller share at the end. In fact it is general that the male plays a very important part in raising the offspring of monogamous passerines. Obviously the non-activity of the Cape Weaver male in the early part of the season is directly related to the polygamous habit. Once one female is settled with her clutch, the time-consuming activity of building the next nest and attracting the next female begins. At the end of the season, this successive activity drops off. It is most likely that the special effect of polygyny is that it overrides the tendency of the male to feed the chicks. This tendency will however remain, but be latent. Towards the end of the season, the overriding effect will be reduced, allowing the latent behaviour to come to the surface. At the same time, the late season feeding behaviour of the male will have a definite adaptive value at a time when there are decreasing food supplies. This again brings back the problem of whether there is or is not a genuine second peak of availability of insects in November. The impression given is that although there may be an increase in certain sorts of insects, particularly imagos, there is a decrease in the availability of that main chick food, insect caterpillars, in November. What causes the male to respond to begging calls of his chicks at the end of the season but not at the beginning or middle is unknown. It is possible that the relative sound level is greater at this time as the general noise of the colony dies down, since by November the amount of displaying by adult males has dropped off. It is even possible that the chicks at the end of the season are hungrier and therefore create more noise. The result is presumably the enhanced survival of end of season broods to the advantage of the male. A third possibility is that the existence of this behaviour in the Cape Weaver male is related to its "intermediate" status as an insectivore/graminivore. The suggestion would be that the species has not developed its polygnous habit fully and therefore the task of raising the chicks is not quite entirely left to the female. This explanation depends on the validity of other observations of other polygynous weavers. It took some very close observation of the Cape Weaver before the extent of the above behaviour was realised. It is suggested therefore that similar examination of other polygnous weaver species will probably reveal similar adaptations. In every other way the Cape Weaver seems completely adapted to a polygnous mating system.

6.11 Weight Fluctuations

Another method of assessing food availability is by its apparent effects on the weight and body condition of the species. Often cause and effect difficulties make it hard to judge whether increased weight reflects increased food availability or increased feeding effort and vice-versa. But if such changes are combined with other factors, such as change of diet, then the picture is clearer.

Weight measurements were taken from birds caught in the field in the course of normal bird-ringing and specimen-taking studies. Weight was recorded to the nearest gram. Birds were aged and sexed where possible. The great majority of birds were caught coming into roost and were weighed within an hour of being caught. Most of the data were collected at the Tygerberg colony but some were collected at other roosts in the SW Cape. The total sample size was 3439 spread over the four and a half years of study.

The results for the 1970-72 period when sampling was more complete, are summarised in Table 6 : 12 and shown graphically in Figs. 6 : 13, 6 : 14 and 6 : 15. Only data on birds the sex of which could be assessed reasonably exactly were included in the summary. All doubtful records were excluded (See Section 3).

The first point emerging is that with very few exceptions, the mean weight of the different age classes vary very little throughout the year. The data for 1972 were the most complete and had reasonable sample sizes. They show that the difference between maximum and minimum means was from three grams (females) to five grams (subadult males). This represents less that a ± 5% fluctuation around the mean body weights of the age/sex classes. The actual range in weight of these classes has been discussed in Section 3.

Despite the small size of the fluctuations, the large size of the samples are sufficient to show that many of these changes are statistically significant. Examination of, for example, the fluctuations of the mean weights of Adult/Eclipse males in 1972 shows a variation of ± 2 gms. about the mean weight of 50 g. The highest mean is recorded in August, the lowest in December. Testing these changes by pairs of mouths, it was found that the January/February and February/March change was significant ($p < .01$; $t = 2.98$ and 3.01 respectively).

Age/Sex Class	J	F	M	A	M	J	J	A	S	O	N	D	Year	Samp Size
Ad/Eclipse M	49(14)	51(24)	49(26)	50(23)	49(17)	51(22)	51(10)	52(1)	51(4)	50(4)	-	48(3)		148
Sub ad. M	48(15)	49(12)	47(6)	46(2)	49(2)	50(12)	51(3)	51(13)	49(41)	49(18)	-	48(3)		127
1 Y M	47(27)	47(70)	46(75)	48(44)	48(48)	49(36)	50(40)	49(7)	49(17)	48(23)	-	46(9)	1972	396
F	40(34)	40(66)	40(64)	41(60)	40(77)	41(110)	42(48)	42(15)	41(14)	43(13)	-	40(23)		524
1 Y F	38(11)	41(1)	-	39(1)	-	42(7)	41(1)	-	-	41(25)	38(1)	-		47
Ad/Eclipse M	-	-	-	-	54(21)	49(6)	50(13)	-	53(5)	-	50(3)	50(5)		53
Subadult M	-	-	-	-	51(3)	50(17)	49(38)	48(7)	51(7)	-	48(18)	50(11)		101
1 Y M	44(4)	-	-	-	54(10)	47(4)	47(23)	-	51(1)	-	48(25)	46(37)	1971	104
F	41(4)	-	-	-	43(10)	41(25)	41(74)	42(13)	43(3)	-	40(35)	40(20)		184
1 Y F	37(5)	-	-	-	-	40(1)	35(1)	-	-	-	38(2)	40(28)		37
Ad/Eclipse M	40(9)	46(2)	49(9)	51(1)	47(2)	49(2)	50(32)	51(24)	-	51(15)	50(12)	49(2)		110
Subadult M	39(7)	50(1)	47(7)	-	49(1)	-	48(125)	49(70)	-	47(10)	49(9)	47(3)		223
1 Y M	43(5)	52(1)	-	-	-	38(1)	45(2)	42(1)	-	46(6)	47(17)	44(2)	1970	36
F	33(33)	40(1)	38(13)	38(1)	36(1)	42(7)	41(134)	41(61)	-	43(23)	40(37)	39(7)		318
1 Y F	32(1)	-	-	-	-	-	-	-	-	-	-	38(2)		3

TOTAL: 2421

Summer | Autumn | Winter | Spring | Summer

Breeding Season

TABLE 6 : 12 The mean weights per age/sex group per month for the years 1970/1972. All weights in grams.

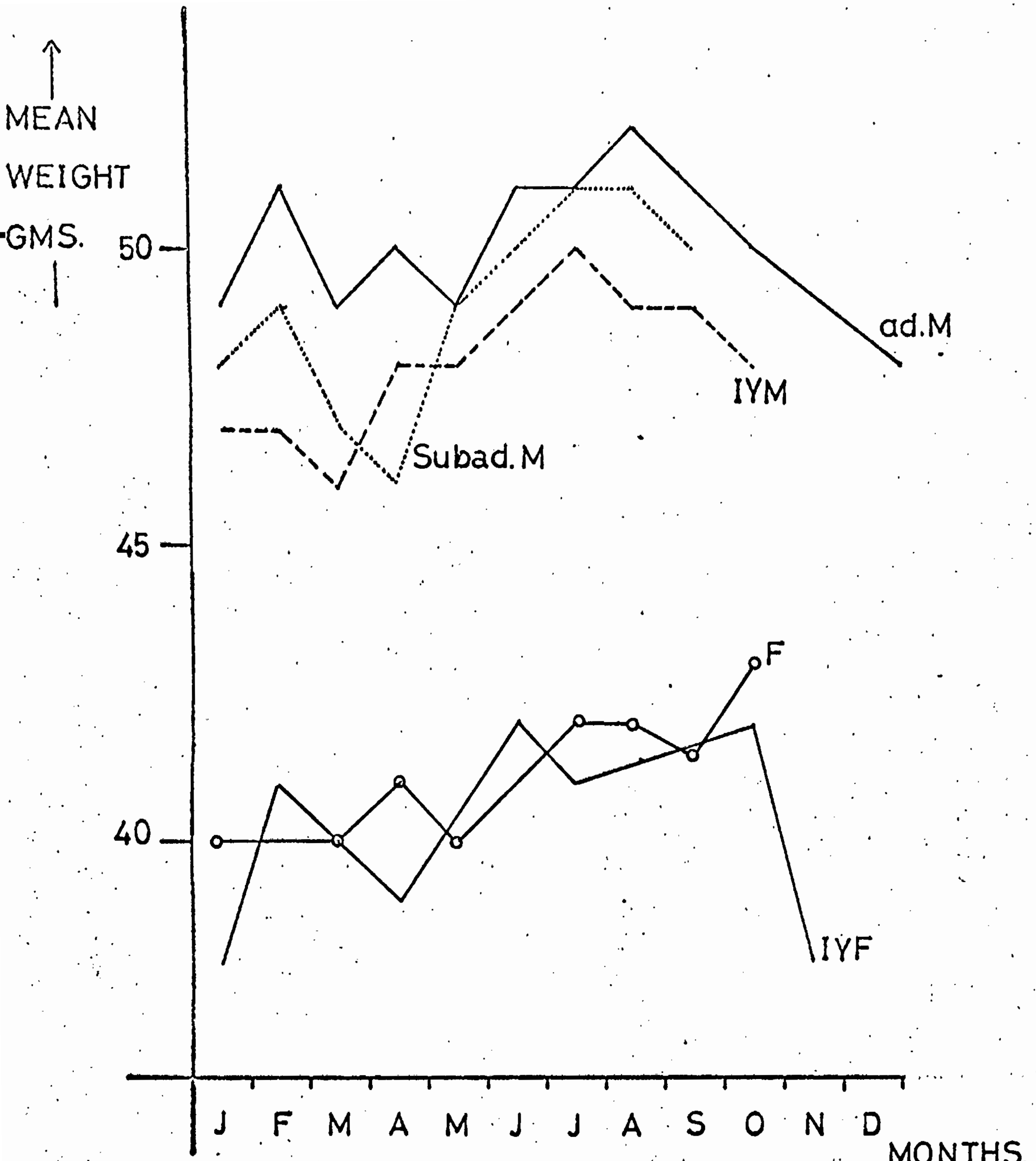


FIG.6:13 Weight Fluctuations per Age/Sex Groups in 1972.

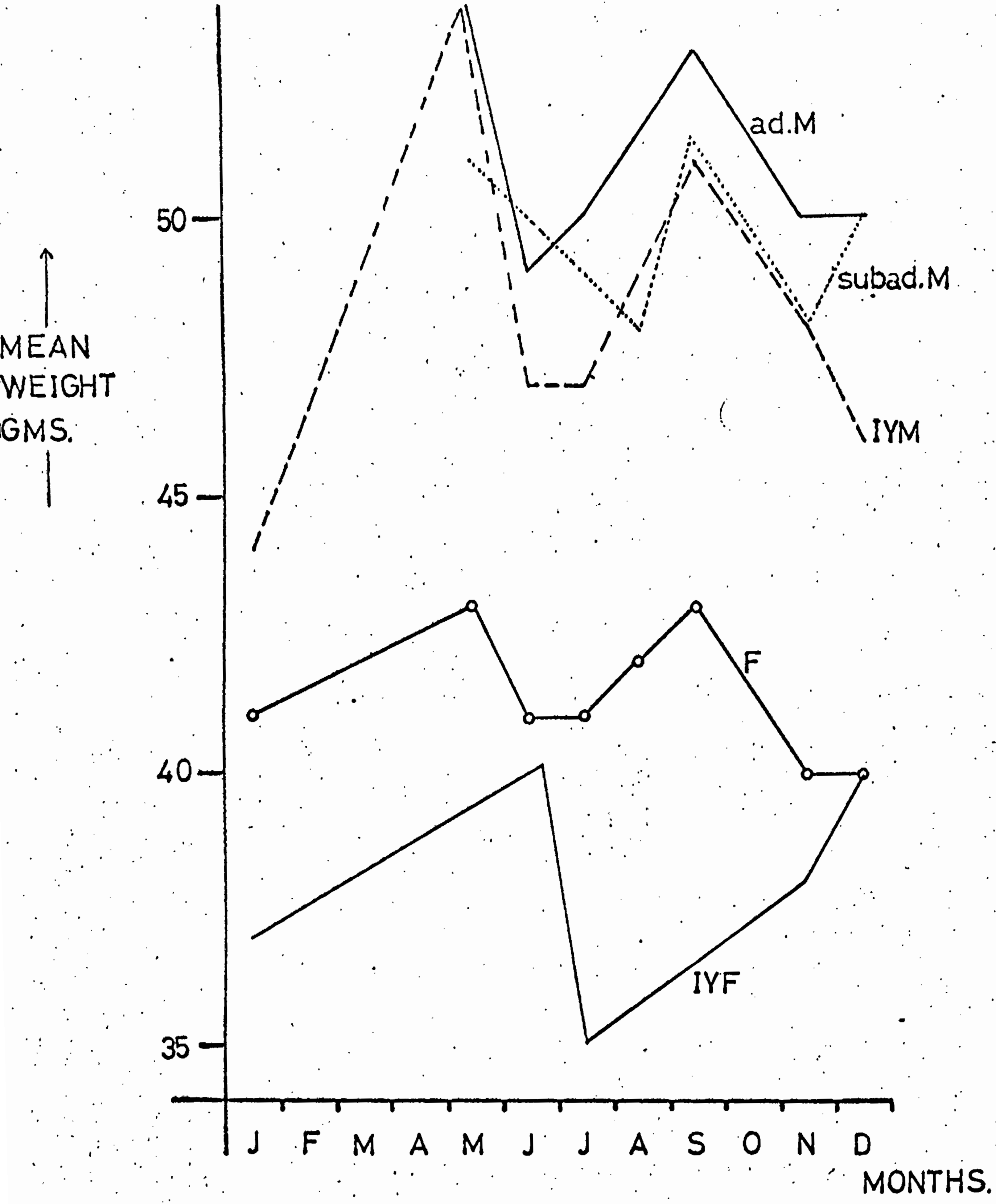


FIG. 6:14 - Weight Fluctuations for Age/Sex Classes in 1971.

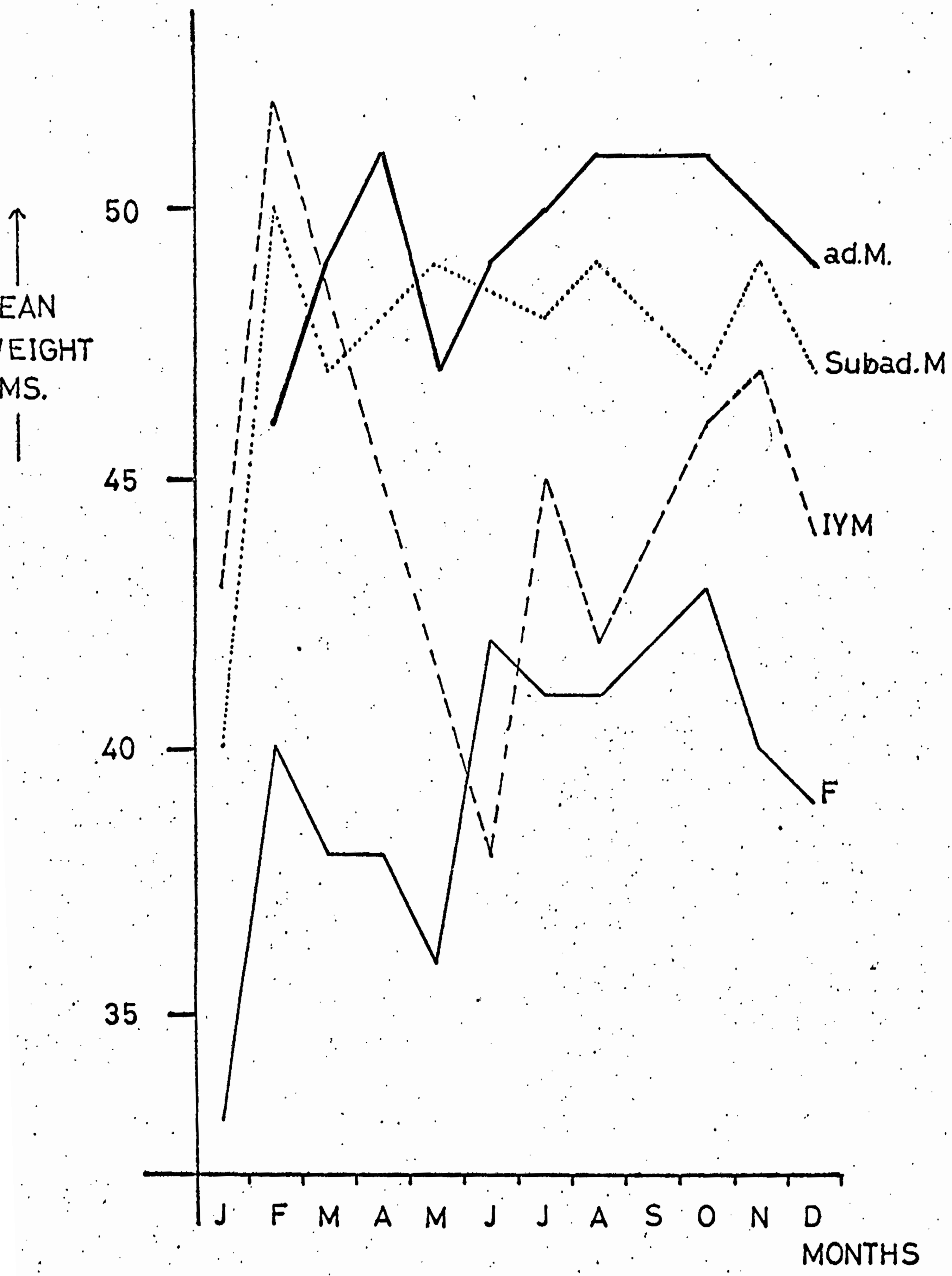


Table.6:15 Weight Fluctuations per Age/Sex Groups in 1970.

The only other change found to be significant was the increase in mean weight from May to June ($p < .05$). Similarly if the female means for 1972 are tested, the changes April/May, May/June are all significant at the 99% level.

Even given that these changes from month to month are significant, to interpret them in terms of the bird's annual cycle is not easy. Looking at all the figures, there seems to be a general upward change Jan./Feb. and down again in Feb./March. There are two important factors at this time of the year, one is moult and the second is that this is the middle of the dry summer. It is possible that the increase in mean weight is related to the proportion of birds in moult decreasing and the proportion of those in new heavier feathers increasing. The apparent drop between Feb./March can be explained in terms of food shortage. However, if there was serious food shortage at this time of the year it would seem likely to have a much more obvious affect on the mean weight of the classes. Such factors as feather replacement would seem to fit in with changes of this order but not serious food shortage. It may therefore be that there is only a minor food shortage at this time of year.

It is perhaps important that there is a general increase in mean weight in all years where there are good sample sizes in the period May/June. The evidence from dissections revealed that this is the time of an increased availability of insects possibly resulting from the first autumnal rains. The weight increase would therefore tie in with an improvement of the protein body condition of the bird (for further discussion, see below). But it should be pointed out that the increase

Adult/Eclipse Male	Sample Size	Mean Weight gms.	Mean Standard Deviation
Summer	69	49.8	2.26
Autumn	40	49.6	2.28
Winter	32	51.0	2.89
Breeding	9	50.7	1.89

Summer/Autumn : $t = 0.49$ Not Significant ; Autumn/Winter $t = 3.59$, $p < .002$

Winter/Breeding: $t = 0.45$ Not Significant; Summer/Breeding $t = 1.89$ $p \simeq$ significant $> .05$

Subadult Male:	44	48.6	2.82
	4	47.5	3.43
	15	50.2	1.95
	72	49.4	2.75

Summer/Autumn : $t = 0.35$ Not Significant : Autumn/Winter $t = 0.85$ Not significant

Winter/Breeding : $t = 2.22$ $p < .05$: Summer/Breeding $t = 2.76$, $p < .01$.

1Y Male	209	46.5	3.28
	92	48.0	2.35
	76	49.5	3.08
	47	48.5	3.45

Summer /Autumn : $t = 13.6$ $p < .001$; Autumn/Winter $t = 8.3$ $p < .001$
Winter/Breeding : $t = 2.7$ $p < .01$; Summer/Breeding $t = 6.6$ $p < .001$

Female	184	40.0	1.86
	137	40.4	1.99
	158	41.3	1.92
	42	42.0	1.93

Summer/Autumn : $t = 8.3$ $p < .001$: Autumn/Winter $t = 17.3$ $p < .001$
Winter/Breeding : $t = 6.2$ $p < .001$: Summer/Breeding $t = 18.3$ $p < .001$

TABLE 6 : 16 Weight changes per season of Age/Sex Classes giving statistical significance of the differences.

is still of a very low order.

Another way of examining weight changes is to consider them on a broad level in terms of the birds annual cycle. In Table 6 : 12 the year has been divided up into four unequal seasons. These comprise the summer season during which the Cape Weaver population is moulting and the environment is becoming increasingly dry. The autumn contains the first rains of the year, during which testis size increases in mature males. Winter is the season of cold and rain before the breeding season begins again. The year consists mainly therefore of a breeding and a moulting season with two intermediate stages in between. The data is tabulated in seasonal form for December 1971 - November 1972 in Table 6 : 16, giving the mean standard deviations of the categories and the t test and significance values.

Various trends in the data are clear. First the highest seasonal mean weights are found in winter and the breeding season. In three out of four classes, the winter weights are the heaviest. The degree of statistical significance between the seasons varies with different age sex classes. The only difference that is consistently significant between the four classes examined (the first year female data was considered too scattered to be worth testing) was the difference between summer and breeding season mean weights. The greatest difference occurred in the 1YM and F classes. In view of the process of maturation which would affect both these classes (since the F class includes birds $<$ 1 year old), this perhaps is not surprising. The fact that all seasonal means for 1YM were significant also points to the effects of maturation.

In conclusion, it is suggested that the most striking point emerging from the study of Cape Weaver weights is their lack of fluctuation. Although there does seem to be a difference in breeding weight and summer weight. the order of this difference is still very small. It could be merely due to the effects of moult and the replacement of tattered thin feathers for new heavy ones. If food availability is having any effect, then it is small. This suggests as has been pointed out in other contexts that food availability in Southern Africa does not fluctuate so conspicuously as it does in northern temperate regions. The absence of weight fluctuation also supports the evidence (see below) that the Cape Weaver does not carry out any migratory movements and is highly resident at least in the S. W. Cape.

Since the above study constitutes the first thorough study of passerine weight variation in Southern Africa, there is little local data with which to draw comparisons. In northern temperate regions most passerines achieve their heaviest weights in early winter (Baldwin and Kendeigh. 1938) when fat is deposited especially to assist survival through cold nights. Fry (1970) found Ploceus cucullatus males to be 4% lower in weight in spring than in winter, the reverse found for P. capensis. The difference in female P. cucullatus was not significant.

A similar absence of weight variation to that of the Cape Weaver was also found by both Fogden (1972) and Ward (1969) for tropical passerines. Ward found a variation of only 2 g. or 7% of body weight in Pycnonotus goiavier during the year. It was suggested there were too many variables affecting body weight to make it a real indication of body condition. Standardisation of collecting time to feeding time is difficult. To some extent this was overcome in the weaver by weighing most of the birds at roost times. But factors such as time between catching and weighing, stress in holding boxes etc. may well have affected weights. The apparent tendency, for which no quantitative data was obtained, of the weavers to go to roost with full crops in winter may also influence results. In dissections, conspicuous changes in fat content comparable to those of migrants were not observed but some fat deposits did exist.

Ward also suggested that individual variation may well be higher than mean variation. To test this in the weaver, a sample of 60 retrap records was examined for weight changes between ringing and recapture. Only those retraps in which the age classification was the same at retrapping as at ringing were taken to avoid partly the effects of maturation. The time elapsed was anything from a few days to two and a half years. Fig 6 : 17 shows the results in histogram form. The mean weight change was 2.6 gms. This is well within the range found in the mean seasonal changes and clearly it is exceptional (10%) for changes of more than four grams to occur.

In one of the longest times elapsed, two years, five months, four days, a female's weight was identical to that originally recorded. However, as expected the range is larger than that given by the mean values and can be as much as 10 gms or 25% of the normal weight.

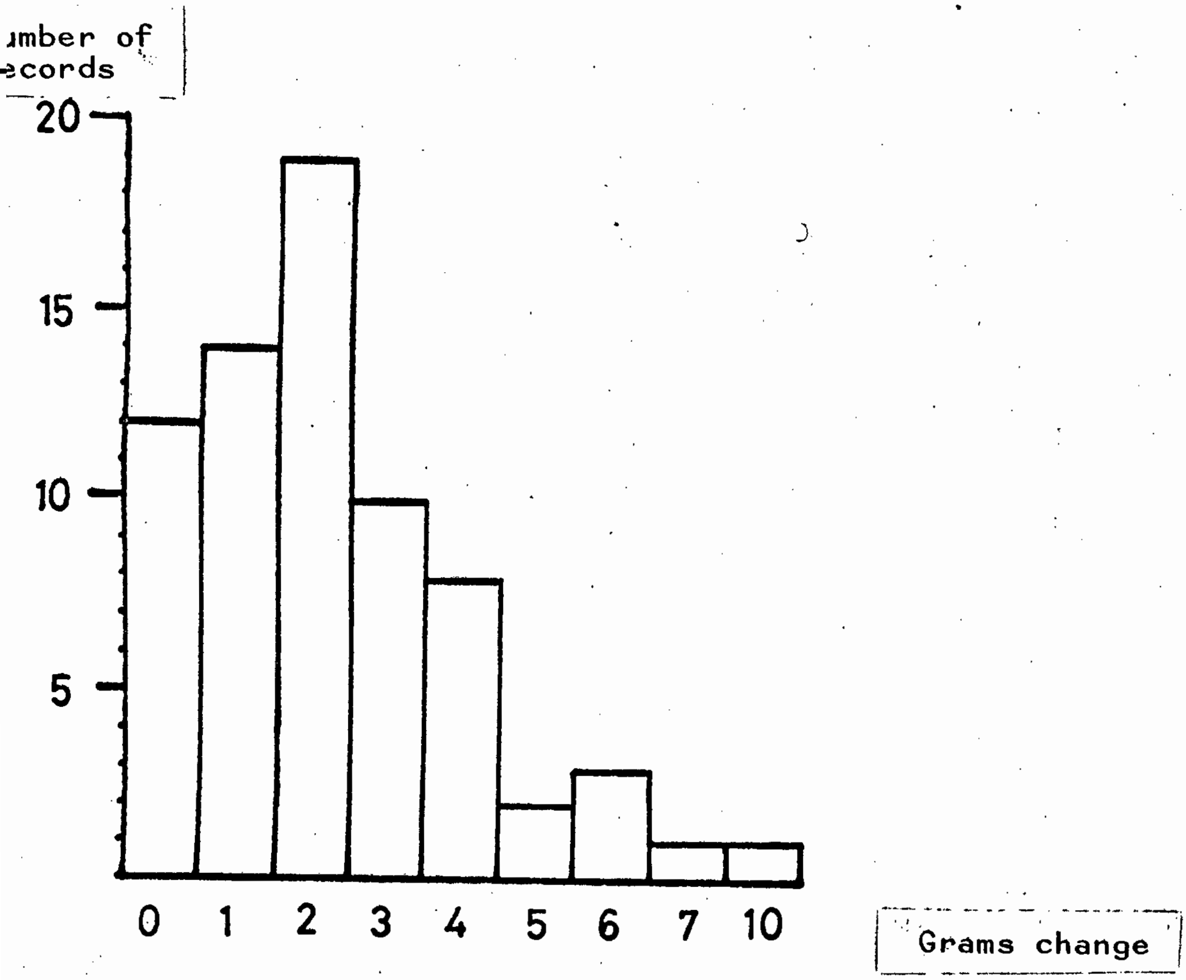


FIG.6:17

Histogram of weight changes in a sample of 60 Retraps, between weight at ringing and weight at retrapping.

SECTION 7 -
SEX RATIO IN CHICKS AND ADULTS

7.1 Introduction

The primary sex ratio in any species is the ratio at fertilisation. In birds, the male sex chromosome is XX and the female XY, the reverse situation to that found in mammals. But the principles governing the segregation of the gametes are exactly the same and produce at fertilisation a sex ratio of 1 : 1, after Fisher's theory of sexual selection (1930). The principles hold good whatever the mating system of the species, whether it is polygamous or monogamous. In birds, no sex-linked mortality factors have been proved to exist, though there is no reason why they should not exist. For example, eggs hatching into males might be more vulnerable than eggs which hatch into females and more easily killed by cold. It is said that in humans (Lyster (1970)) the male embryo is the weaker of the two sexes. But no such comparison has, as far as I know, been carried out in birds. It is generally assumed that such mortality factors do not exist and the primary sex ratio is usually considered as being the same as the ratio at hatching (Mayr 1939).

The presence or absence of an imbalance of sex ratio, whether at primary (hatching), secondary (fledging) or tertiary (adult) levels, is crucial to the understanding of any polygamous mating system. If an excess of females is present in a polygamous system, then it would be reasonable to suppose that the mating system had evolved in response to the imbalance. It was, therefore, vital to establish whether or not the sex ratio was equal at all stages of the Cape Weaver's life cycle.

7.2 Primary and Secondary Ratio - Method

Chicks were taken from two different reed-bed colonies, on dates spanning two breeding seasons. If there was more than one chick in the nest, they were tied together to allow subsequent comparison of the contents of individual nests. The chicks were killed with chloroform.

The sex ratio of the chicks was determined by dissection. It was found that the sex of very young chicks could be ascertained quite easily from hatching onwards. The ovary at about one day old was 1 - 2 mm. long, a single opaque flat structure. The testes were about 0.5 mm. long, slightly oval in shape and looking like creamy white pin-heads. The two testes were clearly visible to the naked eye. It was found to be easier to carry out the dissection when the material was very fresh, even still warm. At the same time as sex was noted, wing-length, body weight and stomach contents of the samples were recorded (for latter, see Section 6).

As pointed out, it is possible that a sex-linked mortality factor exists at the egg stage. Such a factor would result in addled eggs being present in the nest. Therefore no chicks were sampled from nests containing addled eggs. Environmental factors such as wind blowing eggs out of nests or predation by snakes or rodents may also cause egg loss but they can be assumed to act independently of sex. The primary ratio was estimated from a sample of very young chicks, the age of which was not exactly known. Chicks with wing-lengths less than 11 mm. were estimated to be up to five days old. If the nest was not sampled immediately after hatching, sex-linked mortality factors could affect the result. Again the precaution taken was not to sample any nests containing dead chicks. Sampling was carried out by feeling with the fingers. At an early stage in the nestling period when there would be no great size disparity between dead and living chicks, any corpses would have been detected. Adult females were never observed to remove dead chicks from the nest, though they did remove egg-shell pieces. Predation and environmental factors at an early stage in the nestling period can also be assumed to be independent of sex, since sexual dimorphic characteristics will hardly have developed by then. It is concluded that by observing the above precautions, an estimate of primary-sex ratio from the ratio in very young chicks would be reasonably accurate.

The primary sex ratio is the only fixed ratio,being genetically based. The secondary and tertiary ratios are the product of the interaction between various environmental factors such as starvation and predation, and the primary ratio. If a chick died soon after hatching but the nest was not sampled until the survivors were near fledging then it is quite likely that its body will have been over looked. In these circumstances the bodies become flattened and impacted into the bottom of the nest. But such death would only affect the secondary ratio and would constitute a normal influence on that ratio. Similarly, predation could be related to sex at the later stages in the nestling period because sexual dimorphism is likely to have been established. Males will be larger and may beg more vociferously, attracting more predation.

Although my own observations and those of Skead (1947) showed that predators will normally take the whole nest contents, Collias and Collias (1971) observed predation in which only part of the brood was taken. But such predation would again constitute a normal influence on the secondary ratio, and so will not affect results.

7.3 Primary and Secondary Ratio - Results

A total of 216 Cape Weaver nestlings of all ages was collected and sexed by dissection. Table 7 : 1 gives the results in detail according to wing-length. The latter was used as an index of age. It was assumed that growth took place in a regular manner, more or less independent of food availibility.

It can be seen that the sex ratio found was 110 males to 106 females which does differ significantly from 1 : 1.
As stated above, the ratio of the youngest chicks is the closest approximation to primary ratio and was 15 males to 26 females which is also not significantly different from 1 : 1. The immediate conclusion is that the primary and secondary ratios in the Cape Weaver are 1 : 1. But there does seem to be a general trend in the ratios by age from an excess of females soon after hatching to an excess of males towards fledging. In the first two age categories, Table 7 : 1 shows that females predominate, while in the last four, males outnumber females. In the 41-50 mm. group, the chi-squared value is 6.2, $p < .05$ and there is a statistically significant larger number of males.

WING LENGTH	SEX RATIO	
mm.	Males	Females
0 - 10	15	26
11 - 20	24	29
21 - 30	25	18
31 - 40	21	19
41 - 50	11	2
51 +	14	12
TOTAL:	110	106

TABLE 7 : 1 Numbers of male and female chicks of different wing lengths showing the general but not statistically significant trend of an excess of females becoming an excess of males by the end of the fledging period.

None of the other categories differ from 1 : 1. It is suggested that, given larger samples, the trend may become significant at least in all the later nestling stages. But the statistical significance of only one age/size group suggests that this may be a product of chance factors.

On the available evidence, the primary ratio, at hatching must be concluded to be 1 : 1. But there are elements in the Cape Weaver which could cause a bias in favour of males at fledging i. e. at the secondary ratio level. The main element is that the species is sexually dimorphic. The degree of dimorphism in adults has been described in Section 3 and comprises a mean wing-length difference of about seven mm. and a mean weight difference of about 10 gms, comparing adult males with adult females. This dimorphism extends into the nestling period. The mean weight of chicks near to fledging is 41.7 g. in males (sample 24) and 37.0 g. in females (sample 20).

This is coupled with a size difference in the early stages induced by incubation starting on the first egg (see Section 4). Presumably the start of incubation is not related to the sex of the eggs and so sometimes males will hatch first, sometimes females. The dimorphic advantage of the males should either be reinforced if it is hatched first or if second or later, it may take most of the fledging period before its size advantage is established. Of the specimens taken, 32 were derived from nests which contained both sexes. In one nest, both weight and wing-length were identical in the male and female chicks. Of the remainder, 18 nests contained males larger than females and 13 females larger than males. If time of hatching was the sole criterion for which sex was larger, then a ratio of 15.5 : 15.5 would be expected. The ratio found does not differ significantly from this. But the material covers pairs or trios of chicks of all ages. As pointed out, the effects of dimorphism would be only apparent in the later stages of the fledging period. Taking only those nests in which all the chicks had wing-lengths of more than 50 mm., it was found that in six out of seven nests, the male was the larger and heavier sex.

It certainly seems that in competition for food between nestlings, in the latter part of the fledging period, the male will usually have the advantage in size. The male's large size will also allow larger food reserves which will assist in lasting out periods of food shortage. Against this, the male's larger size will mean higher food requirements.

In times of food stress, this higher food requirement might cause higher male nestling mortality. On the other hand, one would think that the competitive advantage and food storage ability would operate to the extent that a smaller chick would be most likely to die first.

Haigh (1968) found similar phenomena in the Red-winged Blackbird Agelaius phoeniceus. Males weighed 10 g. more than females at fledging and were significantly larger. Of 58 chicks found dead in the nest, Haigh found a ratio of 39 M : 19F. I find this difference significant - chi-squared = 6.9 and $p < .01$. The fledging ratio was nearly 1 : 1 but the primary ratio of a group of nests in which the age of chicks was known, was 1.33 : 1. I have back-checked his ratio assuming an average of three chicks per the 21 nests studied and on numbers of 37 males : 26 females, the difference is not significant from 1 : 1 but, of course, favours males. His samples were considerably smaller than the above. It seems that in the Redwing study, the larger males were at a disadvantage according to Haigh because of their higher food requirements. It may be that poor food availability occurred during his study. It would also have been relevant if he had included the age of the dead chicks to see at what stage death occurred.

In conclusion, the data presented show no definite evidence of an excess of females at hatching (primary ratio) and certainly no significant excess of females fledged. It is speculated that large samples might reveal an imbalanced ratio favouring females at hatching. Such an imbalance would offset the effects of competition at the later nestling stages. It seems very likely that large samples would certainly reveal a significant excess of males being fledged. Such a situation would, of course, be the opposite of that required for the operation of a polygynous system based on sex ratio irregularities.

7.4 Tertiary Ratio - Method

The assessment of sex ratio of any freely moving animal whether mammal bird or other, presents considerable problems. Many of these were discussed by Mayr (1939). They encompass such factors as the relative brightness of the plumage of the sexes. The more brightly coloured sex, usually the male, will tend to be seen more easily than the dull-plumaged female. If the behaviour of one sex is more conspicuous than the other, for example if one is noisier, then that sex will appear more numerous. These factors all affect a visual assessment of the sex ratio. The behaviour and plumage of the sexes will also affect other sampling methods. More brightly coloured males may catch the eye of the hunter, causing a disproportionate number of males to be shot. If birds are netted, the alarm calls of trapped males may attract other males into the net but not females. This technique is used by quail-hunters who either use a decoy bird or a simulated quail-caller to bring males into shooting range or into their trapping area. All these examples would produce a false impression of the natural tertiary sex ratio.

In the Cape Weaver, all these factors could apply to certain sampling procedures. As mentioned above (Section 3), the bright plumage of the male was not at all conspicuous when the bird was not displaying. When specimens were being taken by shooting it was nevertheless found that significantly more males were shot than females. The main reason was that males advertised their presence by singing.

Females, of course, do not sing. Similarly when shooting specimens at a new colony near Lamberts Bay, only males were shot. This was due to the colony being an early season one in which the males were busy establishing territories and building nests. Females rarely put in an appearance during the day and only arrived in the colony in numbers in the evening. Specimens were taken in the middle of the day, hence the presence only of males in the "bag". When mist-netting once at a colony near Darling, nets were set early in the afternoon. The colony was at an early stage of development. Not only were males solely caught but it was noticed that trapped males tended to attract others into the net. Males swooped at birds struggling in the meshes and in doing so, often became caught themselves.

But the main sampling of the population was carried out in a standard manner by catching birds coming in to roost. Often the operation was timed so that nets were not put up until half an hour before dusk. Within 20 minutes, the nets would be full to capacity. The result was that there was little time if any in which adult males caught could attract others in. Also the evening roost time is one of the most frantic for territorial males as they try to prevent a continuous stream of arriving roosting birds from settling in their territories. Birds coming into roost usually swooped into the reeds in flocks of 20 - 50 and hit the nets on the way. Others were caught by being frightened out of the reeds into the nets. It is possible that there is some segregation of sexes in the flocks, especially in the non-breeding season, though this was never observed in the field. But the flocks presumably hit the nets randomly. Once in the roost, the flock structure apparently broke up and if disturbed, the whole roost would fly off en masse.

It is therefore concluded that the above sampling method has no apparent bias in favour of one or other sex.

The second possible cause of error was the sexing method itself. The great majority of birds sampled were released. Only a few were killed and dissected for sex. In Section 3 the difficulties found in sexing the Cape Weaver in the hand were outlined. Using wing-length as a parameter to distinguish young males from females, it was estimated that the number of males mistaken for females was approximately equal to the number of females identified as males. Employing the criteria described, the estimate of sex ratio should therefore be accurate.

7.5 Tertiary Ratio - Results

Cape Weaver populations were sampled on a total of 122 catching dates, during the study period, in areas spread over the S. W. Cape and on a few occasions, in the E. Cape. A total of 3882 birds were sampled. The majority was sampled by the method described above but some were caught during the day and others poisoned or shot. Most birds were sexed in the hand and released, but some were killed and sexed by dissection. For the reasons given above, all birds caught by methods other than that advocated, were deleted from the sex ratio determinations, except for the poisoned birds which were included. Poison was considered to act randomly.

Of the remaining sample of 3617 birds caught on 102 catching days, the ratio of males to females was 1919 : 1618 (chi-squared value 13.5, $p < .001$). In the whole sample, there is therefore a significantly larger number of males than females.

On a day to day basis, there is a lot of variation in the samples. On 64 of the 102 days, more males than females were caught. On 4 days, the number of each sex was equal and on the remaining 34, females were most numerous. Sample sizes varied from one bird to 111. Most of these variations were not significant but on 12 sampling dates, significant differences were found. The details are given in Table 7 : 2. It can be seen that on twice as many dates, males outnumbered females. In terms of the annual cycle, it appears that females tend to be most numerous from October to January, i.e. from mid-breeding season to the early dry season. The male is apparently the most numerous sex for the rest of the year, particularly in Spring. This seasonal operation is not clear cut since a surplus of males was on one occasion recorded in November.

There are two ways to explain this seasonal difference. One is that the apparent surplus of females coincides with a flood of juveniles into the population. It may be that these juveniles were incorrectly classified as females. As explained in Section 3, a juvenile male cannot be recognised until its wing-length is 86 mm. or more. It was shown above that overall the number of juvenile males misidentified as

Date	No. of Males	No of Females	Probability value	Dominant Sex
23.8.69	25	12	$< .05$	M
5.9.69	16	6	$< .05$	M
16.10.69	1	8	$< .05$	F
29.10.69	18	34	$< .05$	F
12.1.70	31	64	$< .001$	F
15.8.70	44	17	$< .001$	M
3.11.70	14	29	$< .05$	F
17.5.71	11	2	$< .05$	M
23.5.71	22	6	$< .01$	M
12.11.71	28	10	$< .01$	M
25.2.72	70	39	$< .01$	M
6.9.72	75	20	$< .001$	M

TABLE 7 : 2 Sampling dates on which the male : female sex ratio differed significantly from 1 : 1.

was counterbalanced by the number of adult females (wing lengths $>$ 87) misidentified as males. But at certain times of the year the proportion of recently fledged birds will mean a temporary apparent swing in favour of females. An alternative explanation is that the sampling method does not rule out the possibility of flocks of segregated sexes influencing the results. As explained, no observations were made of such flocks, but feeding flocks were not often observed. If a sample size is small, then it might be possible to catch only one flock at a time and hence introduce a bias. An impression was gained at the catching areas, that there might be some flock segregation as birds being ringed tended to come in runs of one sex or the other. It was possible that this was an artefact occurring in the holding boxes. After being removed from nets, birds were placed in boxes until they were processed. The larger males may have been able to sit on top of the smaller females giving a false impression of segregation. The point is however worth further investigation. If such flock segregation does occur, it would be expected to produce a random variation of which sex was most numerous. There would be no reason for one sex to be more numerous at one time of the year than the other, as was found above.

A third explanation is that the polygynous mating system would tend to produce an excess of females at the breeding colonies by mid-season by which time most breeding males would have at least two or three mates breeding in his territory. Although most of the sampling was carried out at breeding colonies, these colonies were also roosting colonies.

One would have to suppose the disappearance or emigration of non-breeding males at this time of the year. There was no evidence for any such absence of non-breeding males.

In conclusion, it is considered that the excess of females at certain times of the year was the result of a sexing error. As a general phenomenon, it is thought that there is a small excess of males at all times of the year in the Cape Weaver populations. The ratio found can be summarised as 1 . 13 males to one female. The combined nestling ratio was 1. 04 : 1, but this includes all ages. The ratio in the largest class was 1. 17 : 1 but the sample is very small. It may be that the adult ratio directly evolves from the secondary ratio and that there is no appreciable change due to a differential sex mortality. This point is further discussed under Section 8.

7. 6 Discussion

It is shown above that there is a tertiary sex ratio bias in favour of males in the Cape Weaver. A secondary sex ratio bias in the same direction is also thought to exist.
The main factor involved is suggested to be the sexual dimorphism in the species. Such dimorphism is a common phenomenon in many birds but in only a few species have these ratios been examined.

Nestling Ratio

Mayr (1939) gives a number of examples of imbalanced nestling ratios. Most of the examples given of apparent differences from a 1 : 1 ratio in nestlings are either badly substantiated or doubtful in some other way. Both Mayr and Lack (1954) quote widely McIlhenny (1940) who found an unbalanced sex ratio both in the Red-winged Blackbird and the Boat-Tailed Grackle, *Cassidix mexicanus*. In the former species, 77% of the nestlings were male. In the Grackle only 30% were males 125 males : 287 females, to be exact. Both differences are statistically significant from a 1 : 1 ratio. McIlhenny does not state exactly how he sexed his nestlings except that it was done on appearance and was easy. Williams (1940) also studied the Red-winged Blackbird but in the eastern USA, not the west. He examined in detail the development of sexual dimorphism as expressed by physical differences in the chicks. He found that nestling sex could not be determined on appearance until at least the ninth day whereas McIlhenny says that he could sex chicks on appearance at any age over four days. Williams found that the eastern Red-wing showed a 1 : 1 ratio at the nestling stage. Subsequently Selander (1961) has checked the Boat-tailed Grackle again by dissection and found a 1 : 1 ratio. McIlhenny's method seems to have been erroneous and can be dismissed.

Lack also cites an example, originally from Byerley and Jull (1935), of extensive records on poultry, where males formed 49.2% of the newly hatched chicks. For this difference to be significant, the sample size would have to be about 100,000 birds at 49200 males to 50800 females. It seems unlikely that a sample of this size exists and so this data cannot be regarded as a valid exception to the 1 : 1 ratio. The same applies to the percentage ratios of the Pheasant, Ruffed Grouse and Domestic Pigeon. All are likely to be by-products of sample size, rather than genuine differences.

The only other sample quoted by Lack is that of the Sparrowhawk Accipter nisus where 20 out of 27 nestlings examined were females. This is significant difference from 1 : 1, ($p < .01$), but, as Lack says, no mention is made of what stage the chicks were sexed. The Sparrowhawk, like the Cape Weaver, is dimorphic in size, although it is the female which is the larger sex. If the nestlings were all sexed at the end of the fledging period, differential sex mortality may have already occurred and would logically favour the larger sex.

One of Mayr's conclusions, in fact his final one, was that in birds, the primary sex ratio is frequently unequal. As can be seen from the above, he had no grounds for this statement.

Since 1954, data on nestling sex ratio have only occasionally been published. In all cases known to me, only one species has been found to have a primary or secondary ratio other than 1 : 1 (Dhondt 1970 - on Parus major). However in other studies, all involving sexually dimorphic species, a preponderance of males has been found, like the Cape Weaver, but the difference has never proved significant.

(e.g. Selander 1960 and 1961; Morel and Bourliere 1956; Ward 1965; Landauer 1957; Zimmerman 1966). In all these cases except Landauer's, the sample sizes have been comparatively small. Ambedkar (1964) studying polygynous ploceines in India, found a ratio of 50 males to 38 females, which is again not significantly different from 1 : 1.

Dhondt's data on the Great Tit Parus major are characterised by large samples, a total of 1650 chicks examined. His data are split between two areas, urban and "rural" and he contrasts the ratios of the two and finds them significantly different with urban areas fledging more males than females when compared to rural areas. When the data for all the areas are combined a ratio of 794 : 856, males : females, is found. This is not significantly different from 1 : 1. The ratio for urban areas where there is a higher nestling mortality is 113 : 94 in favour of males. In the rural areas, it is 682 : 761 in favour of females. The urban figures are not significantly different from 1 : 1 but the rural ones show a significant excess of females. It should be pointed out that Dhondt's method of sexing was for most of the samples from external appearance backed up by experimental dissection. His results are most interesting because they show an effect of differential mortality in the nest. Low mortality produces an excess of females, but high mortality produces an excess of males. It implies that the primary ratio favours females and if unaffected by mortality factors during the nestling period, produces a female excess. This would agree with the tentative suggestion proposed for the Cape Weaver. In the Great Tit, the male is also the larger of the two sexes. Dhondt did not interpret his results as I have above. He was interested only in the differences between his two major areas. Nevertheless he explained the difference in terms of dimorphic competition favouring males.

The problem posed by the above seems to be the apparent contradiction between Dhondt's and Haigh's studies. In one the females suffered higher mortality in the nest and in the other, males. Both authors explain their results in terms of dimorphism, the one by saying that males outcompete females and the other by saying that the larger males require more food. Lohrl (1968) showed that the nestling to gape quickest and to reach highest is fed first by the parent. Perhaps the explanation is that Haigh's data comprised nestling deaths at all ages and that males are more vulnerable at an early age. Dhondt's data was only on nearly fledged chicks when dimorphism will have asserted itself and males will certainly outcompete females. However this still does not explain why males are more vulnerable than females at an early age. On hatching males and females must be the same size. Perhaps the male has to grow faster and higher energy requirements makes it more vulnerable.

The important point emerging from the above is that Dhondt's work seems to support the suggestion of a primary ratio favouring females in the Cape Weaver. This can be elaborated to say that in perfect conditions of no nestling mortality, a surplus of females will result. In normal conditions, an excess of males will be produced unless there is severe chick mortality at an early age, which swings the ratio in favour of females again.

Tertiary Ratio

Although there have not been many critical assessment of tertiary sex ratio which avoid the pitfalls mentioned in 7 : 4 above, the impression is that in most bird populations, there tends to be an excess of males. This is not unexpected in view of the male usually being the brighter plumaged, more noticeable sex. But such detailed studies that have been carried out indicate that the excess of males is in fact genuine. Some ratios found in full-grown bird populations have been given in Table 7 : 3. In all examples, males outnumber females except for the October figure of the Quelea quelea Where exact numbers are quoted, these have been tested and found to be significant from 1 : 1, with the same single exception. Where males predominate the actual ratio varies from 3 . 8 : 1 in the Quelea to 1. 46 :1 in the Indigo Bunting. The Cape Weaver ratio was 1. 13 :1. The figures for the Red-winged Blackbird and the Quelea are so strongly in favour of males that they suggest that some artefact must be involved. What this could be is not known in the former. In the latter, Ward (1965) offers no good explanation for how the population can change from 81% males in July to 50% by September. In subsequent work (Ward 1971) migration has been predicted for the species in the area. Males tend to arrive and construct nests in the breeding area before females arrive, so there may be segregation in the flocks at the end of the dry season which could explain the results. Otherwise there would appear to be the possibility that 62% of the population competing for available food with breeding birds. In which case the whole population would be inherently unstable and unlikely to survive long.

Males	Females	Species	Author
51186(3)	17062(1)	Agelaius phoeniceus	Burt and Giltz (1970)
154(1.5)	102(1)	Molothrus afer	Darley (1971)
1.66	1	Ducks	Erickson (1943)
86(1.5)	57(1)	Merops bulocki	Fry (1972)
1.46	1	Passerina cyanea	Johnston (1970)
147	158	Quelea quelea (October)	Ward (1965)
467(3.8)	123(1)	Quelea quelea (June)	Ward (1965)

TABLE 7 : 3 Number of ratios of males to females recorded in some published studies.

The only data published on sex ratio in South Africa, are those in Rowan (1964). In view of the above, it is interesting that Rowan estimated a preponderance of females in two ploceines, the Masked Weaver *Ploceus velatus* and *Euplectes orix*. Estimated ratios were 55 : 95 and 55 : 106 in the respective species, in both cases favouring females and in both cases highly significant from 1 : 1. However the data suffered from inadequate knowledge of a method of sexing any birds other than birds in or going into adult/eclipse plumage. Rowan made an attempt to predict the number of males in the "intermediate" group on the basis of birds subsequently recaptured as males. Elsewhere it is stated that males take at least a year to acquire adult male plumage and may be recognisable as potential males at an age only slightly less than this. As presented there is no evidence given that the recaptures on which the calculations were made more than a year after the original captures. Such a time elapse would be necessary to allow young males time to acquire identifiable male plumage. Hence it is considered that the estimated ratios cannot be accepted and therefore do not contradict the results found in the Cape Weaver and the other species above.

In conclusion, it is apparent that in most birds, especially passerines, breeding pressures have tended to produce plumage and size dimorphism in sexes (see Sibley 1957). It is suggested that the degree of dimorphism in such circumstances, is likely to be small, the male is likely to be only larger than the female on average and by a matter of about 10 - 20% as in the Cape Weaver.

Only in species where competition for food has been avoided by specialisation in the sexes, can dimorphism be expected to reach the extremes found in some birds of prey and the Huia *Heteralocha acutirostris*. It follows that in most birds with limited dimorphism and the sexes eating approximately the same food (for the Cape Weaver - see Section 6), an excess of males will be present in the adult population as a result of their larger size favouring them both at the nestling and at the free-flying stage. However this excess will not be large otherwise there will be counterproductive competition between a large number of non-breeding males and the breeding population. At the individual level, there presumably must be selection pressures such as extra food requirements, flight efficiency, manoeuverability and predation which prevent dimorphism from becoming too pronounced. In terms of the mating system, it is clear that there is no correlation between sex ratio and polygyny. In fact dimorphism accentuated by the extra competition for males tends to push the ratio in the opposite direction to that "required" for the mating system. Therefore in theories on the evolution of polygyny, imbalanced sex ratios producing an excess of females cannot be considered as contributory factors.

SECTION 8. - MORTALITY AND PREDATION

8.1 Introduction

It is repeatedly suggested that one of the factors promoting the evolution of polygyny is differential mortality and predation on the sexes. Lack (1968) proposes that there is a surplus of females in the breeding season for two reasons. The first is that in males, maturity is deferred until their second breeding season, while females can breed in their first season. The second is that if young males did try to breed, it would be dangerous for them to do so.

The term 'deferred maturity' refers not to the sexual capabilities of the bird but to the onset of full adult breeding plumage. Evidence presented in Section 4, suggested that males may in fact be able to produce viable spermatozoa by the end of their first breeding season after fledging. Selander (1965) pointed out that though the young male Grackle Quiscalus sp. may be able to produce sperm, the testes tend to be proportionately still small and the amount of androgen secreted comparatively small. Reduced aggressiveness as a result of this, plus only the partly developed adult plumage, put the young male at a serious disadvantage against adults in aggressive encounters and in competition for territories. Smith (1972) showed clearly the disadvantage suffered by a male Agelaius phoeniceus if its red epaulets were obscured i.e. experimentally reducing an adult male to subadult plumage. In terms of the evolution of deferred maturity, Lack states it appears to have evolved because young males would be very unlikely to obtain mates in the face of the extra-severe competition in polygynous species.

Additionally, he proposes that it must be dangerous for young males to attempt to breed, otherwise they would make the attempt and therefore would benefit from having full plumage.

This theory will be further discussed below. As far as mortality is concerned it suggests that if young males adopted full plumage, they would suffer heavy mortality. It follows from this that the bright plumage of polygynous males tends to produce higher mortality and only adult males are experienced enough to reduce this effect. Hence, once breeding is over, the adoption of a non-breeding plumage. The latter point was discussed in Section 3 and it was suggested that there was no evidence for such an anti-predator function of the non-breeding plumage. An adaptation to flock-feeding was proposed instead.

It is apparent from the above that it is important to establish the extent of mortality in the two sexes and to investigate any possible affect that bright plumage might have on predation.

8.2 Method

The only methods of investigating mortality are those of observation and the use of large scale marking schemes. A total of 3882 Cape Weavers was ringed using numbered rings stamped with a return address in the standard manner. Recovery reports of birds were followed up with questionnaires. to determine the exact date, locality and manner of death or finding. In addition 221 retraps were made in the course of routine ringing operations. These give an indication of the relative survival of the two sexes.

8.3 Results - Recoveries

A total of 36 recoveries (birds found dead) was reported by members of the public and myself. (The latter refers to the shooting of one of the marked birds while randomly collecting specimens 40 km. away from the ringing site).

The results are presented in Table 8 : 1. It can be seen that the number of females recovered exceeded the number of males by 18 : 13. Five pulli were also recovered. The time elapsed between ringing and recovery varied from a few weeks to three years. But this does not affect the relative death rates of the sexes. The difference between the number of males and females recovered is not significantly different from 1 : 1, but clearly there is a tendency for more females to be recovered than males. This should be seen against a sex ratio favouring males i.e. the tendency is stronger than indicated.

Table 8 : 2 shows the manner of death of the 36 recoveries. The greatest number were shot, followed by "found dead". As pointed out, my own experience showed that shooting tended to select males, but this was not shown by the recoveries where the ratios were 7F : 3 M : 2 pull. It is however obvious that the recoveries are very much man-orientated and not related to natural predation. Cape Weavers are regarded as pests both of fruit and cereal crops in the S. W. Cape. They are therefore persecuted to some extent. Birds are shot to protect fruit trees especially the more valuable such as export grapes, apricots and figs. Several of the recovery reports specifically mention crop protection as the reason

Age/Sex at Ringing	Number Recovered
Adult Male	2
Eclipse Male	-
Subadult Male	3
1 Y Male	8
Adult/Unsp. Female	16
1 Y Female	2
Pullus	5
Total:	36 - 13 males : 18 Females : 5 pulli.

TABLE 8 : 1. Number of Recoveries (birds dead) according to Age /Sex Class.

Found Dead	11
Shot	12
Caught/Killed	7
Killed by cat	3
Killed by man/method unknown	2
Cause of Death Unknown	1

TABLE 8 : 2 Cause of death of Cape Weaver recoveries.

for the killing. There is the fairly wide-spread practice of placing a series of walk-in traps around the edge of the crops in an attempt to reduce damage. Some farmers claim to kill several thousand ploceids per year,. the main victims being the Cape Weaver and the Cape Sparrow Passer melanurus. Poisoned grain is the chief technique used by grain farmers to kill weavers.

It seems probable that man causes far more deaths in the Cape Weaver populations in the S. W. Cape than is caused by any other factor except possibly starvation.

One of the weaknesses in the theory that it is dangerous for males in relatively bright plumage to breed, is that it would appear to be equally hazardous if not more so for females having to raise their broods more or less unaided. There is a lot of evidence which shows that breeding in general is a hazardous occupation (Coulson 1960, Snow 1958, Summersmith 1963 in Lack 1968). In the passerines covered by these studies, mortality tends to be higher in summer, presumably in adults, than in winter despite the better conditions in summer. The reason given is that breeding takes place in summer. Furthermore Coulson showed that in the European Starling Sturnus vulgaris, female mortality was 70% in the first year while male mortality was only 39%. Again the reason given was that females breed in their first year and males not until their second. Perrins (in Lack 1968) found the same phenomenon in the Great Tit Parus major. Yet Lack is using the reverse of this same argument to explain deferred maturity in polygynous species by saying that young males do not breed in their first year because it is dangerous for them to do so.

The contradiction is caused by Lack considering polygynous species to be a "special case". I cannot accept this and would suggest that if anything any additional mortality suffered by the male as a result of bright plumage is more than offset by the hazards the female must face in incubating and rearing the brood unaided.

Of the 36 recoveries made, only 12 were recorded during the breeding season as shown in Table 8 : 3. Both adult males were recovered in the breeding season. The histogram does show a slight peak in the breeding season and a second one in December. But the sample size is altogether too small to draw any clear conclusions. The time of recovery will also be related to the efforts of farmers to protect their crops rather than to any natural pressures. Of the adult birds recovered in the breeding months (August to November inclusive), it is interesting to note that the proportion of males to females is 2 : 8. This does seem to show perhaps females are more vulnerable than males during the breeding season. During the breeding season, the male spends most of his time at the breeding colony. As suggested by Craig (pers. comm.) for the Red Bishop, on the appearance of a predator the male Cape Weaver only has to dive into the reeds or the interior of the colony tree to be comparatively safe. The female having to feed the chicks has to make repeated forays into relatively unsafe and unknown territory and at that stage is likely to be vulnerable. The warning system of the colony is sufficiently good to make incubation not at all hazardous.

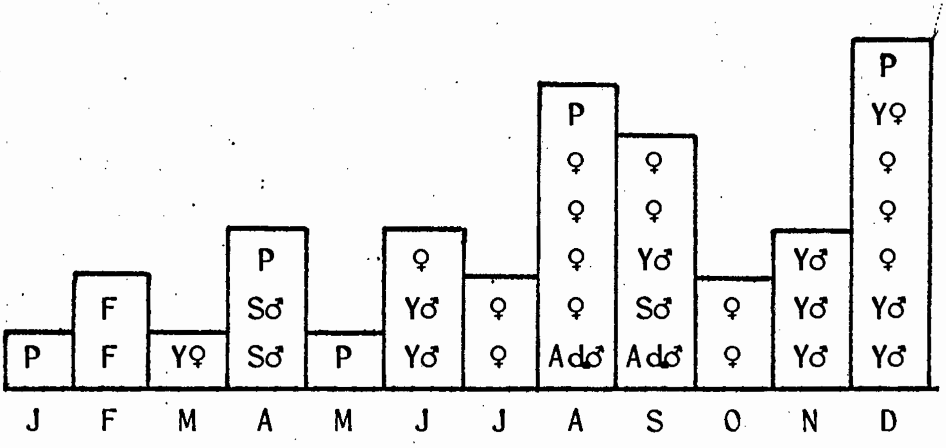


Table 8:3 Seasonal distribution of recoveries according to Age/Sex Class. (P=Pullus, Y♀=1Y♀, S♂=Subadult ♂.) Each symbol represents an individual recovery.

8.4 Results - Predation

As far as I know, no actual observation has ever been made of an adult weaver being taken by a predator. The only indirect record is that of a full-grown Cape Weaver being taken by a Spotted Eagle Owl Bubo africanus, and the ring being subsequently found in a pellet. One observation of nestling predation made by myself was that of a brood of nestlings eaten by a Moorhen Gallinula chloropus. In the main study colony, at least one pair of breeding Moorhens was present. On the one occasion, the Moorhen was seen swimming beneath a weaver nest built into a group of reeds standing in water. The Moorhen, apparently attracted by the sound of the chicks begging, scrambled up the stems of the cluster of reeds supporting the nest and thrust its head into the nest. It pulled out and swallowed a nestling. The process was repeated for the second nestling. The adult male weaver dive-bombed the Moorhen during the procedure, but never actually struck it. The Moorhen's only reaction was to duck.

Other predators of weaver nestlings have been recorded especially the Boomslang Dispholidus typus (Skead 1947). This snake was very common in the study area. No records of predation by snakes on adults have ever been seen, though other adult passerines have been recorded as being taken by snakes e.g. Pycnonotus capensis by Bitens arietans (Liversidge 1970). Adult weavers are likely to be at their most vulnerable when roosting. Snakes, mongooses, and others would all be potential predators in these circumstances. No evidence of such predation was however secured but it could still be a factor under natural conditions. It still seems unlikely that the predation pressure on free-flying birds at any stage other than immediately after fledging is a significant evolutionary pressure in the species.

A short experiment was carried out with a stuffed cobra on a small colony. Although the cobra caused some alarm calls to begin with and tended to collect a group of up to 11 birds of both sexes, no attempt was made to attack the snake. This could be a result of a lack of movement in the snake and therefore the rapid habituation of the birds to its presence. However Rowan (pers. comm.) has observed Cape Weavers, in a mob, attacking a snake. As the snake moved through the bush, the mob followed it.

Collias and Collias (1971) studying Ploceus cucullatus did find some tendency to strike at snake predators and occasionally even at avian predators such as the Banded Harrier-Hawk Polyboroides typus. Little reaction was found on another occasion to a Gabar Goshawk Micronisus gabar.

It therefore seems a fair conclusion that anti-predator behaviour is not highly developed in weavers generally. In view of the conspicuousness of the polygnous species' colonies and roosts, it seems a reasonable assumption that the level of predation is low.

The difficulty about the above is that it is based entirely upon present-day conditions in an entirely man-affected environment. A high percentage of the recoveries of adult birds resulted directly from human action. The question is whether this represents the pressures under which the social system of the Cape Weaver evolved. Are the pressures which promoted the deferring of maturity still in operation today? It is possible that human predators do not react in the same way to plumage differences as do natural predators. Lack (1968) points out that it is difficult to study the pressures which selected for deferred maturity since today there are no test cases in which maturity is not deferred. Under natural conditions, one would expect to find some perpetuation of the same pressures by, for example, higher male mortality. Therefore although the data show quite clearly that females suffer heavier mortality than males and this is quite explicable in terms of nest duties and smaller size, it should be remembered that the predation or mortality observed was not strictly natural.

8.5 Retraps

The age/sex distribution of the 221 retraps made, are given in Tables 8 : 4 and 8 : 5. Table 8 : 4 gives a summary of all retraps regardless of the time elapsed between ringing and retrapping provided this was at least one calendar day. The ratio of males to females retrapped was 139 : 82. This difference is highly significantly different from 1 : 1 (chi-squared 14.7; $p < .001$).

It was felt that there might be extraneous factors operating in the immediate vicinity of the colony whereby, for example, pulli which had not properly left the colony area, perhaps being fed still by their parents, might not be as subject to mortality than if they had moved away. The data was therefore reworked for elapsed periods of six months or more between ringing and recapture. The data are presented in Table 8 : 5 and show that there is still a significantly larger

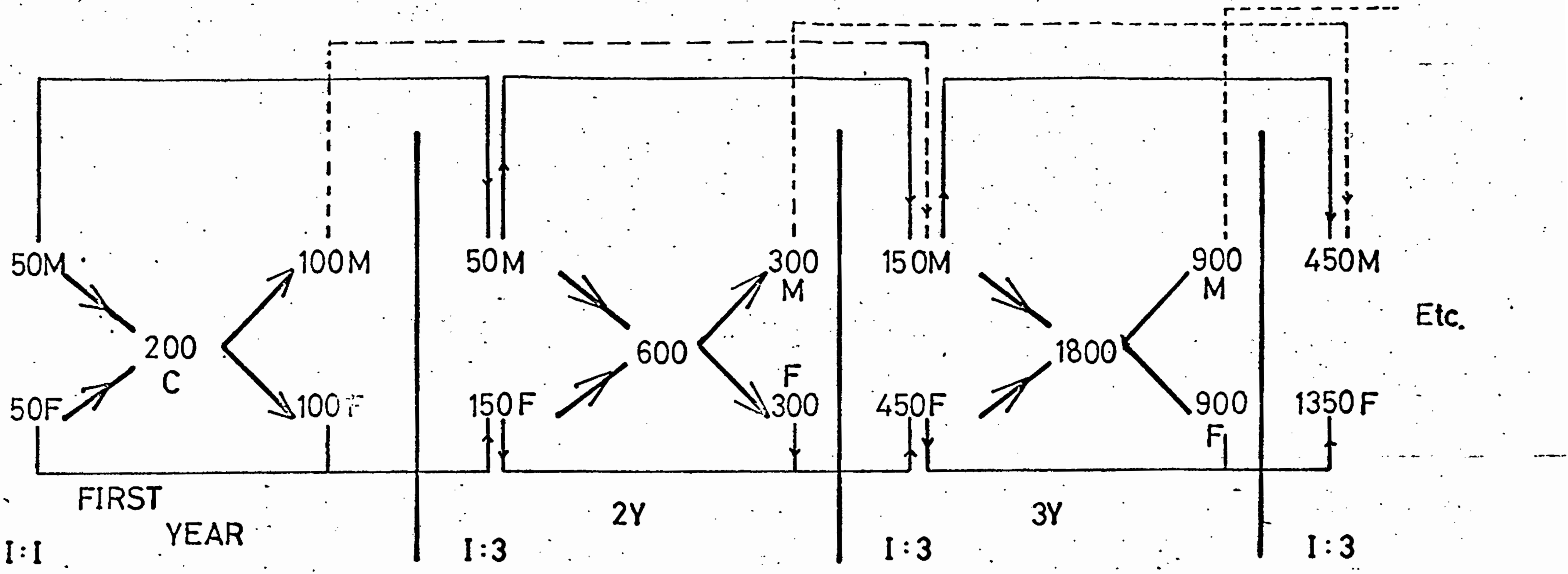


Table 8:4

Theoretical sex ratio system assuming that a population began with 50 breeding birds of each sex; maturity is delayed by one year only in males, secondary ratio of 1:1; each ♀ produces 4 chicks per year.

Age/Sex Class at Ringing	Number of Retraps	
Adult/Eclipse Male	12	
Subadult Male	28	Total Males = 98
1 Y Male	58	
Female	53	
1 Y Female	3	
Pullus (sexed at retrap as Male)	41	Total Females = 56
Pullus (sexed at retrap as Female)	26	
	221	

TABLE 8 : 4 Retraps according to Age/Sex Class.
Time elapsed between Ringing and Retrap > 1 day.

Age/Sex Class at Ringing	Number of Retraps	
Adult/Eclipse Male	7	
Subadult Male	10	Total Males = 35
1 Y Male	18	
Female	28	
1 Y Female	2	Total Females = 30
Pullus (Male)	21	
Pullus (Female)	5	

TABLE 8 : 5. Retraps according to Age/Sex Class.
Time elapsed between Ringing and Retrap > 6 months.

number of male recaptures than female, the ratio being 56 : 35 (chi-squared 4.84; $p < .05$). There are some differences in the two tables. In Table 8 : 5, both the full-grown and the total ratios significantly favour males, while the pullus ratio is not significant from 1 : 1. In Table 8 : 4, the pullus ratio is significant and so is the total, both favouring males, but the adult ratio does not differ from 1 : 1.

The retrap rate of the sexes is influenced by two factors. The first is the relative tendency for the birds to return to the same breeding or roosting site. The second is the relative mortality. If the retrap rate is to be taken as an index of survival in the sexes, then it must be assumed that the emigration rate and the return rate is the same. If one sex tends to disperse to other colonies, more than the other, then no deductions on survival can be made.

Since a number of retraps of all age/sex classes was made, one can say that all the age/sex classes did return. Almost all the retraps were recorded at the main study colony. In the first two dry seasons, the dam dried up and all the birds were forced to disperse. It was only up to six months later that the dam was reflooded and it became tenable as a colony and a roost. Subsequently the dam was kept flooded all the year round and there were birds roosting there throughout the year. No noticeable changes in roosting population were observed which would have indicated a tendency to disperse at certain times of the year.

From the recovery information, it was noticeable that the three furthest records to Swellendam (190 km), Philadelphia (40 km.) and Zuider-Paarl (38 km.) all concerned females. The rest of the recoveries were all within about 15 km. of the ringing site. Whether these three records signify that females disperse further than males is debatable. It has been suggested that in other ploceines like Euplectes (Crook 1964) that females in the breeding season move around from one colony to another in search of a suitable mate. Males on the other hand once they have established territories, remain sedentary until at least the end of the breeding season. But there is no evidence to support this idea and none to indicate how faithful weavers are to their colonies. The retrap data in Tables 8 : 4 and 8 : 5 do show that birds return to the colony but the large remainder which did not return could either have perished or dispersed to other colonies. As a general phenomenon, breeding site faithfulness appears to be strongly selected for in most birds in the event of successful breeding.

In the absence of information of the degree of dispersal of the sexes, one can only conclude that the differences given between the sexes, both with long-term (> 6 months) and short-term (< and > 6 months) retraps, could be due to either mortality or dispersal differences. However the fact that the retraps produce the same result as the recoveries means that it can be taken as tentative support of the proposal that females suffer heavier mortality than males.

The differences between Table 8 : 4 and Table 8 : 5 in the ratios of the age groups show that a significant difference between the male and female pullus retrap rate only develops in long-term retraps. This may be due to chicks being dependent on their parents for some days after fledging and mortality or dispersal factors only having an effect when the fledglings have moved right away from the colony. In the full-grown category, a significant difference is only shown in the larger sample which includes all retraps not just long-term ones. The fact that both ratios favour males but only the larger is significant suggests that the difference may only be a matter of sample size.

8.6 Discussion

The evidence presented above, although not extensive, does indicate a heavier mortality in females than males, despite there being a slight excess of males in the population. I think, therefore, that Lack (1968) is wrong to consider that polygnous species constitute a special case, where the excess of females is partly induced by higher male mortality. Lack based his comments on Selander (1965) who claimed to establish a higher mortality in males of the polygynous Boat-tailed Grackle. Selander however had only indirect evidence of this supposed mortality. He deduced it from apparent changes in sex ratio and the sex ratio was also assessed indirectly, not by dissection or even by close examination of the birds in the hand. The techniques used were either for incoming roosting flocks to be counted by two observers or from photographs of bird flocks assembled for roosting.

In this Grackle there is considerable sexual dimorphism both in size and plumage. Selander states that the sexes can be readily distinguished in the field. While it is clear that adult males (iridescent black) and adult females (dull brown) are easily distinguished, Selander does not make it clear whether young males can be separated from adult females. The juvenile male and female plumages are certainly similar as shown in his earlier paper (1965). It is stated that there is considerable variation in the young males after their post-juvenile partial moult. Figures given for first-year males show that they are larger than adult females and that there is no overlap, but size is notoriously difficult to judge under field conditions. By both methods used by Selander, the main sex determinant would be the dark black plumage of the male compared to the dull brown of the female. Selander concluded that his figures showed that males suffered twice as heavy mortality than females in the course of the winter. If this was so, it is surprising that he was not able to support the conjecture with mortality figures from ringing studies. In view of these weaknesses in the data, I feel that Selander's conclusions cannot be accepted without further investigation.

Furthermore, the examples quoted above, Section 8 : 3 of mortality in other passerines, most of which are monogamous, also invalidate Lack's contention. A further example of passerine mortality is that of the Bobolink <u>Dolichonyx oryzivorous</u> (Martin 1973). Martin records his surprise that in this species which is polygynous, dimorphic and which performs a 19000 km. annual migration, the survival rate is high and there is evidence that the species is comparatively long-lived.

It seems therefore that the Cape Weaver and probably other polygynous species do not have any different mortality pressures from those of other monogamous passerines, especially those that are dimorphic or where the male does not breed until its second year. As stated in the introduction, Lack stated that if there was the least chance of young polygynous males obtaining mates, then they would still attempt to breed unless it was dangerous for them to do so. This suggests that because males do not attempt to breed, it is therefore dangerous. The danger aspect has been dealt with, but there is still the implication that males do not attempt to breed in their first season after fledging. In the Cape Weaver, this is certainly not so. Young males are continually arriving throughout the day, moving through the colony, inspecting nests etcetera. But they are seldom given the chance to remain in the colony for any length of time. Almost always they are chased by resident territory-holding males from the moment they land in the colony. Towards the end of the season, the aggression of the males either decreases or the aggression of young males increases, or both. Some young males manage to set up territories and build nests on the edge of the colony. None was observed even to build a nest anywhere but on the edge of the colony and none was observed even to attract a mate, although attempts were made to do so. On one or two occasions young males were observed to attempt to copulate with a female giving the precopulatory display to a resident adult male (see below Section 11). It was promptly chased from the scene. All these observations point to the fact that young male Cape Weavers are repeatedly trying to obtain mates in their first season.

This of course implies that it is not dangerous for them to do so which supports the general contentions given above. If this is the case then we are still faced with the problem of how deferred maturity evolved in the Cape Weaver and in polygynous species as a whole.

It is suggested that there are two possible reasons. One is that the level of predation under which deferred maturity was evolved was far higher than it is today and so at the time when the plumage was evolved, it was dangerous for young males to have bright plumage and be inexperienced. More positive and more likely is that the one main difference between polygynous species and monogamous ones is, obviously, the mating system and as a consequence the competition for mates. I therefore agree with the first part of Lack's idea that it is the intensity of competition which has been the main selection pressure evolving deferred maturity. Even if the young male did attain full plumage he would not be able to compete against the marginally larger and heavier, and more experienced adult male (See Section 3). However, unless there is some additional factor, one must accept that the young male would be more competitive if he did have full plumage. It is suggested that with such a premium on experience, it is to the young male's advantage to be able to visit regularly the colony and to attempt to build nests and defend a territory. Collias and Collias (1964, 1972) have shown in aviary studies how vital experience with nest-building is for the young male. Birds deprived of nest-material in their first year often totally failed to build successful nests when provided with nest material later on.

If the young male Cape Weaver had full-breeding plumage, it is suggested that this is such an aggression releaser, that he would at no stage be allowed to remain in the colony at all even towards the end of the season.
By having a less aggressive subadult plumage, he can occasionally enter the colony and practise making nests at least to some extent. This experience will be to his advantage in the following season. It should be pointed out that young males are also known to make "practice" nests well away from colonies. My impression was that these nests were made earlier in the season, and young males tended to move in to the colonies later in the season, perhaps when adult male aggression is dropping off.
This suggests that there is more to practise than just making nests; defence of territory and participation in the colony if only on the periphery may also be important.

Since deferred maturity is known to occur, it is interesting to see the theoretical effect that this would have on sex ratio at a breeding colony. Given that males breed at about two years old and females at one year old, a scheme has been drawn up in Table 8 : 4, based on an original population of 50 adult males and 50 adult females. As can be seen, the system stabilises at a ratio of 3 : 1 in favour of females.
The degree of polygyny present in the colony will be discussed further in Section 13 below.

SECTION 9. BEHAVIOUR - TERMS, DEFINITIONS, METHODS

9.1 Introduction

The only previous description of the display of the Cape Weaver is contained in the paper by Skead (1947). The displays of the bird are described in very general terms which tend to be somewhat anecdotal. For example, the display of the single male is described as "a ruffling of the feathers and a rapid shivering of the wings, accompanied by almost incessant song of some form or other", i. e. very little detail is given and it is therefore difficult to make comparisons with other weavers. This is indicated by the slight misclassifications in the details of the Cape Weaver's behaviour in the monograph on the behaviour of the Ploceinae by Crook (1964), which are based on Skead's paper. In the broader outlines, Crook's classifications are generally correct. Since his study is so fundamental to any other behavioural study of weavers, the details of his classification as far as the Cape Weaver is concerned have been given in Table 9 : 1. The minor errors in the scheme will be corrected where appropriate in subsequent sections.

Of the other African species of the genus Ploceus, only P. cucullatus and P. nigerrimus in West Africa have been described in detail (Collias 1959, 1963, 1967, 1970; Crook 1963). P. phillipinus, an Asian representative of the genus, has also been studied to some degree in India (Crook 1960). Prolonged observation and special techniques such as frame by frame analysis of cine-films of the birds, have allowed

Environment Class III	Dry non-forest, arid Savannah and thorn scrub with vast seasonal fluctuations in food availability and in the general aspect of the landscape.
	Nests in trees or bushes
Notated non-asterisk	No personal knowledge
Population Dispersion Type VI	Gregarious but breed in dense "colonies" consisting of numerous small contiguous territories of size much less than 6 sq. metres placed normally in a restricted locality which often has some obvious characteristic likely to be protective. Visibility around each nest commonly good.
Pair Formation Type II b	Advertisement display of particularly dramatic form precedes courtship. Sex chasing is omitted and courtship is entirely restricted to a small area around the next or nest group.
Territory Defence Type	Mobile
Nest Advertisement Type B	Nests sited in trees, particularly those of colonial species, are advertised by advertisement posturing given on or near the structure. Elaborate usually ritualised displays are performed which attract the female not only to the nest but to her first contact with a potential mate.
Evolutionary Grade II	Primary granivores of savannah. Mostly polygamous with sexual and seasonal (male) dimorphism.

TABLE 9 : 1 The classification group into which *Ploceus capensis* is placed by Crook (1964).

detailed description of almost every single movement involved in the displays of these species. A similar level of description has been the initial aim for P. capensis as a prerequisite to the longer term studies on, and the understanding of, the biology of the species. Long term studies have not been carried out on any of the above.

9.2 Displays and their Motivation

A description of passerine behaviour can best be divided into three sections territorial behaviour, courtship behaviour, and maintenance behaviour. The former two are more important than the latter from the evolutionary point of view and show the greatest species specificity since, of course, they are primarily involved in sexual and ecological isolation. Each form of behaviour is made up of a number of movements which in the first two types, have developed a communication element, becoming normally ritualised displays. Each display is produced as a result of an initial internal drive or motivation. Theoretically it might be thought that territorial and courtship behaviour were different underlying 'drives', the former being concerned with the tendency to 'fight or flee' and the latter with the tendency to give sexually-based responses, following the simplistic one drive, one response system of Tinbergen (1952). Other workers such as Beach et al. (1955) and Larsson (1963) indicate that other types of stimulation not directly concerned with the type of response, may affect the response produced, i.e. if you starve a bird. you will inhibit its sexual behaviour. These ideas gave rise to the idea of a 'general drive' hypothesis which, according to Hinde (1966), requires that the production of a given behaviour 'is determined equally by all the motivational factors and stimulation acting at the moment.'

The conclusion seems to be that neither the general drive theory nor the single drive theory are correct and that the tendency to produce a given response is determined by a single major drive which is affected by a general drive amounting to the general state and level of activation of the body.

Courtship behaviour is therefore produced by a sexual drive affected by the non-sexual state of the bird such as whether it has just completed a territorial encounter (which would almost certainly increase the intensity of the sexual behaviour). However to separate the two important forms of behaviour in terms of drive is a purely arbitrary action.

9.3 Territorial Behaviour

The overlap of these two types (Territorial/Courtship) of behaviour is again indicated by Andrew (1961) after Hinde (1952) both of whom use the term 'reproductive fighting' to describe territorial behaviour. The adjective 'reproductive' stresses the strong sexual component of this form of fighting which distinguishes it from normal fighting. Normal fighting occurs over some commodity outside the breeding season, be it for space, food, shelter etc. Reproductive fighting does however seem to be a clumsy term which is marginally misleading implying that the fighting is directly to do with copulation i.e. perhaps it is best used to describe the fighting between male and female early during pair formation, prior to copulation. But particulary in P. capensis, fighting occurs long before the females start arriving regularly in the area and for this reason I prefer to use the term 'territorial behaviour' instead of that used by the above authors. Territorial behaviour can then be defined purely functionally as the behaviour exhibited between territory-holding males and other males (holding territories or not) during the breeding season. Agonistic displays shown between territory holding males and strange females entering the territory unsolicited are also included here. The latter produces the same displays as can be given to strange males. Territory here is defined as 'any defended area' after Noble (1939), so displays not necessarily to do with breeding, such as individual distance disputes between immature birds, but occurring in the breeding season are included.

9.4 Courtship Behaviour

As stated in Andrew (*loc. cit.*) it has for a long time been accepted that the components of courtship may be sexual, aggressive or fear responses. This seems to leave out an important part of courtship and that is the tendency to approach, usually of the female towards the male. This is not contained in the 'sexual' part of the definition above except in the longest possible view, since the approach may not directly be appetitive of copulation. This again applies particularly to *P. capensis* because the female approaches the male in courtship display sometimes several days or even weeks before the pair-bond is sufficiently established to allow copulation. Here the attraction of the male's display or of the colony as a whole produces a tendency to approach in the female. Perhaps it is the gregarious drive of P. capensis which is partly responsible for the approach 'drive'. Certainly the immature males are also drawn to colonies.

Andrew also includes alert, nesting, parental and begging behaviours under his courtship category. It seems extremely debatable whether the alert responses are necessarily connected with courtship, so these displays have been included under maintenance behaviour. Begging behaviour also cannot be considered a constituent of courtship, except when produced by adult birds, presumably females, in such species where, for example, courtship feeding occurs. The display-response system between adult females and nestlings belongs more properly under the maintenance behaviour section.

9.5 Maintenance Behaviour

This behaviour is simply concerned with the general health and efficiency of the bird's body which includes the so-called comfort movements (preening, bathing etc.) plus feeding, locomotion, predator avoidance (alert) etc. These behaviours differ from the two main types above in that most of the movements are directly functional and have not been ritualised. They are important in considerations of the ontogeny of behaviour as many displays seem to have developed from exaggerations of straightforward movements. (see McKinney 1965).

9.6 Display:

The basic units of the two main types of behaviour are their displays. Perhaps the best definition is that given by Hinde (1964) as 'a term denoting movements that have become specialised through the course of evolution to serve as signals in social communication'. When one thinks of displays, the movement aspect is the first to spring to mind, but displays are often accompanied by characteristic calls which reinforce the signal function. In the Cape Weaver there is one example where mechanical sounds such as the snapping of the beak, reinforce a visual display. Sometimes calls are given without body movement. In any case, such vocalisations or sounds given by the species must be considered as part of the display repertoire.

In descriptions of bird displays, there seems to have been very little uniformity or attempt to follow previous authors. Each worker has tended to invent new terms for describing a particular display of *his* species. Thus Collias (1970) calls one display of the male *P. cucullatus*, the 'Upright Wing-flapping display' and another, the 'Inverted Wing-flapping display'. Crook (1963) in his earlier description of exactly the same species, had referred to these as 'Upright Wing-beating display' and 'Wing-beating display of Nest advertisement' respectively.

In the following record of the behaviour of *P. capensis*, I have tried to follow the terminology of Crook, the earlier worker, particularly as laid out in his monograph (1964).

It is also important in the description of one species of passerine to bear in mind the displays of other species of passerine. Although much of the courtship behaviour of

P. capensis is specialised to colonial ploceines, many of the maintenance and some of the territorial behaviours appear homologous to those of the passerines in general. For this, the terminology of Andrew (1961) has been followed where possible.

9.7 Method

The Cape Weaver is usually insufficiently tame to be observed without the observer being concealed to some extent. The great bulk of the observations were carried out at the main study colony from a hide placed on stilts in the middle of a small dam. The view from the hide covered almost the whole colony and the windows did not have to be concealed with branches as is the case with very 'nervous' species. Provided that the observer did not move close to the windows and remained in the shadow, the weavers behaved normally, ignoring the observer completely. Most of the birds in the breeding colony were between 3 and 20 metres from the hide with the bulk of the activity going on at 5 or 6 metres range. Most behavioural interactions were observable with the naked eye, but for some details and for such requirements as reading the colour-ring combinations on individual birds, binoculars 7 x 50 were used.

Birds were also observed at several other colonies using vegetation cover or a transportable hide, for concealment. Observations were carried out at experimental aviaries as well as in the wild. Hand-reared birds could be observed from two metres range without concealment, or initially as close as one liked but wild-caught birds never 'tamed down' sufficiently not to necessitate the use of a hide.

Data were recorded usually straight into notebooks, but occasionally a tape-recorder was used and the information transposed later. For details of the actual movements involved in displays, a 35 mm. Canon camera, with a 450mm telephoto lens, increased to an effective 900 mm. with extension tubes, was used. Photographs of postures were usually taken a 1/500 sec., which was sufficient to 'freeze' most movements. Ciné -films were also taken of displays and display sequences, using a Bolex 16 mm camera. The largest telephoto lens available was a 6" (152mm.) lens and the maximum speed of the camera was 64 frames per sec. (equivalent to 1/100 sec. in a still camera). The latter speed, although sufficient to freeze most movements of larger birds like Sula capensis, was insufficient for P. capensis. However frame by frame analysis of the film did give some indication of how the displays were constructed.
For some vocalisations, a Uher 4000 Report-L tape recorder was used, usually at the fastest speed of the tape (190.5mm per sec.) which gives an audio range of 40-20000 cycles per sec. and as a result, the purest sound available.
For recording purposes, the microphone on an extension lead, was normally placed within three feet of the bird, the vocalisations of which were required for taping.

SECTION 10. - TERRITORIAL BEHAVIOUR

The agonistic behaviour of weavers consists of a series of displays which vary in intensity. The displays are all concerned primarily with the acquisition and subsequent defence of the territory. They will be first described individually and then compared with the territorial displays in other weavers.

This section concerns itself mainly with the description of the Cape Weaver's behaviour. The quantification of the behaviour is described in Section 12.

Attack-predominating Behaviour

10.1 Ocular Fixation

The plumage of the Cape Weaver has already been described. One of the most noticeable sex differences is the contrast between the deep warm brown colour of the female's iris and the pale glinting gold of the adult male's iris.
This feature stands out sufficiently to be detected at least at 20 m. range by the naked eye and is also one of the first parts of the appearance to change when the female-type-plumaged first year male changes into immature-male plumage. The next significant morphological change is the blackening of the beak in the advanced immature male, the beak being pale horn grey in the first year bird.

The contrasting black and gold against the yellow of the plumage are accentuated in the lowest intensity of territorial display, when the territory-holder merely turns towards the intruder and stares at it. The plumage state is also important and is usually fluffed out particularly in the region of the breast and crown of the head.

The combined effect of this simple posture is to drive away intruding birds which event will only occur where the escape motivation is already very high in the intruder.

10.2 Supplant-Flight

The supplant flight is normally the next stage in intensity. It consists of a sudden flight at the intruder. It does not appear to have been ritualised in the sense that there is nothing exaggerated about the action. Sometimes the aggressor swoops upwards before landing, but usually it is a direct straight-line flight. If the supplant flight is preceded only by ocular fixation, it follows that it will only be directed at an intruder having a strong tendency to flee. It is normally performed if the intruder does not move on after ocular fixation. Because of the high escape motivation, the supplant flight is not followed by a chase by the territory holder away from his territory. In fact the intruder usually flees as the holder starts to fly, so that by the time the holder has landed near where the intruder was perched, the latter is already outside his territory and usually outside the colony altogether.

10.3 Bill-raising

The above term is a descriptive one used by Andrew (1961).

Although it is not a particularly good description since it only describes one facet of the display, it has been followed to prevent further proliferation of terminology. Crook (1964) surprisingly does not record a bill-raised display in any species of weaver and Andrew on the basis of earlier papers makes the same assertion. The discrepancy will be discussed below.

The bill-raised display in the Cape Weaver is one of the most characteristic of the species' displays. One of the important parts of the display consists of raising the bill from the horizontal plane, up and down repeatedly, up to about 45° above the horizontal. The general appearance of the display can be seen in Fig. 10 : 1. The general body plumage is sleeked in common with over 30 passerines which are recorded as giving a similar display, but not completely sleeked. The chest feathers are thrust out. The impression is rather as if the breast muscles are being expanded, like a parading boxer, rather than the breast feathers being thrust out individually. This gives a rectangular look to the front of the body. The dark line on the upper breast is also clearly visible in this display and seems to accentuate the posture by the formation of an almost continuous dark line, running from the tip of the upraised beak to half-way down the breast. The display is a little reminiscent of the sky-point in Sula capensis (Jarvis 1971) where the dark skin on the throat and upper breast is shown off in display. Like the Cape Gannet too, the Cape Weaver lowers the wings a little and holds them slightly out from the body, so that a gap appears between the carpometcarpal joint ("shoulder") and the body.

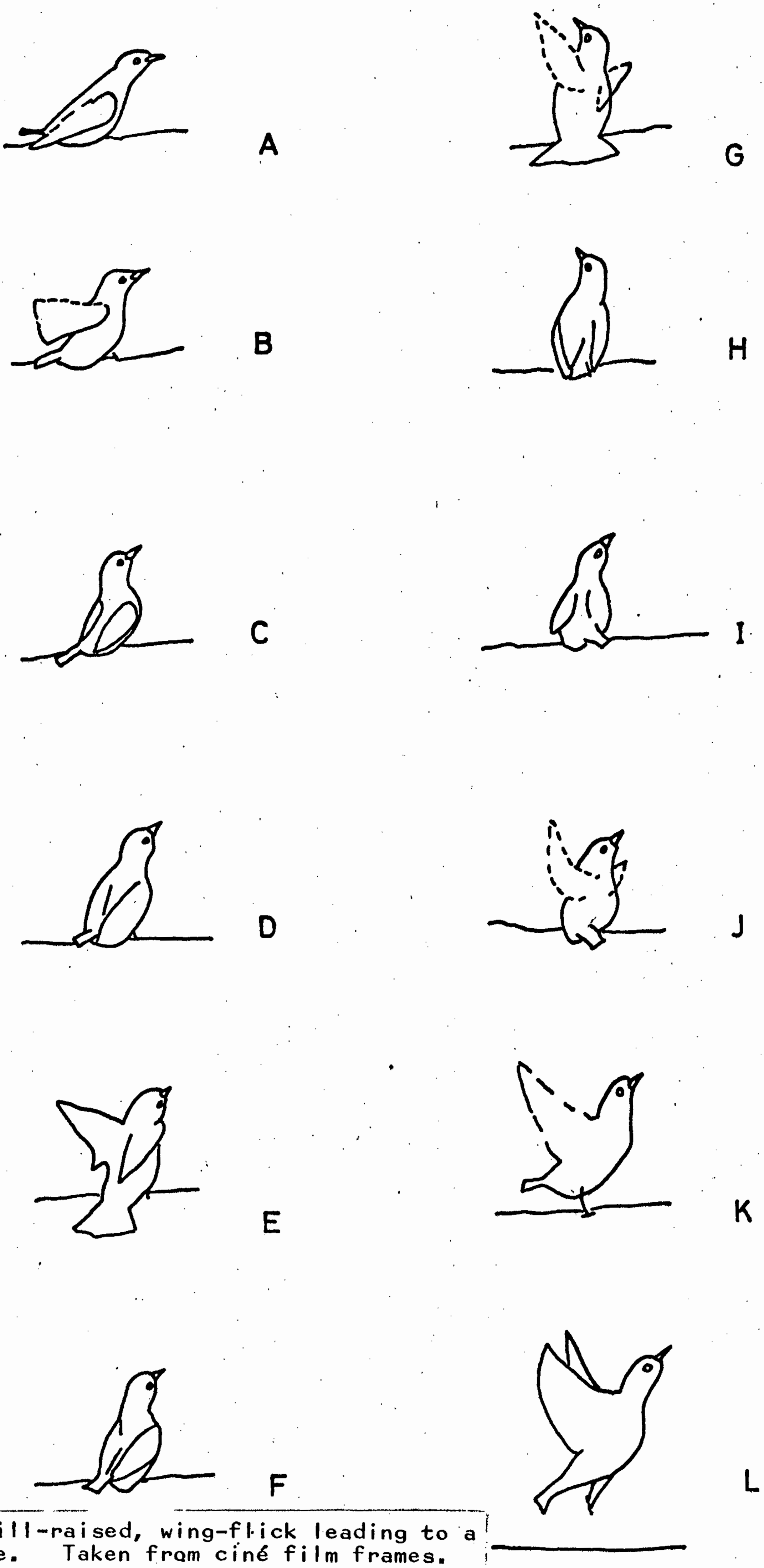


FIG.10:1

equence of bill-raised, wing-flick leading to a pplant chase. Taken from ciné film frames.

The bill-raised posture can be given by itself when an intruder enters an adult male's territory. Almost always, however, it is accompanied by a strong wing and tail flick. The flick of the wing is concentrated on the primaries which are lifted away from the body by up to 30 degs. but usually about 10 degs. and then flicked back into place.
The tail flicks in the vertical plane upwards from the normal position and back to.the normal position i. e. there is no element of tail depression. Sometimes the tail is fanned a little at the bottom of the flick movement. In the bill-raised display at its lowest intensity, the tail only tends to be flicked and at its highest intensity, the wing and tail are flicked together.

When an intruder appears in the territory, the bill-raised posture is adopted. The territory holder may then hop in an exaggerated fashion two or three times, and then it will hop towards the intruder in an exaggerated supplant flight.
At this stage the intruder normally flies away.

10.4 Supplant Chase

The displacement of the intruder by the approach of the holder in bill-raised , wing/tail flick, and exaggerated hop display, is usually followed by the holder chasing the intruder right out of the holder's territory, through other male's territories and out of the colony. Fig 10 : 1 shows the sequence from a bill-raised position (A, C, D) using flicks (B, J), wing and tail flicks (E, G) ending in a supplant chase (K, L). Sometimes the supplant chase continues for more than 100 m. beyond the colony edge. At this point, the holder flies back to the

territory. These chases occasionally involve more than one chaser since neighbouring males may join in , particularly when an intruder is chased through their territory. If the intruder is very persistent and flies around the colony, the chase may go on for several minutes round and round the colony. The holder was never observed to catch an intruder in the air but remained one or two metres behind it.
The supplant chase is almost always performed on large subadult males or males coming into adult plumage, by the fully adult territory owner.

10.5 Aggressive Dance, Song and Lunge

This display is restricted entirely to encounters between two territory holding neighbouring males in full adult plumage. The first stage of the display is the adoption of the bill-raised posture by one male (male A, but could be either) and the characteristic accompaniment of the wing/tail flicks and exaggerated hops. This usually carries one male to the edge of his territory. The neighbour male B on seeing this display also goes into a bill-raised stance and hops towards male A in exactly the same manner. At this point both A and B appear to positively select a patch of vegetation whether it is a thick spray of leaves at the end of a branch or a small clump of reeds. In this way neither male is exposed to a full frontal view of the other. They then 'dance' around the clump both producing exaggerated small hops but no vocalisations. Each bird moves round to the furthest point from the other round the clump, like children chasing each other round a table, but they face each other the whole time so that one male is not actually chasing the other. The dance leads them back and forth araund the clump. One male will then stop and fluff up his plumage particularly raising the feathers on the crown. It will cling to the vegetation so that its body is about vertical. The bill is held at about right angles to the body and is opened. The 'aggressive wheeze call' is given. This consists of a prolonged song (see later) of many grating syllables strung together and decreasing in intensity from a harsh buzz down to a soft prolonged last syllable. It could be written as 'cheeze-wheeze-wheeze-wheeze .... wheeeeeze'. The song last usually from 20-40 secs. The head is not moved during song production. Male B meanwhile continues to produce the elaborate bill-raised posture but will stop occasionally when A is singing and lunge at A through the clump of vegetation. These lunges never touch the other male. They are usually aimed in the region of the head but fall short by about 5 cm. or more. The lunges consist of an elongation of the body and a jabbing movement of the head. The movement is reinforced by often easily audible clicks as the lunge culminates in a snapping of the beak (see Displays above). The bill-raised part of the display is also reinforced by a much more pronounced wing-flicking than occurs when that display is given by itself. Often aggressive dances occurring outside the field of view of the observer were drawn to his attention by the flapping noise produced by disputing birds. The noise was similar to the flapping of fighting Streptopelia doves.

In the aggressive dance, no vocalisations are produced by B. The dance may continue thus for a half minute or more with A continuously wheeze-calling and B producing the bill-raised display punctuated with periods of lunging. A then completes one bout of song and reverts to the bill-raised posture. This usually causes B to go into 'wheeze-call' posture and to start singing. The roles are completely reversed and B sings while A hops and occassionally lunges. The aggressive dance continues in this manner with display roles reversing every now and then, until either A or B break off the contact and flies back into the centre of its territory, usually to a nest. Although A and B give the bill-raised display simultaneously, they were never observed to give the wheeze call at the same time.

10.6 Redirected activities

These movements were noticed chiefly as an adjunct to the aggressive dance. The male B performing the bill-raised hop while A wheezed, would direct his activity to the surrounding vegetation. Another typical noise emanating from these dances was the sound of tearing vegetation. The male B would snap at a strand of reed and with a jerk of the head snap and tear the reed off. The 'nest material' would be held in the beak for a few seconds and then dropped. Sometimes the reed stems would be pulled at in a movement quite similar to that of the grass-pulling Herring Gull Larus argentatus (Tinbergen 1952 and 1953) except that the movement in the Cape Weaver would be accompanied by exaggerated wing and tail flicks. Displacement nest-building was also noticed with the male performing exaggerated sewing movements and sometimes vigorously tucking in loose strands protruding from the nest.

All these types of redirected displacement activities are clearly derived from nest-building movements. They are perhaps an indication of how important the nest is in territorial behaviour. Since the nest also features strongly in courtship, all nest - involved displays have been included under that one heading.

10.7 Fighting

Fighting involving direct physical contact does not occur very often. It was only observed, in connection with territory, between males in full adult plumage (although physical exchange do sometimes occur between male and female in pair formation). Fighting usually occurs when a territory-holding male returns to his territory from a foraging or nest-material collecting trip, and finds an intruder male in his territory or stealing nest material from one of his nests. The aggressor immediately dives at the intruder hitting him in mid-flight. The fight develops with the feet being used for gripping, the beak for lunging and the wings for beating. Such fights occasionally resulted in both birds fluttering into the water. The underneath bird is submerged and gives an alarm squawk, which usually causes the aggressor to relinquish his grip and allow the intruder to fly off.

Fighting can also sometimes develop from an aggressive dance where birds A and B both lunge simultaneously and a form of 'fencing' match results in which the lunges do contact the body (usually the upper breast). Such fencing matches are very short perhaps lasting 5 - 15 secs., when one bird retreats and is chased by the other. Then normal fighting as above, results and the loser usually wet, flies back to the centre of his own territory. Although feathers were observed to be lost occasionally during these encounters, no loss of blood was seen. Despite the handling of several thousand weavers, none was found to have wounds or blemishes which might have been caused by fights with conspecifics.

10.8 Head-forward posture

This posture is standard to most passerines (Andrew 1961) and consists of lowering the body and elongating it so that the head, body and tail form a continuous line. The beak is opened about 30 degs. and feathers raised slightly especially on the back. The posture is often accentuated by the production of a short high-pitched 'growl' as the bird thrusts the open beak at its opponent. Head-forward in the weaver is not primarily concerned with the defence of the breeding territory. It was noticed commonly among non-breeding birds and their efforts to maintain an 'individual distance'. In the study colony, it was most frequently observed between non-breeding birds coming in to roost shortly before dusk. There was competition for preferred roost perches. The head-forward differs from the lunge which was more of a woodpecker hammering aimed just short of the opponent and which was silent, while the head-forward was usually accompanied by the growl. The head-forward was especially common in the experimental aviaries where it was used by birds trying to retain one of the limited number of favourable perches.

10.9 Fear-predominating behaviour

The above has described those agonistic displays in which the 'fight drive' is the most important. There are a few displays which do not appear to have been highly ritualised which signal that the bird has a strong tendency to flee or submit to an aggressor. Perhaps the reason that they have not been ritualised is that generally a bird does not want to show to a competing conspecific that it is at a disadvantage.
This can rarely have any selective advantage.

10.10 Alert.

Here the plumage is sleeked and the head is extended or appears so as a result of the neck feathers being sleeked. The head of the bird has a very angular appearance, a high cheek-boned look and the bird glances about as if expecting an attack from any quarter at any moment. The 'alert' bird can be put to flight with very little aggression being shown towards it by another. The posture is commonly seen in immature males visiting the colony. They are attracted to the colony and particularly to nests.
If the territory-holder is absent, they will move into the area and inspect the nests, occasionally manipulating strands. While indulging in this inspection the bird will periodically go into the alert posture when an adult male flies nearby, so that the bird is continually switching from sleeked to normal plumage and back. When the owner eventually does return, the alert posture is adopted before his arrival and the immature male takes flight before the owner has settled. The alert is also given when a strange bird immature or adult male lands in the colony for the first time in a particular sequence.

10.11 Look avoidance

Here birds, especially those arriving at dusk, appear to avoid ocular fixation by territory owners. The owner may be displaying agitatedly in their direction particularly if more than one bird lands in his territory simultaneously, but the intruders turn away and fail to react to the display. The movement does not appear ritualised or remotely comparable to such appeasement movements in other species (like the chick in Rissa tridactyla (Cullen 1957) or head-flagging in Larus ridibundus (Tinbergen 1959), but it nevertheless results in intruding birds occupying positions in another bird's territory which would not normally be tolerated. It is also debatable whether look avoidance really constitutes a display as it really amounts to a failure to respond in the normal way i.e. a negative display rather than a positively communicating one.

10.12 Fluffed Posture

This is also typical of birds coming in to roost. In addition it was seen in a young chick which had just fledged and had flown inadvertently into another territory. The head is contracted into the shoulders, the feathers fluffed out as if it were cold. The bill is slightly raised. Birds preparing to roost, some time before they would actually start to sleep, adopted the fluffed posture and this enabled them to perch in a territory where they would not normally be tolerated.
With the exception of the observation on the chick, the fluffed posture was not noticed during the other hours of daylight.

The posture is submissive and prevents or reduces attacks by aggressive conspecifics. Perhaps the clearest illustration of the function of the posture was seen in the aviary birds. Here the bird (a female) which, at least early on, was consistently 'bottom' of the aviary hierarchy (for greater detail, see below), regularly went to roost half an hour before any of the other birds. One of the most favoured perches was chosen, and the bird adopted the fluffed posture, with the bill withdrawn into the feathers but slightly raised. Sometimes the head was moved round so that the bill was tucked between the scapulars. Both these postures inhibited attack from the other birds when, later, they started settling and disputing for roost perches. Occasionally one bird would approach the premature sleeper, as if wishing to take over the perch, but not knowing where to direct the attack. Occasionally after moving from side to side near the sleeper, the second bird moved off again. Sometimes pecks were directed in a gentle exploratory way at the feathers of the fluffed bird. These 'attacks' were usually ignored or would be met with a rapid head-forward and growl which usually had the effect of displacing the normally superior aggressor. The inhibitory effect of the fluffed posture was clearly shown in these behaviour sequences.

10.13 Comparison with other Ploceines

The 'tail-depressed threat' recorded in P. cucullatus, Q. quelea, P. phillipinus and other species (Crook 1964) was not observed in P. capensis at all. On the other hand, the posture described above as 'bill-raised' is not mentioned for any species of ploceine.

This seemed contradictory and indicated that perhaps one posture was being mistaken for the other or that it had been overlooked in one or other case. Illustrations of the tail-depressed threat in Q. quelea (Crook 1960) make it clear that there is no element of bill-raised in this posture except when the opponent is sitting above the displayer. i. e. the bill-raised is not ritualised to that position. But, as pointed out, the bill-raised display is a common one in many passerines, (Andrew 1961), so its absence in the weavers observed or reported on by Crook is more surprising than its presence in the Cape Weaver. The exposure of the black upper-breast line in the bill-raised posture may be why this display is recorded only in the Cape Weaver. Some other species like P. ocularis have black bibs and throats but none are described as having a dark upper breast line.

The aggressive dance of P. nigerrimus (Crook 1963) appears quite similar to that of P. capensis, with the exception of the bill-raised component. Crook indicates that P. nigerrimus opponents sing simultaneously although this contrasts with the general description of the aggressive dance (1964) in which the alternation of song with lunging is stressed. Collias describes the alternation of song with lunging and the apparent inhibitory effect of the song. In P. capensis, attack is not inhibited entirely as the singing bird will be subjected to lunges and beak-snapping directed a few inches from his head, but actual physical contact does not result until the dispute breaks into simultaneous lunging. If the wheeze-call is produced simultaneously in P. nigerrimus, it must serve another function besides inhibition of attack.

Another detail recorded by the above authors in territorial behaviour is the quivering of the wing tips. Crook records this as a component of the tail-depressed posture, as part of the threat display, and as a displacement activity produced from attack/non-attack conflict in courtship. Collias indicates that wing-quivering occurs in high-intensity disputes. In the Cape Weaver, wing-quivering was observed only as a displacement activity related to the courtship of the female, and not in interactions with other rival males at all. It has not therefore been mentioned above, but included in the courtship section.

One of Crook's general conclusions is that the degree of mobility of the territorial behaviour is related to the size of the territory. This is hardly surprising since if a bird has to defend a large territory, it must have highly mobile displays in order to protect that area. A correlation is said to exist between the degree of mobility in the actual aggressive dance and the territory size. This correlation seems to break down except when very large differences in territory exist. Territory size in <u>P. capensis</u> is small, being about 1.5 sq. m. but the mobility is nevertheless high in the dance. One bird is usually static (and wheeze-calling) while the other hops about energetically. Also supplant chasing occurs sometimes several hundred metres away from the bird's territory. The correlation is therefore very loose and really only applicable to the extremes of territory size and does not hold with finer distinctions.

Arising from this two-level system of territorial behaviour, the aggressive-dance and the long-distance supplant chase, is the apparently unusual situation of a two-level defended area. It was noticeable that when a subadult male entered the colony, it would quite often end up being pursued out of the colony by several territory-holders. Usually such chases were started by the male in whose territory the intruder landed. But as the pursued bird flew over other territories, the other males joined in. Presumably such a situation arises because the supplant-chase extends outside the territory. Also a number of records were made of territory-holding males chasing subadult males out of other males' territories. Such a defence system does not seem to have been recorded for other polygynous birds. This is interesting because it amounts, at least partly, to the males operating together as a colony. This must make it that much more difficult for young birds to gain a foot-hold in the colony until the aggressive levels in the males are beginning to drop off at the end of the season.

This extra territoriality can be regarded as an additional adaptation of the species to polygyny in that it ensures less competition for females between territory-holders since the young males are so effectively kept out of contention.

SECTION 11. COURTSHIP BEHAVIOUR

11.1 Introduction

The courtship display of the Cape Weaver is the most noticeable feature of the species and, generally, of the genus Ploceus. As has been explained, courtship strongly overlaps with territorial behaviour and early season displays in the male have considerable territorial significance, and conspicuous aggressive components, while in the female, the tendency to approach is combined with a strong tendency to flee from the aggression of the male.

Each display will be described individually and then compared with the courtship displays in other weavers.

11.2 Nest-arrival Display

This display is prevalent early in the season when a great deal of nest-building is undertaken. The adult males make repeated sorties into neighbouring fields to collect grass and then fly back to the colony with grass strands of 20 cm. or more trailing out from their beaks. As they fly over the edge of the colony, they often swoop up, increasing their altitude by one or two metres and then glide down to their nests. The approach flight contrasts with that of the female later in the season which flies to and from its nest with no such swoop or glide. This indicates that the latter has some signal function namely the accentuation of arrival and territory ownership.

The male lands usually immediately below the nest and as he lands, he gives the 'nest arrival' song. This is a short chatter usually 1 - 5 secs. long. It is very similar to the full display song, except that it is shorter and less elaborate. After the nest-arrival song, the bird normally starts building the nest.

11.3 Wing-quiver

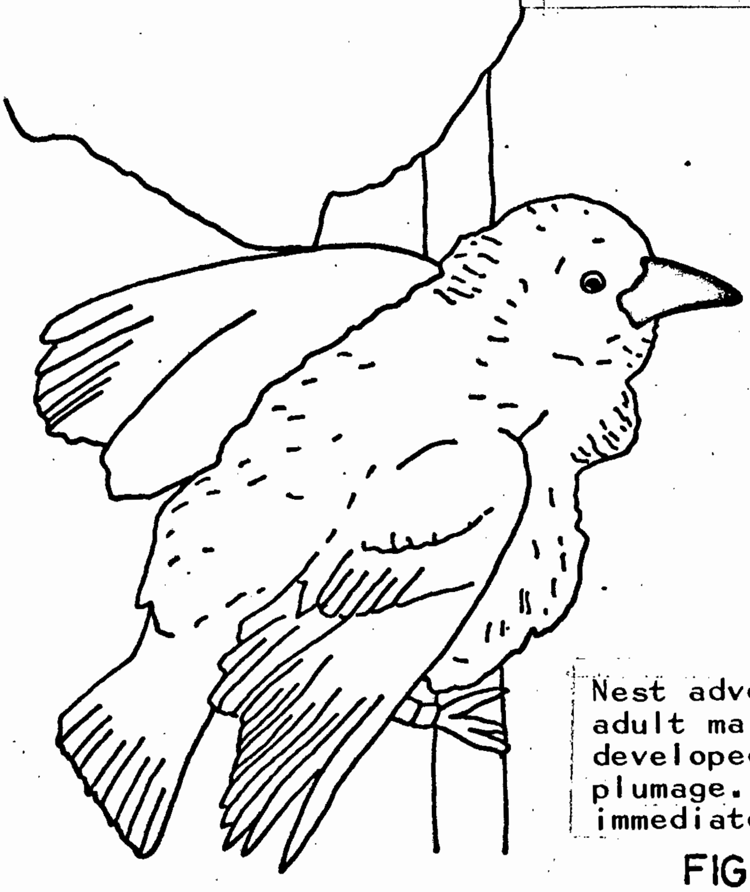
The wing-quiver is the display given by the male immediately on seeing a potential mate enter his territory or the adjacent area. The feathers are fluffed up but not to their fullest extent and the wings lowered slightly and quivered. The quiver of the wings is concentrated in the primaries and is very rapid, giving a blurred impression which is quite distinct from the single exaggerated flick of the wings in the bill-raised posture.

Bursts of low intensity advertisement song are given in conjunction with the wing-quiver. The feathers of the crown are also prominently raised in this display. The wing-quiver is usually performed a little way away from the nest and the classic pose is shown in Fig 11 : 1 where the male is perched, at the end of the twig supporting one of his nests, on the look-out for passing females.
The wing position is clear and the black streak on the breast is visible, because the chest feathers are fluffed.

If a likely female is seen, the bird will immediately fly down to the nest and go through the ritual of nest advertisement.

FIG:11:1

Wing quiver being given by an adult male on the look-out for passing females. Perch position is the end of a reed stem above labelled nest.



Nest advertisement by the adult male showing the fully developed fluffing of the plumage. Perch position - immediately below nest.

FIG:11:2

11.4 Nest Advertisement

This display is orientated entirely to the nest but can be made at a nest in any stage of development from the initial ring onwards. The displayer normally places himself below the nest entrance, but sometimes a partial display is given standing on top of the nest, or at early nest stages, inside the initial ring.

The position of the feet when the bird is below the nest depends on the surrounding vegetation. In nests built in trees, the feet cling to one side of the entrance, since there is plenty of room to hang below. If the nest is built in reeds, the movement of the displayer is restricted and it perches on a reed stem as near as possible to the entrance with the body orientated mostly upright. If there is space between the reeds, the bird hangs on in the same manner as those with tree nests. (Compare Fig 11.3 with 11.4).

The display begins as a repeat of the wing quiver, the body plumage partly fluffed, the wings quivered and a low intensity advertisement song being sung. The display intensity then increases. The degree of fluffing increases to a maximum like that shown in Fig 11.2. The fluffing is prominent on the crown and the back of the head like a judge's wig. The feathers of the middle back, rump, throat, chest and belly are all raised as shown in Fig. 11.2. The wings are held out further than in the wing quiver posture. Notice the perch position in Fig. 11.2. This is typical of birds nesting in reed environments.

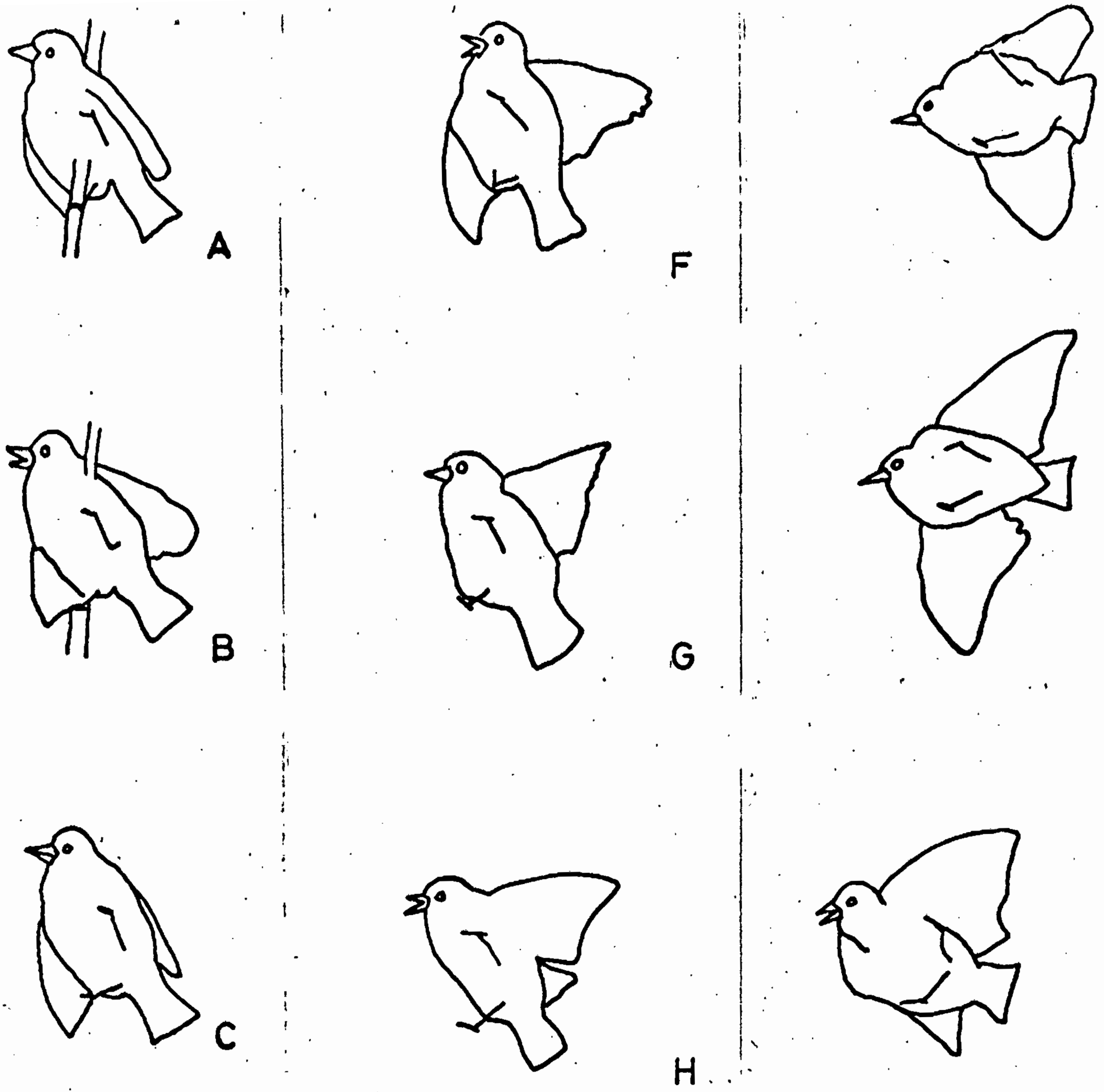
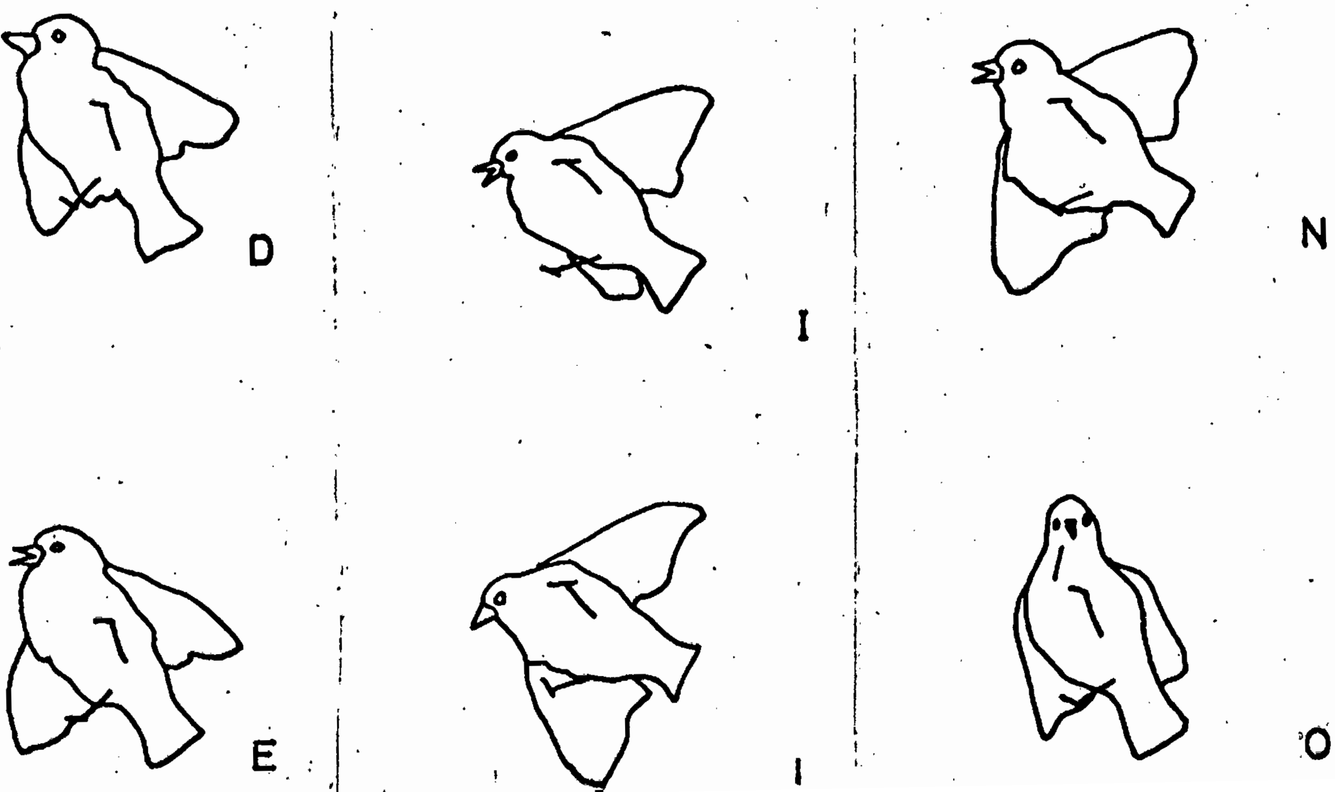


FIG.11:3- Full advertisement display sequence of adult male. Note swivelling of the body typical of birds displaying in nest environment.



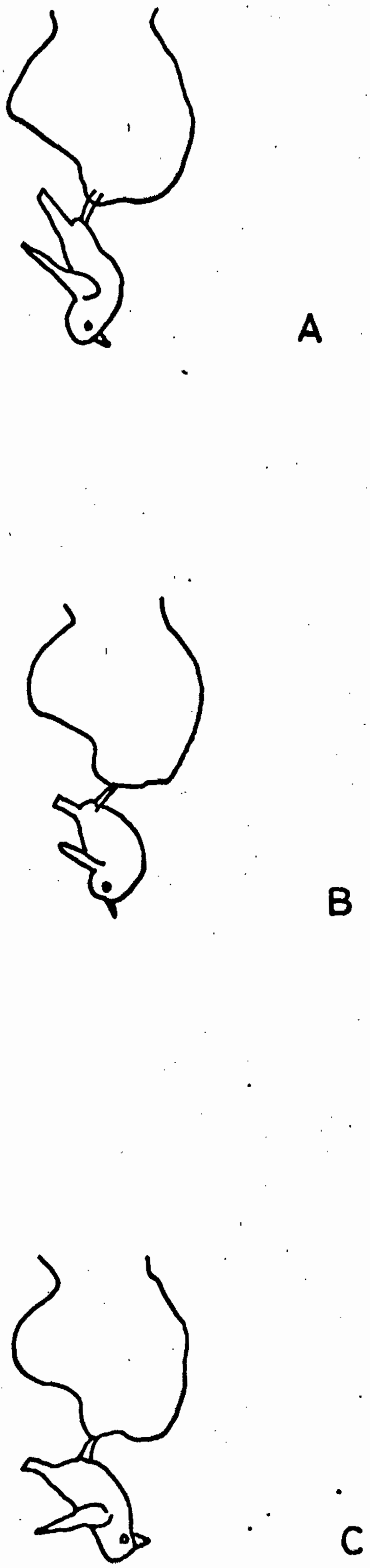


FIG.11:4

Full advertisement display seen in side view in a tree nest where there is freedom of movement below the nest.

If the female approaches to within about 6 m. of the nest the display increases further in intensity. The song becomes continuous with a full range of chatterings and wheezings emanating from the open beak - the 'swizzle' song (Skead 1947). It is not clear which of the display songs Skead referred to, but the name 'swizzle' seems appropriate to the cacophany of chattering, reeling and buzzing calls given in this song.

The wings are opened almost to their fullest extent and are then flapped while open in a slow quiver. The slow quiver is continued while the degree to which the wings remain spread varies. The development of this display is shown in detail in Fig 11.3. At the top of the illustration, A shows the bird in the wing quiver position (reed environment), the wings being quivered slowly (the impression being not of a blurr but of distinguishable movement) and gradually opened to their fullest extent as shown in F.

The highest intensity develops where the whole body is pivoted on the perch position and swung about (shown H to L) and the angle of the body is lowered to just below the horizontal. Within the body movement, the head is thrown from side to side and the bird sings continuously.

When the male is hanging free, the movements are the same but the foot-hold position allows the body to be swung about in a greater number of directions. Fig 11.5 shows the sideways outline which indicates the body angle. The head position may be anything from right up by the legs (C) to hanging down almost vertically (A).

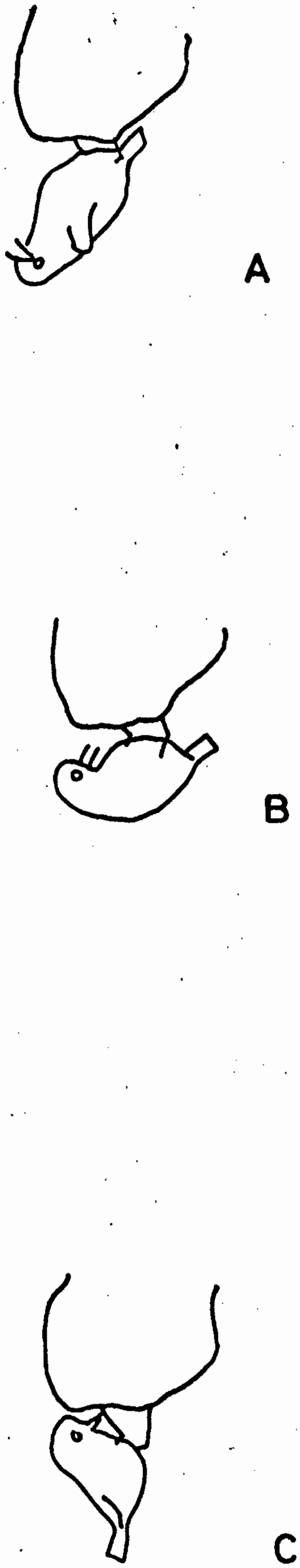


FIG.11:5 - The nest-advertisement display showing the varying positions of the head in relation to the nest.

Fig 11:4 shows an exaggerated version in which the bird's beak is pointing in the opposite direction to the nest and the body line is vertical.

The body can also be moved in the sideways plane and pivoted from side to side through about 15 degrees and the head can be twisted to almost any angle, usually directed at the approaching female.

11.5 Female Wing Quiver

If the female is attracted by the displaying male, she will first fly to a perch near the nest, but still a few yards away from it, and there she gives a wing quiver. This is almost identical to that of the male except that the general body plumage is not fluffed but is partly sleeked. The quiver is fast, giving a blurred appearance and the lifting movement of the wing is from the shoulder so that the angle increases from the wing tips. The wing is therefore not drooped like the male's, but is tipped forward at the shoulder pivot, raising the vibrating wing tips away from the rump.

After the wing quiver, in an idealised sequence of events, the female flies down to the nest and perches close to the entrance.

At this stage the sequence of behaviour becomes more difficult to describe because a number of different situations may develop according to the degree to which the pair-bond has been cemented. But for the purpose of this initial description, an idealised sequence will be described and the variations on the theme, later.

11.6 Female Nest Entry

The female is perched at the nest entrance and may give wing quiver displays, some of which may become quite pronounced, the wings being raised away from the body. This is shown in Fig. 11.6 where Part A is the arrival of the female, the male being positioned below the nest giving the full advertisement with song and display. Part B shows the female's low intensity wing quiver in which only the distal part of the wing is quivered. In Part C, the high intensity wing quiver is seen where the wings are nearly half-open. This display may be accompanied by the female directly attacking the male with lunges aimed at his head and chest. This occurs if the male is very close to the nest entrance and is therefore 'in the way' of the female. The end result is that the female manages to scramble into the nest.

11.7 Circular Flight and Nest-wheeze song

As the female enters the nest, the male's advertisement display switches to its highest intensity, the circular flight, or to the nest-wheeze song.

The former consists of a further increase in 'agitation'. The male hops back and forth 'frenziedly' beneath the nest giving an even more strident version of the advertisement song. Instead of the even mixture of rattles, churrs and buzzes, the song becomes interspersed with more strident, sharp, scolding phrases. Any neighbouring male which is normally tolerated, will be attacked if it comes at all close, and the displaying male may take off in a circular flight

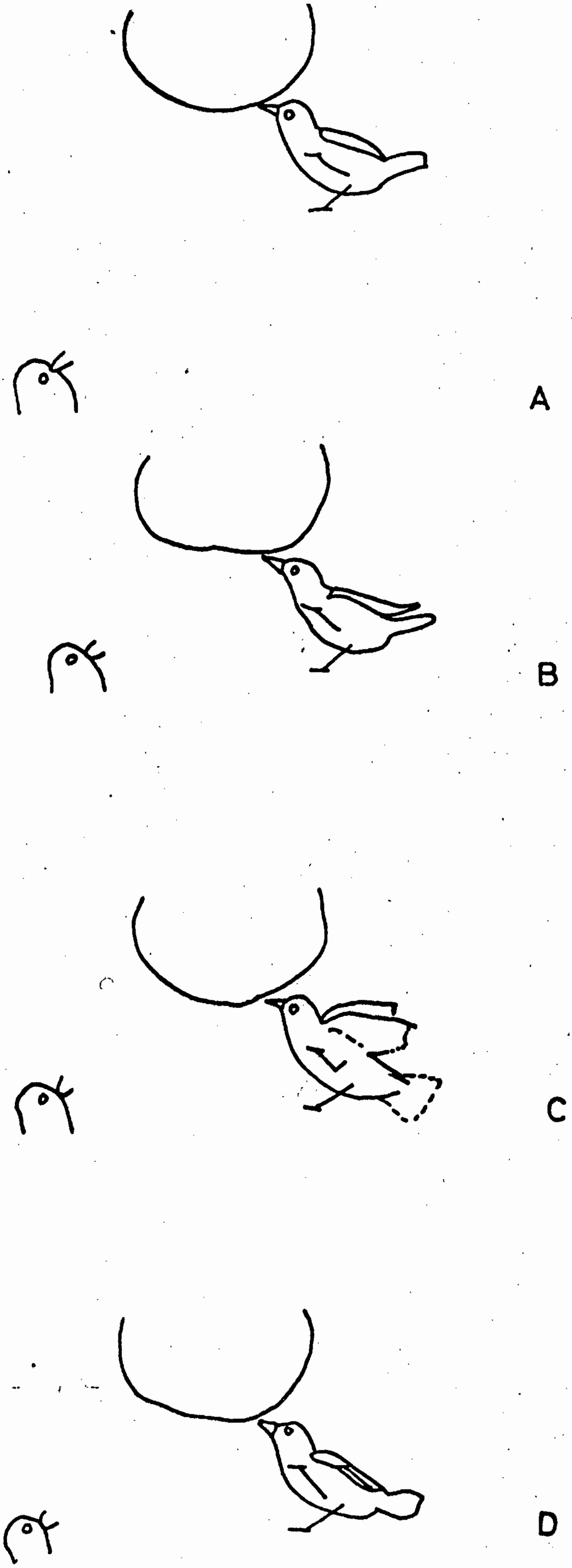


FIG.11:6

Female Nest Entry Sequence. The female is giving a wing quiver display and the male is giving an advertisement song below and to the left of the nest around the nest. During this flight, the male sings all the time and dive-bombs other males who are sitting peacefully in their own territories. The displaying male sings stridently while flying. Landing back beneath the nest, he will either continue with the lower intensity advertisement display, or switch to the wheeze call.

This call is very similar to the aggressive wheeze call described above in connection with the aggressive dance. It also consists of a long drawn out 'wheeze, wheeze .... wheeeeeeze', a buzzing call. The male perches just below the nest into which the female has recently entered. The feathers are half-fluffed out and the characteristic pose is shown in Plate 11:7 where the wheeze call is being given right into the mouth of the nest.

11.8 Female Look-out posture

When the female enters the nest, she obviously becomes invisible to the observer. Very often, however, her activity consists of pushing and pulling at the walls of the nest chamber and the resultant bulging is visible. She then hangs her head out of the nest entrance. The amount of head visible beneath the nest varies from a few millimetres of the beak tip to half the head. The beak is pointed vertically at the ground. This display is very characteristic and may continue for some minutes. The head is not moved during this time. Presumably the bird is sitting in the egg-chamber whilst holding this position. The female will not 'look-out' until the male has stopped wheeze-singing and has moved away out of reach

PLATE 11:7 The adult male giving the wheeze call directly into the entrance of the nest into which the female has just entered.

of the nest entrance. Sometimes when the female appears, the male will fly to the nest entrance again, but if so, the female will defend the nest by jabbing down at the male's head, until he is forced to move out of range. The female's attack can be vigorous and one was observed actually to grip the male by the top of the head and keep him hanging there for a few seconds before he managed to shake free.

11.9 Female Precopulation Display

The female flies out of the nest and perches nearby. The head is hunched into the body and the tail fanned and quivered. The wings are lowered a little and vibrated as in the wing-quiver except that the wings are lowered at the shoulder rather than being pivoted forward from the shoulder. As the tail is fanned, it is also tilted up occasionally exposing the cloaca. At its highest intensity, this display is accompanied by a reedy copulation call, and the tail may be fanned and tilted so high that she may topple over and lose her perch.

11.10 Male Copulation chatter and Copulation

The male reacts to the female's precopulation display by giving a short sharp chatter and flying to her, landing on her back and copulating in the normal passerine manner by sideways lowering and twisting of the tail to bring the cloacas together. The male's wings are opened during this action and the female maintains a hunched position. The copulation does not last more than a few seconds whereupon the female will hop to another perch within the male's territory and rest and preen. The male will often fly back to his nest and continue the advertisement display sometimes supplemented by further circular flights.

The female precopulation display is highly attractive to any male and neighbouring males or even transitory immature males may attempt to mount the female.
In the territory-owner's circular flights such males are dive-bombed or chased out of the territory.

Conclusion:

Table 11.8 presents an idealised ethogram of the courtship sequence described above. The table has been drawn to show a simple stimulus/response system. The sequence may in fact occur occasionally in the wild but each stimulus and each response is affected by so many variables that the ethogram is a great simplification.

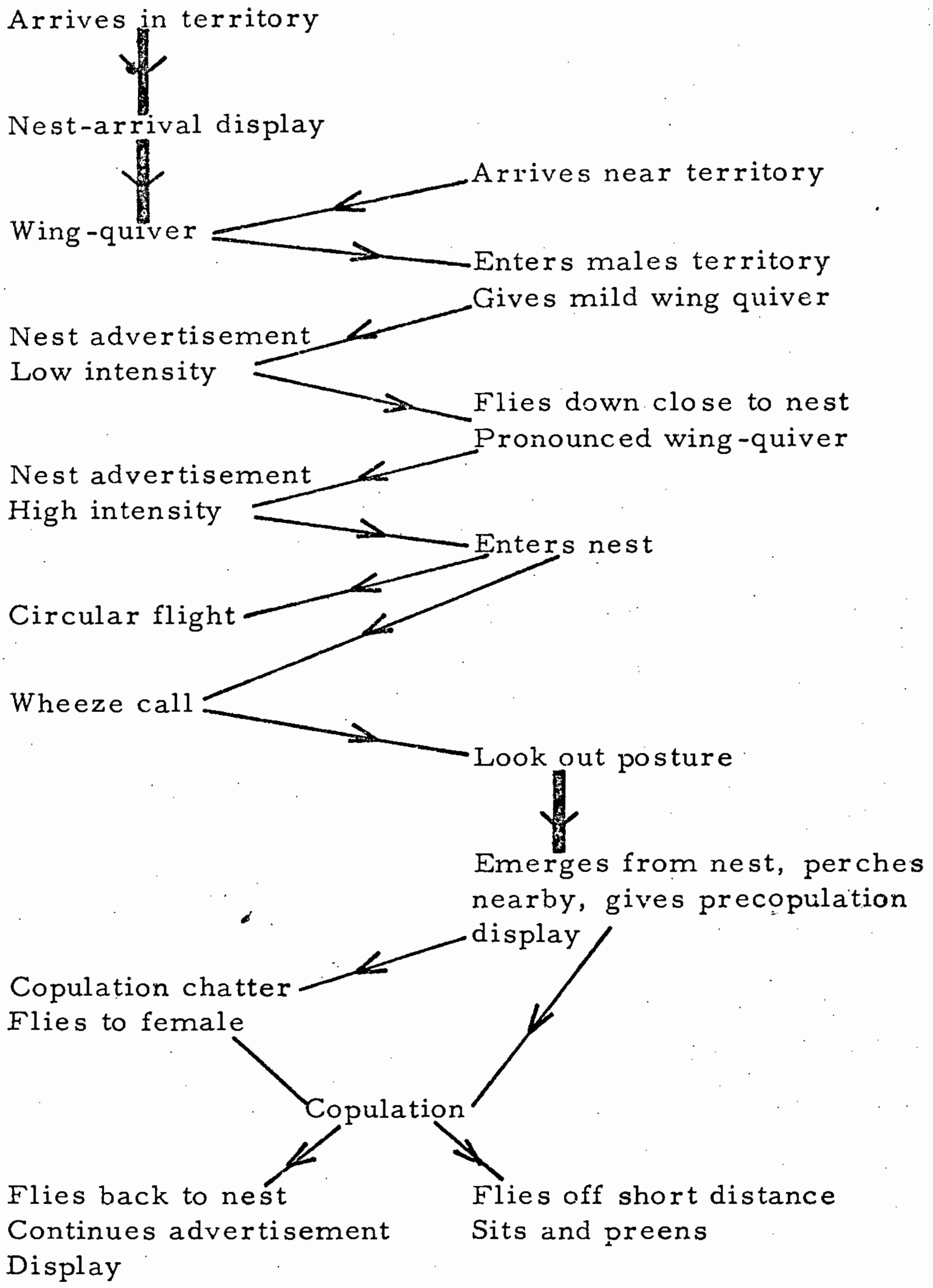


TABLE 11.8 - An idealised ethogram showing the complete courtship sequence in the Cape Weaver.

SECTION 12. - BEHAVIOUR VARIATIONS AND HIERARCHY STUDIES

12.1 Introduction

In the previous two chapters, a basic description of the Cape Weaver's behaviour patterns have been given and an idealised ethogram of courtship has been presented. Whether or not a bird will switch from one behaviour to another in such a sequence is governed by two major considerations and a host of minor ones.

The first major factor is the state of development of the pair-bond between the male and his current mate at the moment of observation. At an early stage of development, only a small proportion of the courtship sequence will be completed, before the female either flies away or enters the nest. At a late stage, the female's presence will produce only a minimal reaction from the male.

Minor effects such as the environmental conditions at the exact time of the encounter, - temperature, rain, sun, time of day, - all influence the behaviour sequence. Circumstances such as which behaviours have just been performed can also affect the outcome.

Some of the variations in display were monitored and have been outlined below. A special study of hierarchy in captive birds was also carried out.

12.2 Song Length : Seasonal Variation

The first display shown in the ethogram (Table 11.8) is the nest-arrival display, the most distinctive part of which is the short song. In the very early part of the season, this song appeared to be very short, in the middle, it sometimes developed into a part advertisement song and at the end, it was short again. Observations were made at about the same time of day i.e. during the last four hours before dark. A stop-watch was used to record the length of the longest arrival songs made in a given period. Usually a group of about 12 adult males was observed at one time. Two or three birds might arrive simultaneously and as soon as they started singing the stop-watch was started and the length of the longest song recorded.

12.3 Results

The results of 86 observations of the length of the nest-arrival song during the season are given in Table 12 : 1. The mean for the whole sample was 2.44 and the range 1.0 - 5.4 secs. The song is therefore uniformly short. The data were then divided into early season records and late season records and the means compared. It was found that late season nest-arrival songs were significantly shorter than early season ones ($t = 3.97$, $p < .001$). It may be noticed that the sample size in the late season is comparatively small. This was not due to the number of periods of observation being small but to the difficulty in finding any birds which were actually giving nest-arrival songs, especially late in the season when few new nests would be under construction.

12.4 Advertisement Song Length

In contrast to the nest-arrival song, the advertisement song

	Early Season				Late Season				
Date 1970	22.6	23.7	24.7	30.7	20.8	8.10	21.10	2.11	6.11
Mean Display, Time secs.	2.8	3.1	2.1	2.5	1.8	1.9	1.6	1.8	2.05
No. of Observations	13	14	13	24	7	6	4	3	2
Total Obs.		64					22		
Total Time		168.8					43.5		
Mean Time		2.6					1.9		
St. Deviation		1.29					0.23		

TABLE 12:1 Variation in length of the nest-arrival song display during the season

	Early Season	Late Season
Total Obs.	19	86
Total Time: Secs.	239.4	1928.1
Mean Time	12.6	22.4
St. Deviation	34.28	61.87

TABLE 12.2 Variation in length of the advertisement song display during the season.

appeared to be shorter at an early stage in the season and longer at later stages. The nest-arrival song is independent of females and related to the nest, while the advertisement song is part of the stimulus/ response system of courtship. It was therefore produced primarily by the presence of females although, as will be shown below, there was some social stimulation effect from other males as well.

The results of 105 measurements of the advertisement song are given in Table 12 : 2. The mean duration of the song was 20.5 seconds and the range was very large from 2.7 to 131.5 seconds. The mean and the latter extreme shows how long this call can go on for and gives some idea of its importance as part of the advertisement display. The data were again divided into early season and late season observations and the difference tested statistically. The difference between the early season mean of 12.6 secs. and the late season of 22.4 secs was found not to be significant. The main reason for the lack of significance despite the large difference in the means, was the high values for the standard deviations. The presence of a female to produce the advertisement song and display appeared so important that if the female moved off quickly, the song duration would be short and if she stayed, it would be long.

Circumstance also affected the sequence of nest-arrival and advertisement songs. It seemed that the latter was dominant over the former since, if a female was present near the nest when the male returned with building material, he would not give a nest-arrival song but start straight into the full advertisement.

Generally the advertisement song was produced only in the immediate vicinity of the most recently constructed nest in the male's territory. On one occasion, the song was given from the mouth of a partly-built Red Bishop nest. The display attracted a female who entered the "nest" but left shortly afterwards. The male then attempted to pull the edges of the bishop's nest together before giving up and flying off. Advertisement displays were also given at early stages of nest-building even when only the initial ring had been completed.

12.5 Nest-building behaviour

Little has been said about nest-building behaviour partly because it is of little direct importance to the social system. Males were observed to build up to 30 individual nests in the season of which only a small proportion would be utilised. A nest normally took about three days to complete. The division of labour between the sexes will be described in Section 13.

One curious form of behaviour involved in nest-building was that of tearing up old nests. This activity was very conspicuous at times since it appeared to require considerable effort by the male and the torn bits and pieces would often be flung in every direction. The function of the activity appeared clear in that it was a response to the limited space for nest-building. Often within a territory, there would only be a limited number of suitable branches or read-stems placed about the right distance apart for the construction of the initial ring. The space cleared by tearing down the nest would usually be used as a site for a new nest. The nest torn down was also often one which had not been accepted by a female. But little consistency could be detected in the behaviour. Sometimes nests were left intact throughout the season; sometimes nests from which chicks had fledged were torn down; on one occasion a nest left standing throughout the winter was torn down the following spring. But however inconsistent, the behaviour does serve to clear areas for new nests in the restricted territories of this highly colonial species.

Another behaviour pattern concerned with the nests was that of nest-material stealing. This was frequently observed throughout the season but appeared more common early on. Its frequency will become apparent in the time-and-motion studies described in the next section. On occasions, the extent of nest-material stealing by one bird on a neighbour's nest was such that the whole structure of the neighbour's nest was in jeopardy. It was noticeable how the thieving males showed typical fear-predominating postures of sleeked plumage while they were in the neighbour's territory. One male while stealing nest-lining material from the inside of the nest darted its head in and out of the nest apparently attempting to watch for the returning territory-holder while still obtaining the material. When a male was "caught" he provoked a fierce attack from the owner, usually a flying lunge attack that was once observed to knock the intruding bird into the water.

The importance of the nest-stealing behaviour is that it puts an even greater premium on the male remaining in the territory than is already the case in terms of competition for mates. If a male spends too much time away from his nests, then on his return his building work will have been undone and the nest even virtually destroyed. On the other hand, the successful nest-material stealer need hardly ever leave the colony in order to collect building material. This will ensure that this nests remain relatively intact and he can repel any intruders.

12.6 Male Activity Budget - Method

Observations totalling 28 hours, 34 minutes were made on the amount of time spent by different adult males on their daily activities at different times of the year. The main purpose of these observations was to compare the activity budgets of different males in relation to the extent of their polygyny. This aspect will be discussed in the next section. But if the data for the individual male are lumped, it gives an idea of how the activities of males change during the season. The various activities were divided into 12 categories as follows:-

A - Absent from the colony
B - Building a nest
C - Displaying - full advertisement display.
F - Fighting - ritualised territorial fighting such as aggressive dance.
H - Supplant of an intruder in or near the territory.
K - Feeding of chicks by the male (See Section 6)
M - Returning with nest-material
P - Preening
S - Sitting in the territory
T - Tail-flick display on intruder or neighbour
V - Stealing Nest-material from a neighbour's nest.
Y - Sitting in a tree or bush outside the territory and colony.

As can be seen, the activities recorded were only those occurring within the colony. Nothing was known of the activity once the birds were absent, though it is assumed that a lot of their time was spent feeding.

The observation method was to record the activity of the males every 15 seconds. Three colour-ringed males, the same three throughout, were observed during the study period.

12.7 Results

The results are presented in Table 12 : 3. The first figure in each column represents the number of times at each 15 sec. record that the bird was indulging in the particular activity. The figure in brackets is the percentage of time spent on each activity. The first point of interest is that there seems to be a trend in terms of time spent in the colony from 82% absence in the early breeding season when some nest building has started to only 10 - 30% absence in the height of the season. This suggests that there is considerable pressure on the male to remain in his territory during the breeding season, partly, as pointed out above, to prevent the stealing of nest-material and partly for territorial and display purposes. Unfortunately, the times of data collection were not standardised and there is likely to be a diurnal variation in activity, [illegible] This will to some extent affect the comparison as shown by the difference in the activity budgets of the 30th and 31st July which were recorded at different times of the day.

		Absent	Build	Display	Fight	Supplant	Chicks	Nest	Preen	Sit	Tail	Steal	Tree
Time	Date	A	B	D	F	H	K	M	P	S	T	V	Y
10.00	24.7.70	575 (82)	71 (10)	12 (2)	-	-	-	8 (1)	-	25 (4)	5 (1)	1 (-)	-
14.45	30.7.70	344 (61)	71 (13)	16 (3)	1 (-)	-	-	12 (2)	-	92 (16)	6 (1)	21 (4)	-
8.30	31.7.70	260 (41)	203 (32)	14 (2)	- -	4 (-)	- -	17 (3)	- -	113 (18)	12 (2)	8 (1)	- -
11.40	6.8.70	371 (55)	84 (12)	59 (9)	8 (1)	-	-	10 (1)	4 (1)	113 (17)	18 (3)	4 (1)	- -
13.40	11.8.70	527 (68)	78 (10)	24 (3)	8 (1)	-	-	8 (1)	3 (-)	100 (13)	20 (3)	5 (1)	- -
17.30	20.8.70	43 (10)	27 (6)	236 (54)	30 (7)	-	-	1 (-)	-	97 (22)	2 (-)	-	-
17.45	8.10.70	199 (36)	131 (23)	76 (13)	8 (1)	-	-	3 (-)	20 (4)	121 (22)	1 (-)	-	-
17.00	21.10.70	281 (32)	228 (26)	89 (10)	13 (1)	6 (-)	-	14 (2)	23 (3)	212 (24)	5 (1)	-	-
8.00	26.10.70	226 (27)	239 (28)	136 (16)	2 (-)	8 (1)	-	12 (1)	32 (4)	182 (21)	11 (1)	-	-
1500	5.11.70	348 (42)	-	32 (4)	-	11 (1)	9 (1)	-	10 (1)	290 (35)	10 (1)	-	117 (14)

TABLE 12 : 3 Activity budget of three males measured through one complete season. Activity was recorded every 15 seconds. The figures fiven are the combined total number of times the males were recorded in the various activities. The figures in brackets are the % values.

In section 4, Fig 4 : 5 shows that the 1970 breeding season was late to start and did not get under way until mid-August when the first eggs were laid. The relatively slow build up in displaying is therefore understandable. The activity budget also shows that a lot of the early season nest building must be more related to territory establishment or even to "practice" than to positive breeding efforts. The extent of nest-building at this stage also seemed to be related to the weather conditions, bright sunny conditions prompting more building. The weather on 31. 7. 70 was recorded as cold at first but very sunny later on. It was also noticed that although females visited the colony several times they were invariably chased off as will be mentioned below.

It is also interesting to note that according to the figures in Table 12 : 3 there was little territorial fighting until just before the nests were first occupied. It might be thought that the exact borders of the territory would be established by much fighting and aggressive dancing early in the season and that by the time breeding was fully under way, the males would have to spend little time in dispute with neighbours. The figures show that this is not so. Another point shown is that there is little supplanting activity in the early season, which supports the contention that young males do not enter the colony much until towards the end of the season. Feeding of the chicks is shown to be very much an end of season activity, for the male.

The proportion of time that males spend sitting around in the territory towards the end of the season is very noticeable and a general trend in this direction is shown in the figures.

The importance of this in decreasing the disturbance to females raising broods has been mentioned elsewhere. Finally the tendency to steal nest material is shown to be restricted to the early season. It is suggested that this is related to the fact that the nest is defended during the breeding season proper by the incumbent female soon after the nest is built. So it is likely that either the territory male or the nesting female will be present to prevent any nest-material stealing.

12.8 Courtship sequence - Female arrival

The degree of familiarity between the sexes has a strong influence on the behaviour sequence. If the female has not visited the male's territory more than a few times, her arrival close to the male precipitates an attack by him. He produces a guttural attack call and will lunge at her directing his blows at her chest and head. The new arrival immediately flees and as she does so, the male stops attacking and chases after her. We thus have the standard situation of male attack followed by sex chase. The female normally flies out of the colony, if not right out of the area. Often she lands in a nearby tree and the pursuing male lands beside her. He then chases her from perch to perch, until he eventually flies back to defend his territory or she flies even further away. This sequence is typical of early season behaviour. The contradictory picture of the male displaying hard to attract a female and then when she arrives, of driving her away again, is a common one. Occasionally this sex chase behaviour was concluded by copulation taking place in a tree up to 100m. away from the territory. After copulation, the male would soon fly back to his territory, while the female normally sat and preened for a while before following suit.

As the pair-bond develops, so the levels of aggression in the male and fear in the female become reduced. Because of the polygynous system this develops further into a stage where there is very little communication between the pair when the male starts attempting to attract the next mate to a new nest. Details of this are given in the next section.

One important aspect of the social system is that by nesting in an adult male's territory, the female, once established, is able to carry out her hood-raising activities undisturbed. It was noticed that late in the season when the males spent more time away from the colony (presumably feeding), - the females which were still feeding chicks gave more 'fear' displays than in mid-season. These displays consisted of sleeked plumage, and tail/wing flicks. They were usually in response to my movements in the hide in the middle of the colony. In mid-season, the adult males usually returned to the colony before I had even climbed into the hide and colony activity was back into full swing before I was settled. At the end of the season, when only six or so nests were still active, the females' "nervousness" to my presence was conspicuous. It is suggested that the main reason for this was the absence of most of the territory holders. This shows the advantage which the female obtains by choosing a mate in the middle of an active colony.

In terms of Crook's (1964) classifications (See Table 9 : 1) in which the Cape Weaver's pair formation behaviour is classified as Type IIb, the above shows that this is not quite correct.

Type II b requires that no sex chasing is performed. But sex chasing does occur in the species though to a varying degree and so, strictly, the behaviour falls between Type IIa and IIb. Nevertheless Crook is quite correct in that the Cape Weaver's nest is the concentration point for the advertisement display. Another minor error in Crook's classification is that the species of course nests both in trees, bushes and in reeds.

12.9 Social Synchronisation of Display

Crook (1964) drew attention to the "flower effect" of a weaver colony observed from a distance. He referred to how a large number of males flapping their wings in display, appear like a tree full of yellow blossom. This was suggested to act as a stronger attraction to passing females than would the same number of males displaying separately. It was Collias and Collias (1969) who quantified the observation and found that larger colonies of P. cucullatus attracted proportionately more females than small colonies.

It seemed likely that a similar attraction system operated in P. capensis. If the flower power is to work, then when one male starts to display, it must stimulate other males to do likewise so that there is some synchronisation. Observations were therefore taken of the number of males displaying at any one time.

12.10 Method and Results

A group of between 10 and 12 territory-holding males was observed. During the first ten seconds of every half minute or every minute the number of males displaying was recorded. The method was repeated for a total of 521 minutes observation time, at all times of the day on 11 different days during the season. The data for all the days have been lumped in Table 12 : 4. This shows for example that in 257 of those ten second periods, no males were displaying at all. On three occasions, 10 males were displaying simultaneously. The observations were computerised separately and the expected number of birds displaying at one time was calculated. The expected results were compared with the observed, in the standard chi-squared test and there was found to be a highly significant difference ($p < .001$). An example of the comparison for one day's observation is given in Table 12 : 5 and it can be seen that the difference is considerable.

It can therefore be concluded that in the Cape Weaver, there is interaction between males which tends to produce some synchronisation of display i. e. males are not displaying at random independently of one another. It would seem very likely that the main selection pressure for this interaction is the flower effect attracting proportionately more females, though no supporting data on this was obtained. In other species such as the Mallard Duck, (Weidmann and Darley 1971), a similar interaction between males independent of the presence of females has been proved to exist.

Number of Males Displaying	0	1	2	3	4	5	6	7	8	9	10	11	12
Number of Records	257	148	112	50	51	42	36	20	8	7	3	-	-

Total No. of Males = 124 ; 11 Observation Days ; 521 minutes observation

TABLE 12 : 4 Social Enhancement Studies : No. of Males displaying at every observation time. See text section 12.8.

Number of Males Displaying	0	1	2	3	4	5	6	7	8	9	10	11	12
Observed Records	34	42	27	17	25	19	15	8	3	0	0	0	0
Expected No. of Records (Computed)	8.98	31.21	49.71	47.99	31.27	14.49	4.89	1.21	0.22	0.03	0	0	0

TABLE 12 : 5 Social Enhancement Studies : Comparison between observed and expected number of males displaying.

12.11 Young Male Behaviour

Little has been said about the behaviour of young males except that on entering a colony as they frequently did, they showed a strong tendency to flee.
On a few occasions, it was observed that adult males apparently mistook an arriving young male for a female and reacted with a short display. This was quickly replaced with tail/wing flicks followed usually by a supplant chase of variable intensity. If a young male entered a particular territory when the holder was absent and a neighbouring holder did not supplant him, he would often spend some time looking in nests and indulging in incipient building movements. Begging chicks sometimes attracted attention. Once a young male was observed actually to enter a nest but he apparently found the technique of swinging up through the entrance difficult. The bird repeatedly swung into the nest mouth before finally gaining entry. He then looked out from the nest before jumping out again and going on to look at another nest.

The behaviour of subadult males changed noticeably during the season. In the early part, my impression was that they chiefly came to the colony at dusk to roost. Towards the end, visits were repeatedly made during the middle of the day. Nest-building was only attempted, on the edges of the colony towards the end of the season. These nests were usually built at the furthest point from the colony's epicentre, and were often placed in thick patches of reeds out of sight of other parts of the colony. Nest-building behaviour did not appear to be well-developed. Nests were sometimes not completed or appeared loose or untidy compared with those of adults.

For nests of young males to be "substandard" is a common phenomenon in other weavers (cf. Collias and Collias 1964).

Young males did defend a small area immediately around their nests against intruders. One young male was observed to see off a bird in full adult plumage. It should be pointed out too that not all males in full adult plumage held territories. It was noticeable that in roosting flocks, which were apparently non-breeding, there were often a number of males apparently in full plumage.

But as a rule the young males held a very inferior position in the colony hierarchy. A general point that was considered worth investigating was to what extent the behaviour of young males was influenced by their subordination to the adults, and to what extent to their undeveloped physiological condition. It was also noticed that young males were often supplanted by females when the former were inspecting colony nests on one of their periodic visits. The relationship between males and females in the colony and away from it, and in the non-breeding season presented a number of problems and a small study of social hierarchy in the species was therefore carried out.

12.12 Social Hierarchy - Method

The original intention of this part of the study was to establish a series of artificial colonies with variable sex ratios and to study the effect of the ratio on the behaviour of the birds. The age composition was to be varied and for example first year male behaviour studied when not influenced by the presence of older males, i.e. to attempt to determine the breeding potential of young males when competition was removed. With these experiments in mind I constructed two aviaries, but difficulties with construction, followed by continual problems in maintaining artificial colonies, mainly due to my avicultural inexperience, were met. Some observations were made on the aviary birds but each of four replacement groups rapidly became defunct. It was also found that since the cage was well away from regular human contact, the birds easily became frightened and observations had to be made from a hide placed next to the cage.

In an attempt to overcome the latter problem, a total of 11 nestlings of various ages was taken from nests and hand-reared. Five were successfully raised to fledging and released into a second aviary. There were three males and two females. The birds were initially hand-tame and could be observed without concealment. But as they grew older, they became wilder and observations had to be made from a hide. They remained however considerably less wild than those caught in adulthood.

It was noticed early on that the smaller birds which subsequently turned out to be females were generally subordinate to the three larger birds. Despite this, they were on occasion able to repulse attacks especially when they were strategically placed. The female would give a head-forward threat combined with a harsh 'growl' which often repelled an attacker. Watson (1970) in a study of caged sparrows Passer domesticus, noticed a tendency for some birds to establish territories within the cage and this gave a false impression of the hierarchy. A dominant male intruding into the small territory of a subordinate, would often be driven off. To avoid this effect, the Cape Weaver hierarchy was tested by placing a new food source in the cage away from the normal feeding areas. The technique usually used was to hang a bunch of grapes from the aviary roof. The bunch was kept small so that the birds were forced to come into contact with each other. The attraction effect of the new food seemed to provoke a higher rate of interaction than was normal at the fixed feeding trays.

All the birds were colour-ringed for identification purposes. Any direct physical attack such as a lunge, a head-forward or a supplanting fight was recorded in terms of victor and vanquished. A supplant might involve nothing more than one bird displacing another from the food, with no apparent threat or resistance taking place. A resisted supplant would be recorded in favour of the resisting bird.

It quickly became clear that both the females held subordinate positions in the hierarchy and that it was much less significant for a male to displace another female than for it to displace a male. The same applied to females. The interactions were therefore.scored as <u>four points</u> for "defeating" a male and <u>one point</u> for a female.

In the course of observations on hierarchy, other notes were kept on the development of behaviour of the chicks.

12.13 Results

The results were presented in Table 12 : 6. The total score made for each bird during the period of observation represents its position in the aviary hierarchy. By using a scoring method, a linear hierarchy is necessarily produced, but the linearity was not rigid and the dominant bird would occasionally be repelled by one of the other birds.

The most obvious point in Table 12 : 5 is that on only two occasions did a female reach an equal score or out-score a male. On all other occasions, the female point score was a long way below that of the nearest male. Although the sample size is small, the aviary studies suggest that females were therefore subordinate to males almost all year round. In other aviary studies, similar findings were made. Collias and Collias (1970) found that male P. cucullatus were always dominant on neutral ground such as at food or water, in the aviary. They also superficially tested dominance in wild birds by placing a supply of food near a colony. A known peripheral male was attacked twice as often as a known territory holder. Males also dominate females by 13 : 0 in observed interactions. Kikkawa (1968) states that male Zosterops lateralis were generally dominant over females, though this was not always statistically significant. Shoemaker (1939) found that captive male canaries dominated females except during the breeding season when females dominated their mates. Watson (loc. cit) found that adult male sparrows dominated adult females in 66% of all encounters. In most studies no correlation could be found between hierarchy position and size, but Fretwell (1969) found that in wild flocks of Juncos Junco hyemalis, the larger birds tended to dominate smaller. His index of size was wing-length.

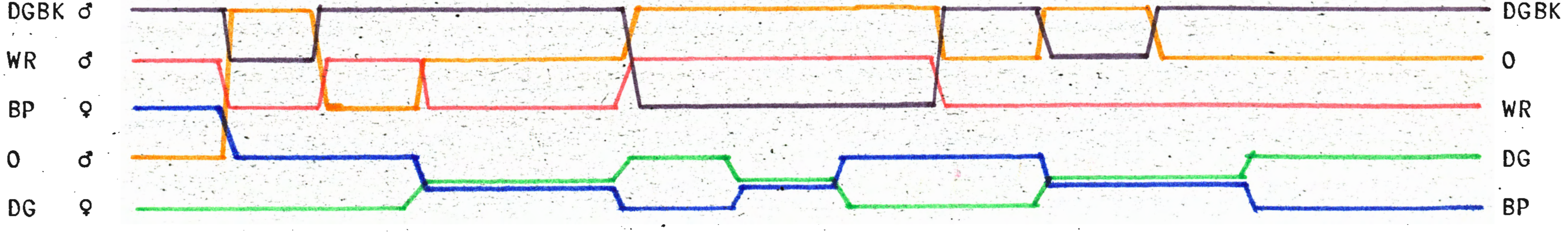
To check on the influence of size in the Cape Weaver, the figures are given in Table 12 : 7. It can be seen that on 2. 11. 70, two weeks after the first observation of Table 12 : 6, the difference in weight between the smallest male 0 and the largest female BP was only one mm. and one gram. This may explain how the female BP managed to score more points than 0 during the first observation session. Thereafter the size and weight differences between the sexes are clear cut and some other explanation must be sought for the increase in aggression in DG in mid-November of her first breeding season after fledging.

On about the 17th November, an egg was laid in a nest built in the aviary. It was not known which female was responsible nor which male built the nest, except that both 0 and DGBK were seen carrying nest-material. It is suggested however that it was female DG because an increase in aggression was found in DG on 9. 11. 71. It would seem likely that this was associated with preparatory nesting behaviour.

Although the above explains the change in female aggressiveness, there seems to be no clear cut correlation between the size of the males and their position in the hierarchy, especially when their positions change over a comparatively short period. In the early part of the study DGBK is clearly the heaviest male, but the difference is not of importance in the later stages. Nor is wing-length significant especially as there seemed to be a tendency to wear the outer tips of the primaries, hence the small wing-lengths recorded for 0 and WR. Of the

TABLE 12:6 - Results of chick heirarchy studies under aviary conditions. The scores given refer to results of interactions between the birds. Four points were given for "defeating" a male and one point for "defeating" a female.

Date 1970/71	12/10	14/10	25/10	16/12	14/1	18/3	22/3	30/3	30/4	6/5	3/11	9/11	18/11	Total
♂ DGBK	82	33	38	26	30	9	16	13	55	35	176	116	88	717
♂ O	8	47	24	5	5	154	61	147	18	78	23	39	42	651
♂ WR	32	8	25	1	4	115	38	103	14	25	12	27	19	423
♀ DG	2	5	0	0	0	2	5	2	3	1	0	9	19	48
♀ BP	14	6	13	0	0	0	5	3	4	1	0	0	0	46



Date	2.11.70		22.12.70		23.3.71		18.11.71	
	Wing	Weight	Wing	Weight	Wing	Weight	Wing	Weight
Male DGBK	86	50	88	41	88	47	87	44
Male O	84	43	88	37	88	48	84	45
Male WR	88	46	88	37	91	46	84	43
Female DG	81	42	81	30	84	39	82	37
Female BP	83	42	82	31	83	40	83	38

TABLE 12: 7 - Weight changes and wing-length changes with data of the five aviary birds.

broader trends in the relative male positions, it seems that DGBK lost his position during the three months January to March, but held the dominant position on most other occasions. The only physiological event that might be related to this, is that January to March was the time in which all three males moulted. It may be that aggression levels change during this time and that this was the main reason for the change in hierarchy.

However, all the above conjectures are based on a very small sample of only five aviary birds. Given larger samples the trends might have become clearer.

12.14 Hierarchy - Discussion

It can be a doubtful procedure to extrapolate from aviary studies to birds in the wild. Where hierarchy studies have been carried out on both captive and wild birds e.g. Kikkawa (1968), a similar situation has been revealed, especially if aviary phenomena such as fixed territories are taken into account. The most important trend shown in the above study on the Cape Weaver is that the female is subordinate to the male at all times except during the breeding season. It is suggested that this will apply equally to wild birds. This would explain the observation that the female can successfully defend the nest area against visiting young males as mentioned above. It would also fit in with the finding that females tend to suffer higher mortality and that the adult ratio favours males. In other words, where competition for food does occur, males would be expected to outcompete females, particularly when males have attained full size.

But such a system could not be absolute, otherwise in times of severe food hardship, all the females would die, leaving a self-extinguishing population of large males. It is suggested that the counter-pressure against social dominance might be the relation between hunger and aggression. Thus the hungrier a bird became the more aggressive or at least more forceful it would become in its attempts to obtain food. In other aviary studies not related to hierarchy, there is evidence that such a system does exist. Studies by Andrew (1957) and Hinde (1959) showed that increasing hunger did not so much increase aggressiveness, but did decrease fear which had the effect of making the birds more forceful. If, as seems likely such a system operates in the Cape Weaver, then the influence of sexual dominance will be considerably reduced at least to the point where it could not operate disastrously, but would still give the male some advantage in competition for food. It should also be pointed out that the Cape Weaver aviary study was carried out only on first-year birds of ages all within a few days of each other. In natural populations, it is possible that a more complex hierarchical system might exist where, for example, experienced females might be able to hold their own or even dominate first year males. This would act as an additional counter-balance to a male-dominated population.

12.15 Other observations on the Aviary birds

As mentioned above, another aim of the aviary study was to examine young male behaviour with and without the presence of adult males. It was hoped to show whether young males were capable of successfully fertilizing eggs when females were available to them.

For reasons stated, the comparison could not be carried out, but an attempt at breeding was recorded in the aviary. Nest material, probably of substandard quality, was provided in the aviary from the beginning of the first breeding season after fledging onwards. About once a week, a pile of freshly cut grass was left lying on the aviary floor. Although the birds were often observed mandibulating bits of grass, and sometimes small areas of the wire netting were weaved into, full nest construction did not begin until about early November. A number of partly-completed nests were built in the aviary but only one nest was completed. On about 17th November an egg was laid in this nest and on the 18th, probably because the nest was over-loosely constructed, the egg was found lying on the aviary floor.

Since female birds can produce eggs whether they are fertilised or not, this observation does not prove anything about young male reproductive capacities. But it does show that females can produce eggs at one year of age, a fact which was also established by retrapping birds in the wild.

On the other hand, the timing of this breeding attempt is interesting. It fits in with the observation that young males in subadult plumage tended to establish territories and build nests on the periphery of the colony only in the late part of the season. It is also shown in Fig 4 : 12 that the testes of young males showed some increase in early November. It is therefore suggested, although there is little supporting evidence, that young males are sexually mature by the end of their first season after fledging. In the wild, however, the competition for mates is so severe, that they never

succeed in obtaining mates or in making successful breeding attempts. The significance of this suggestion will be further discussed below. It should also be pointed out that one first year male Ploceus cucullatus was found by Collias and Collias (1970) to be capable of breeding at one year of age.
This bird was kept in an aviary with first year birds only and successfully fertilised eggs.

SECTION 13 -
POLYGYNY AND THE PAIR-BOND

13.1 Introduction

The theme running through most of the sections presented above, has been the study of the biology of the Cape Weaver in relation to its pair-bonding system of polygyny. That this type of pair-bond is unusual in birds is shown by Lack's (1968) calculation that in the taxonomic families for which information is available, only 7% are non-monogamous. Of the remainder, some are promiscuous or polyandrous and only two families are given as polygynous, namely the Icteridae and the Ploceidae. The delimitation must therefore be based on species in which polygyny is the rule rather than the exception. The literature is liberally scattered with references to isolated or occasional records of polygyny in several other families e.g. Bonner, W. (1964) - Stercorariidae; Catchpole, C.K. (1971) - Muscicapidae; Ryves and Ryves (1934) - Emberizidae; and Scherzinger, W. (1967) - Strigidae. But in these cases, polygyny is usually a product of special circumstances and only a small percentage in any population would be polygynous.

Despite the widespread reference to this mating system in the Icteridae and Ploceidae, only in a few species has the actual degree of polygyny been established. Ambedkar (1964) found a range of 0 - 5 in Ploceus philippinus, while Crook (1960) recorded a maximum of three females to one male (8%), 54% having a normal monogamous pair-bond. Collias and Collias (1959) recorded up to seven females to one male in Ploceus cucullatus. Martin (1971) found that trigamy was the maximum in the Bobolink Dolichonyx oryzivorus. Between 30 - 50%

of Marsh Wrens *Cistothorus palustris* were found to be bigamous (Verner 1963), while only 20% of Dickcissels *Spiza americana* were bigamous (Zimmerman 1966). Finally in a detailed study of the Red-winged Blackbird *Agelaius phoeniceus*, the range was from 0 - 6 females to every male (Haigh Holm 1973).

There has been considerable speculation on the adaptive value of polygyny and on the possible selection pressures which have promoted its evolution. It has been suggested, for example, that the adaptive value to the adult male is that he produces more offspring if he is polygynous than if he is monogamous. The value to the female is more difficult to elucidate and a number of different advantages have been suggested. Only in two cases known to me, have these advantages been quantified and assessed and both concerned icterids (Haigh Holm 1973; Martin 1971). None has been carried out on ploceids in the wild.

The main aim of this section is therefore to quantify the degree of polygyny in the Cape Weaver in terms of the number of mates obtained and the degree of breeding success of different levels of polygyny.

In the polygynous mating system, it has been described how the male establishes a territory, builds a nest and then displays below the nest to attract a female. The male is therefore relatively sedentary. On the other hand, the female arrives in the colony and moves around among the displaying males until she selects one male at one nest. Mate selection appears therefore to be carried out entirely by the female. One of the intrinsic problems in polygyny is to understand why a female chooses to mate with a male which already has a number of mates, rather than with an unmated male which is potentially able to render her more assistance. Observations were therefore made of the comparative behaviour of individual males in an attempt to quantify what characteristics were being selected by the female.

None of the studies of polygynous birds seem to have examined the exact nature of the pair-bond between the male and his females. Both Crook (1964) and Lack (1968) refer to the typical polygynous pair-bond as being successive i.e. once a female has been attracted and established in the territory, the pair-bond breaks down and a new female is attracted. To ascertain if this is correct, the behavioural interaction between the territory-holder and his different mates was quantified and assessed.

13.2 Method

The investigation of the mating system was carried out in detail only at the main study colony at Tygerberg. Observations at several other colonies showed that polygyny was certainly the rule, and these colonies superficially did not appear to differ from the study colony. However, only at the latter was polygyny quantitatively assessed.

This was carried out by two methods. First as many as possible of the breeding adult males and females were colour-ringed with unique colour combinations. The colour-ringing was carried out as part of routine ringing operations on flocks of birds roosting in the same patch of reeds which held the breeding colony. Very little ringing was carried out during the breeding season for fear of disturbing the birds. The result was that though several thousand birds were colour-ringed only about two-thirds of the territory-holding males were colour-ringed and only slightly less than half the breeding females. Where an unmarked male held a territory, it had to be assumed that it was the same bird throughout each breeding season. Similarly an unmarked female feeding chicks or incubating eggs at one particular nest was assumed to be the same female for the duration of that one particular nest. In the case of the males, the presence of one-third unmarked individuals was unlikely to have affected the results since presumably individual territory-holders recognised each other and a strange unmarked male would initially be chased out of the colony. In the case of the females it was more important as will be shown below.

The second part of the polygyny study was to mark every nest and to record the fate of its contents if any, throughout the breeding season, as described in Section 4. The frequency of nest inspection is given in Section 4, Table 4 : 2 and is shown to vary between once every 3.6 days to once every 8.2 days in the four seasons of study. Since the point which concerns us here is the success of individual nests in terms of number of fledged young produced, it can be seen that as with almost all breeding studies, breeding success will be an approximation.

As previously mentioned, the eggs could not be marked, so egg loss could not be measured. Similarly only once was the successful fledging of a chick observed and so, on all other occasions, a chick was assumed to have fledged if its absence from the nest coincided with the expected time of flying (18 days after laying). Clearly the breeding success is more of an approximation the more infrequent the visits, so that the data for 1968 is twice as inaccurate as that of 1970.

With the nests marked and the males colour-ringed, the next stage was to establish which nests fell within the territories of which males. This was carried out by observations from a hide in the middle of the colony. On most days of observation the numbers of the current nests within each territory was recorded. In turn it should be noted that the records did not cover the whole colony but only those territories within sight of the birds. Territories which were obscured by patches of reeds or otherwise out of sight were not monitored. Nevertheless at least two-thirds of the territories were in view.

Since about half the females were unmarked, the number of females was assessed by plotting out the duration of activity in each nest and finding the minimum number of females which could have been responsible. Table 13 : 1 gives an example of the females mated to male RDG/AW (the left and right leg colour-ring combination). The duration of activity is measured from the time of finding of the first egg (when the exact date was not known, this was, where possible, back-dated) to the end of activity in the nest. In a successful nest, this would be the date or estimated date of fledging. Each line in Table 13 : 1 represents the record of one nest observed to be within the male's territory. The minimum number of females that could have produced these results, as shown by the dotted line, is seven. If none of the females had second or third broods then the number of females would be equal to the number of nests, in this case 12.

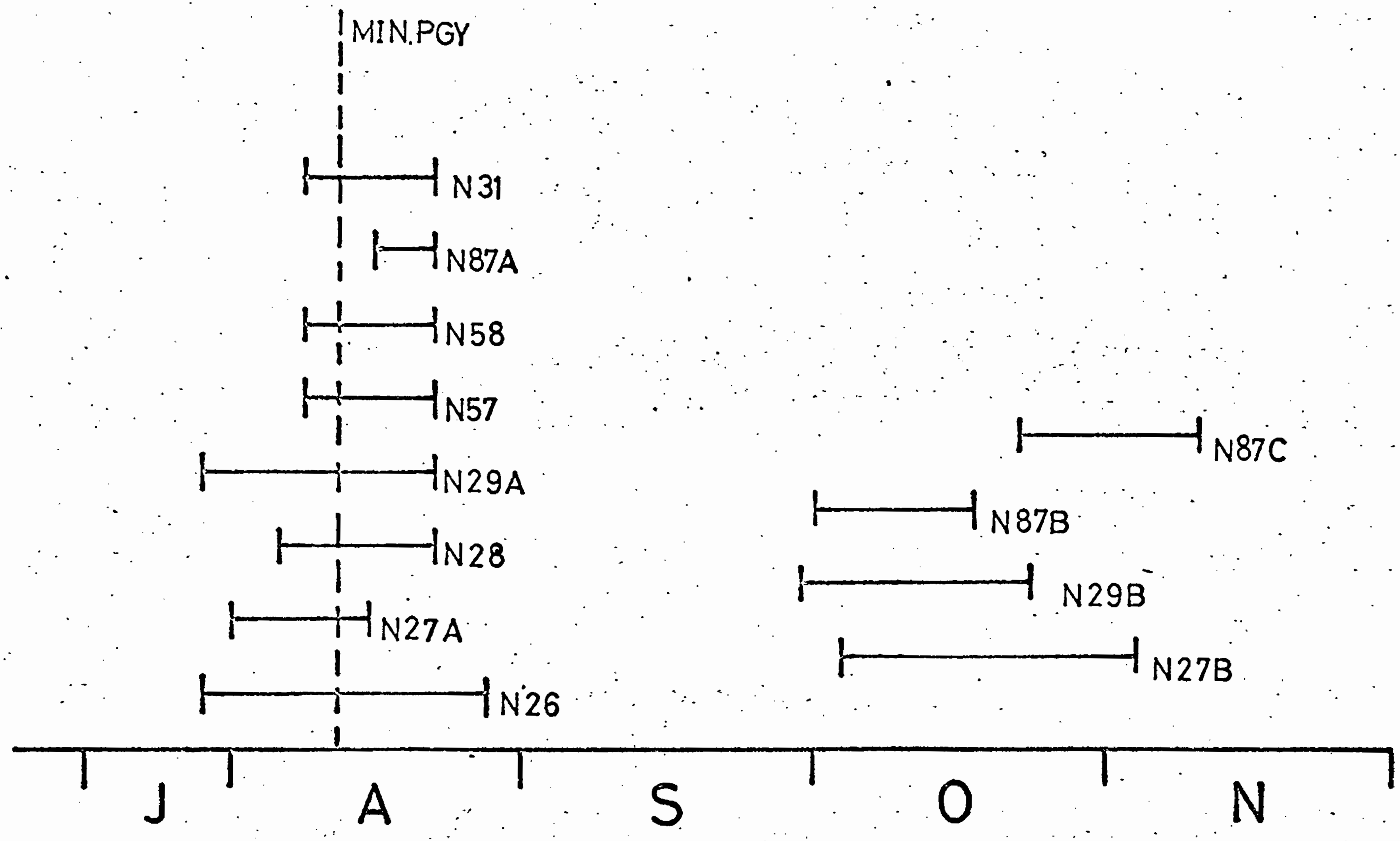


Table.13:1 Method of assessing the minimum degree of polygyny in one male adult Cape Weaver (shown as the dotted line). Each horizontal line represents the duration of one individual nest in the male's territory. The two groups of nests could all have been occupied by different females, but it is likely that the second group is made up of second broods.

The extent of double- or treble-breeding could only be observed from records of colour-marked females. During the four seasons of observation, 65 marked females were present and five instances (8%) of double-broods were recorded. However, in the observations of nest-ownership, most of the effort was concentrated on the males. It is felt therefore that double-broods may have been more frequent than is shown by these figures. Taking the example given in Table 13 : 1, it can be seen that many of the nests failed in mid-August (for details see Section 4). There was then a gap of about a month before further attempts were made to breed in this territory. Such a time lapse would fit well with the possibility that early season females took about a month to replenish their protein reserves before being able to lay a repeat clutch of eggs. It is likely therefore that the actual number of females per male was nearer to the minimum than to the maximum. In the example quoted, seven females are probably a good estimate of the degree of polygyny.

13.3 Results

The complete results of the breeding success aspect of polygyny in the Cape Weaver in the four seasons of study, are presented in the series of Tables 13:2 to 13 :9. The first four tables give the data on an individual male basis.

It could be argued that the data for the unmarked males (=UI) cannot validly be included in the tables since their nests could have been built by a series of different birds. As mentioned, it was necessary to assume that UI males built their nests in the same territory throughout the season. Evidence from marked

1968 POLYGYNY

Colour-Marks of Males	No. of Occupied Nests	Min. No. of Females	No of Eggs Laid	No of Chicks Fledged	Min Polyg. No of chicks Fledged per Female	Max Polyg. No of chicks Fledged per Female	Fledging Success %	Male Wt. gms.	Male Wt. mm.	Date of Measurement
ALG/Y	9	4	18	5	1.2	0.6	27.8	52	-	13.9.68
W/ADG	8	4	19	5	1.2	0.6	26.3	52	90	20.8.69
LG/AO*	8	4	20	5	1.2	0.6	25.0	61	-	20.9.68
UI	5	4	16	9	2.2	1.8	56.2	-	-	-
LGW/AW*	7	4	17	5	1.2	0.7	29.4	61	-	20.9.68
Y/ALG	4	3	10	4	1.3	1.0	40.0	47	-	13.9.68
UI	5	3	10	5	1.6	1.0	50.0	-	-	-
UI	5	3	10	2	0.7	0.4	20.0	-	-	-
DG/AW	5	2	11	2	1.0	0.4	18.2	46	-	20.9.68
A/WO	3	2	7	6	3.0	2.0	85.7	48	90	4.12.69
AR/-	3	2	7	5	2.5	1.7	71.4	-	-	-
AO/DGO	2	2	4	0	0	0	0	51	90	5.11.68
ADG/W	2	1	5	1	1.0	0.5	20.0	50	-	13.9.68
YR/AO?	1	1	2	0	0	0	0	-	-	-
UI	1	1	3	2	2.0	2.0	66.7	-	-	-
UI	1	1	2	0	0	0	0	-	-	-
UI	1	1	3	2	2.0	2.0	66.7	-	-	-
UI	2	1	5	3	3.0	1.5	60.0	-	-	-
UI	1	1	4	3	3.0	3.0	75.0	-	-	-
UI	1	1	1	0	0	0	0	-	-	-
UI	1	1	3	0	0	0	0	-	-	-
UI	3	1	6	0	0	0	0	-	-	-
22	78	47	183	64			34.97			

TABLE 13 : 2 Degree of polygyny and the breeding success of individual males and females in 1969. The weight and wing-length of each male is also given. UI refers to unidentified/unmarked males. * refers to individual males recorded in subsequent seasons.

1969 POLYGYNY

Colour Marks of Males	No. of Occupied Nests	Min. No. of Females	No of Eggs Laid	No of Chicks Fledged	Min Polyg. No of Chicks Fledged per Female	Max Polyg. No of chicks Fledged per Female	Fledging Success %	Male Wt. gms.	Male Wt. mm.	Date of Measurement
WDG/ALG	9	7	26	9	1.3	1.0	34.6	46	86	6.11.68
WLG/AW*	11	6	31	6	1.0	0.5	19.3	61	-	29.9.68
WR/AB	16	6	39	16	2.7	1.0	41.0	50	93	5.9.69
WY/ADG*	11	6	30	14	2.3	1.27	46.7	50	90	28.9.69
DGA/-?	6	6	15	7	1.2	1.16	46.7	50	-	13.9.68
RDG/AW	10	5	31	14	2.8	1.4	45.2	49	91	28.9.69
AO/W	7	5	19	4	0.8	0.6	21.0	47	-	10.9.68
OR/ALG*	10	5	26	15	3.0	1.5	57.7	47	-	13.9.68
LG/AO*	10	5	32	5	1.0	0.5	15.6	50	92	28.9.69
UI	10	5	25	9	1.8	0.9	36.0	-	-	-
UI	8	5	25	8	1.6	1.0	32.0	-	-	-
UI	4	4	14	4	1.0	1.0	28.6	-	-	-
UI	7	4	19	8	2.0	1.1	42.1	-	-	-
UI	10	4	31	12	3.0	1.2	38.7	-	-	-
UI	6	3	16	6	2.0	1.0	37.5	-	-	-
WO/AB?	4	2	12	5	2.5	1.2	41.7	-	-	-
A/WDG	3	2	9	2	1.0	0.7	22.2	52	93	20.8.69
DG/AW*	3	2	10	7	3.5	2.3	70.0	46	-	20.9.68
AR/YDG	4	2	12	5	2.5	1.2	41.7	48	92	21.8.69
YO/AW	2	1	6	3	3.0	1.5	50.0	61	-	20.9.68
UI	1	1	4	2	2.0	2.0	50.0	-	-	-
UI	1	1	3	2	2.0	2.0	66.7	-	-	-
UI	1	1	3	0	0	0	0	-	-	-
UI	1	1	3	0	0	0	0	-	-	-
UI	2	1	7	2	2.0	1.0	28.6	-	-	-
25	157	90	448	165			36.83%			TOTALS

TABLE 13 : 3 : Degree of polygyny and the breeding success of individual males and females in 1969. The weight and wing-length of each male is also given. UI refers to unidentified/unmarked males.

1970 POLYGYNY

Colour Marks of Males	No. of Occupied Nests	Min. No. of Females	No of Eggs Laid	No of Chicks Fledged	Min Polyg. No of chicks Fledged per Female	Max Polyg. No of chicks Fledged per Female	Fledging Success %	Male Wt. gms.	Male Wt. mm.	Date of Measurement
UI	12	6	32	5	0.8	0.4	15.6	-	-	-
WR/AB*	14	6	41	9	1.5	0.6	21.9	50	93	5.9.69
YR/AB?	5	5	11	5	1.0	1.0	45.4	45	88	28.9.69
UI	6	5	18	4	0.8	0.7	22.2	-	-	-
DGW/DGA?	9	4	31	5	1.2	0.6	16.1	47	88	21.8.69
WY/ADG*	10	4	26	5	1.2	0.5	19.2	50	90	28.9.69
-/AW	6	4	14	5	1.2	0.8	35.7	50	-	20.9.68
LG/AO*	8	4	18	8	2.0	1.0	44.4	50	92	28.9.69
WW/ABK	4	4	9	0	0	0	0	44	92	20.10.70
AY/PBK	7	3	23	7	2.3	1.0	30.4	53	92	4.11.69
RY/A	3	2	9	2	0.7	0.7	22.2	52	90	23.8.69
YB/AB	3	2	7	1	0.5	0.3	14.3	47	94	5.9.69
DGBK/A	4	2	11	2	1.0	0.5	18.2	47	91	3.7.70
UI	2	2	6	2	1.0	1.0	33.3	-	-	-
UI	2	2	4	2	1.0	1.0	50.0	-	-	-
UI	2	2	5	0	0	0	0	-	-	-
AW+BK/BW	1	1	3	0	0	0	0	48	92	22.7.70
DGR/AW*	2	1	4	0	0	0	0	47	91	29.10.70
AY+BK/OP	3	1	6	0	0	0	0	52	91	2.11.70
UI	1	1	2	1	1.0	1.0	50.0	-	-	-
UI	1	1	3	0	0	0	0	-	-	-
21	105	62	283	63			22.3%	-	-	TOTALS:

TABLE 13 : 4 Degree of polygyny and the breeding success of individual males and their females. in 1970. The weight and wing-length of each male is also given. UI refers to unidentified/unmarked males.

1971 POLYGYNY

Colour Marks of Males	No of Occupied Nests	Min. No. of Females	No of Eggs Laid	No of Chicks Fledged	Min Polyg. No of chicks Fledged per Female	Max Polyg. No of chicks Fledged per Female	Fledging Success %	Male Wt. gms.	Male Wt. mm.	Date of Measurement
LG/AO*	12	8	33	12	1.5	1.0	36.4	50	92	28.9.69
RDG/AW*	12	7	31	12	1.7	1.0	38.7	47	91	29.10.70
UI	9	5	24	12	2.4	1.3	50.0	-	-	-
UI	9	4	25	12	3.0	1.3	48.0	-	-	-
OR/ALG*	8	4	20	5	1.2	0.6	25.0	47	-	13.9.68
DGP/A?	11	4	24	5	1.2	0.4	20.8	-	-	-
WY/ADG*	6	3	15	6	2.0	1.0	40.0	50	90	28.9.69
ADG/LGLG	6	3	14	1	0.3	0.2	7.1	56	93	1.7.71
A/BP	4	3	11	5	1.7	1.2	45.4	45	86	29.10.69
AW+BK/BB	2	2	5	0	0	0	0	52	94	22.7.70
W/AO?	1	1	3	2	2.0	2.0	66.7	51	85	5.11.68
ALG/LGLG	1	1	2	0	0	0	0	36	90	20.11.69
RY/A	1	1	3	2	2.0	2.0	66.7	52	90	23.8.69
13	82	49	210	74	-	-	35.2	-	-	-

TABLE 13 : 5 Degree of polygyny and the breeding success of individual males and their females in 1971. The weight and wing-length of each male is also given. UI refers to unidentified/unmarked males.

birds showed that once an individual had established a territory, he remained there throughout the season. If one of the neighbours disappeared, the territory could expand to take over the vacated area, but generally the positions were fixed. There was therefore no likelihood that UI males built first in one part of the colony, then in another. It was also unlikely that if a UI male disappeared that his territory would be taken over by a strange UI male. The vacated territory would be more likely to be taken over by a neighbour and observation would reveal this. The inclusion of UI males appears therefore to be reasonable.

The main difficulty in drawing up the tabulated data was that sometimes an individual male would give the impression that he owned more nests, than in fact he did, perhaps by supplanting an intruder from part of a neighbour's territory while the latter bird was absent. If the absentee remained away for the duration of the observation period, records could result over a series of observations which showed more than one male owning a nest. In such cases, the nests were allocated to the male most often recorded as the owner.

In Tables 13 :2 to 13 :5, the number of occupied nests refers to the number of nests which at some stage contained eggs or chicks. It does not reflect the number of nests built in each territory. The maximum number of occupied nests recorded was 16 in one male's territory in 1969, but the maximum number of nests constructed could reach up to about 30.

The minimum number of females per male derives from Section 13.2 above, and refers to minimum number of females which could have accounted for the number of occupied nests in terms of overlapping occupation as explained. The maximum number of females is of course equal to the number of occupied nests assuming that no double- or treble-broods were raised at all.

The number of chicks fledged per female at a minimum degree of polygyny is therefore using the minimum figure for females responsible and at maximum polygyny uses the maximum figure. Presumably the actual success per female is somewhere between the two, but as explained probably nearer to the minimum polygyny figure.

Fledging success (=breeding success) refers to the percentage of chicks hatched from the number of eggs laid, both figures being approximations as is the case in all breeding success studies.

Finally in the Tables 13 : 2 to 13 : 5, the physical dimensions of each male are given. For reasons stated, birds could not often be caught during the breeding season with the result that the weights given were often not even taken in the breeding season concerned. To show how close the date is to the relevant season, the date of measurement is given. Weight was taken to the nearest gram and wing-length to the nearest mm. of maximum chord in the natural position.

The first point which emerges from Tables 13 : 2 to 13 : 5 is that overall breeding success in the three seasons 1968, 1969 and 1971 was very similar; varying from 34.97% to 36.83% or less than 2% range. 1970 was a much less successful season with success at only 22.3%. In comparisons between the degree of polygyny in different years, these differences should be kept in mind.

Second it is noticeable that the success of individual males with the same number of females could vary considerably. For example in Table 13 : 2, in males with four females (4F males), the number of chicks fledged per female was quite uniform, 1.2, for four of the males, but in the fifth, nearly twice as many were fledged. In other words, female ability to successfully raise chicks varied, as would be expected from monogamous species, from individual to individual. Therefore a male obtaining four mates all of which were substandard could succeed in rearing less offspring than a male obtaining only one female which was highly successful. Since mate selection is apparently by female choice, the probability of obtaining some good females is higher the more mates acquired. This effect is shown by the high degree of varying success in males which obtained only one female; in Table 13 : 2, varying from 3.0 chicks fledged to zero.

In terms of the degree of polygyny, the four seasons show that at the minimum number of females, a male can obtain from 0 to 8 females, the top figure being obtained for male LG/AO in 1971. If there were no double- or treble-broods, the range would be from 0 to 16 females, but such an extreme figure would seem unlikely. Taking the minimum figure as the more reasonable, this would still make the Cape Weaver the most highly polygynous species yet recorded exceeding the maximum of seven females for one male recorded by Collias and Collias (1959) in Ploceus cucullatus. It would seem however that such levels are probably normal extremes for ploceids when subjected to detailed study.

A figure often quoted is the sex ratio at the breeding colony. In the Cape Weaver, this ratio is not of course equivalent to the adult ratio since there is a large population of non-breeding males. In the observed breeding population, the breeding sex ratio varied from 2.14 to 3.76 females per male (M : F, 1968 1 : 2.14; 1969 1 : 3.6; 1970 1 : 2.95; 1971 1 : 3.76). This compares closely with figures of 2.00 to 3.57 females per male found in the Red-winged Blackbird (Haigh Holm 1973).

The breeding success of individual males varied from a maximum of 16 chicks fledged in nests belonging to WR/AB in the 1969 season, to zero. This compares with a mean of all 81 males observed in the four seasons of 4.52 chicks fledged per male. The seasonal means were:- 2.9 (1968); 6.6 (1969); 3.0 (1970) and 5.7 (1971). Since the breeding success of the whole population was low only in 1970 and comparable in the other three, it would seem that the success of individual males was more related to the breeding sex ratio than to any seasonal effects. Thus 1968 and 1970 had the lowest female ratio, and the lowest success, while the other two years had almost equal ratios and almost equal male success.

A further point which emerges from polygyny considered at the individual level is that Tables 13 : 2 to 13 : 5 present a number of examples of the success of the same males in different seasons (shown by asterisks*). If the general theory of deferred maturity is correct then a male's success should improve with experience, though it presumably drops off again if a male survives into old age. One male LG/AO was recorded in all four seasons. His number of females fluctuated by 4, 5, 4 and 8 while his number of chicks fledged showed a steady increase 5, 5, 8 and 12. In the other 14 records which include two other males recorded in three consecutive seasons and one male OR/ALG which was recorded only in 1969 and 1971, the high mean polygyny degree in 1969 was followed by a drop in the poor 1970 season. Only LG/AO was able to maintain the same number of females (6) from 1969 to 1970, but the number of chicks fledged dropped by 16 to 9. In males recorded in 1968 and 1969, and separately in 1970 and 1971, five out of seven show improvement in their polygyny level and in the number of chicks fledged. One retained the same number of females but improved the number of chicks fledged and the other dropped one female but fledged more chicks. It can be concluded that given average to good breeding seasons, males will improve both the number of females they obtain and in the number of chicks they fledge. This suggests that experience is an important factor but will tend to be overruled by poor environmental conditions.

Only three females were observed in two consecutive seasons, 1969 and 1970 and there was no marked difference in their breeding success except that AW/BB was double-brooded in 1970, and only single-brooded in 1969.

The above has considered polygyny on the basis of the individual male. But the crux of the matter is whether on the average, polygynous males achieve greater fledging success than monogynous ones and whether females achieve greater fledging success when they mate with polygynous males than when they mate with monogynous ones. Tables 13 : 6 to 13 : 9 have summarised the data for all the males monitored in each season, according to the minimum number of mates they acquired i. e. their harem size. The data has been laid out in exactly the way used by Haigh Holm (1973) to allow direct comparison between the Redwing and the Cape Weaver.

It is at once clear that with only three exceptions (harem 7 : 1969 and harem 3 & 4 1970) the more highly polygynous a male is, the more offspring he will leave and therefore the more successful he will be in evolutionary terms. Taking 1969 as an example (Table 13 : 7), it can be seen that the monogynous male rears an average of only 1.5 chicks while a male with a harem of 6 raises 10.7. These figures were then tested to ensure that differences were real. The overall fledging success was 6.6 chicks per male. The expected number of chicks to be fledged if increased polygyny had no advantage was then calculated and compared with the observed number fledged, using a chi-squared test. The chi-squared value was 43.95 and the difference between the expected and the observed was highly significant ($p < .001$). The number of chicks fledged per male by males with large harems is therefore significantly larger than for males with smaller harems.

On the other hand, there appears to be no clear trend in the number of chicks fledged per female in different harem sizes.

POLYGYNY 1968

Harem Size	1	2	3	4
No of Males	10	4	3	5
No of Active Nests	14	13	14	37
No of Eggs Laid	34	29	30	90
No of Chicks Fledged	11	13	11	29
No of Chicks Fledged per Male	1.1	3.2	3.7	5.8
No of Chicks Fledged per Female	1.1	1.6	1.2	1.4
Fledging Success %	32.3	44.8	36.7	32.2
Chi-squared values	0.31	0.65	0.04	0.35

TABLE 13 : 6 Degree of polygyny for the observed population presented in terms of minimum harem size, in 1968. For further explanation see text.

POLYGYNY 1969

Harem Size	1	2	3	4	5	6	7
No of Males	6	4	1	3	6	4	1
No of Active Nests	8	14	6	21	55	44	9
No of Eggs Laid	26	43	16	64	158	115	26
No of Chicks Fledged	9	19	6	24	55	43	9
No of Chicks Fledged per Male	1.5	4.7	6.0	8.0	9.2	10.7	9.0
No of Chicks Fledged per Female	1.5	2.4	2.0	2.0	1.8	1.8	1.3
Fledging Success %	34.6	44.2	37.5	37.5	34.8	37.4	34.6
Chi-squared values	0.36	1.30	0.05	0.19	-	0.02	1.13

TABLE 13 : 7 Degree of polygyny for the observed population presented in terms of minimum harem size, in 1969. For further explanation, see text.

POLYGYNY 1970

Harem Size	1	2	3	4	5	6
No of Males	5	6	1	5	2	2
No of active nests	8	16	7	37	11	26
No of eggs laid	18	42	23	98	29	73
No of chicks fledged	1	9	7	23	9	14
No of chicks fledged per male	0.2	1.5	7.0	4.6	4.5	7.0
No of chicks fledged per female	0.2	0.75	2.3	1.1	0.9	1.2
Fledging success %	5.5	21.4	30.4	23.5	31.0	19.2
Chi-squared values	3.3	0.86	5.07	0.33	0.14	0.25

TABLE 13 : 8 Degree of polygyny for the observed population presented in terms of minimum harem size, in 1970. For further explanation, see text.

POLYGYNY 1971

Harem Size	1	2	3	4	5	6	7	8
No of Males	3	1	3	3	1	-	1	1
No of Active Nests	3	2	16	28	9	-	12	12
No of eggs laid	8	5	40	69	24	-	31	33
No of chicks fledged	4	0	12	22	12	-	12	12
No of chicks fledged per male	1.3	-	4.0	7.3	12.0	-	12.0	12.0
No of chicks fledged per female	1.3	-	1.3	1.8	2.4	-	1.7	1.3
Fledging success %	50.0	-	30.0	31.9	50.0	-	38.7	36.4
Chi-squared values	0.06	-	0.17	0.89	2.7	-	0.21	0

TABLE 13 : 9 Degree of polygyny for the observed population presented in terms of minimum harem size, in 1971. For further explanation, see text.

Certainly the success rate does not appear to increase in proportion to increased polygyny. In general there seems to be a tendency for the middle levels of polygyny to be the most productive. Success rate appears to be reduced in monogynous and highly polygynous pair-bonds. In the manner described above, the observed number of chicks fledged per female was compared with the expected number, using the chi-squared test. The idea was to find out whether the fluctuations in success per female were significantly different from expected values or not. For example in Table 13 : 7, it appears that for females, a harem size of two is the most successful and that of seven is the least. The chi-squared values are summed and show that in this Table, these differences are not significant. In none of the other three tables were the observed success rates significantly different from the expected rates, taking the samples as a whole, each year. This is an important point because it shows that according to the data, there is no advantage for a female to mate with a male which is already mated rather than with an unmated male. Examining in detail the chi-squared values for each harem size in each year, we find that except in 1970, none of the values exceed 1.5. If the data were considered in pairs of harem sizes, none of the success rates for harem sizes would significantly differ from the others, except in 1970. This again is important because it shows that in times of low breeding success, which was met only in 1970, there is a statistically significant disadvantage for a female to breed either in a harem of one or of three (chi-squared values 3.3 and 5.07 respectively). No suggestions can be offered as to why a harem of three should be so unsuccessful.

The data is however taken from only one male's territory, and so may be a result of some odd circumstance affecting this one male. On the other hand, with a sample of five males, it does seem clear that if females choose unmated males in years of low breeding success, they will achieve lower success than if they pick already-mated males.

13.4 Discussion

The above suggests that in the Cape Weaver, the disadvantage of mating with an unpaired male only affects the result in poor breeding years. If females are able to predict whether a breeding season will be good or bad before they select their mates, then they would select already-mated males in poor seasons. Such an ability to predict the quality of a season would seem most unlikely but it could be expected that females would have evolved behaviour so that they always attempt to select a mated male. The adaptation of course need not be a direct response to the presence or absence of already occupied nests. It could be that it is a response to display characteristics in the male which would tend to attract more than one mate. If this was not the case, then there would be a tendency for females not to breed until as late as possible in order to be able to choose a mated male. Females capable of breeding early in the season would be faced with only unmated males. It would seem generally advantageous to breed as early in the season as possible (cf. Perrins 1965) and therefore more likely that females will pick a mate the behaviour of which is likely to attract subsequent mates.

One point following from this is what is the advantage to the female to pick a mated male rather than an unmated one. Why does this produce a higher success rate? As shown, the higher success rate is only produced in poor conditions. Since the female has very largely to raise the brood alone, (See Section 6), what difference does the male make. It is suggested that the main purpose that the male serves is to ensure that the female is undisturbed and can carry on all nesting activities without having to contend with attacks, territorial or sexual, from other males. It has been pointed about (Section 12) that females were noticeably more "nervous" towards the end of the season when the males appeared to be spending more time away from the colony and therefore leaving their females more subject to disturbance, than at peak breeding times. The evidence for this idea will be discussed below.

In the only other comparable study, that on the Redwing by Haigh Holm (loc. cit.), there are many similarities to the Cape Weaver. It is found that in the Redwing, the male also produces more offspring the more polygynous it is. Haigh Holm also categorically states that in both years of her study, the female also fledges more young in higher polygynous situations than low ones. I have tested her data in the same manner as that used for the Cape Weaver and find that her 1966 data are <u>not significant</u>. The 1967 data are just significant- chi-squared value 11.18 $p < .05$. Haigh Holm did not appear to test statistically either data. She merely points out that the 1967 data more noticeably proves her point and draws attention to the fact that in this year the breeding success is lower (23%) than in 1966 (32%).

The Redwing situation seems therefore to parallel that of the Cape Weaver where only in poor years did the effects of harem size make any difference. Her data for 1967 is shown in Table 13 : 10, and indicates that success values per female are only significantly different from the expected ones at low and high levels of polygyny. This differs from the Cape Weaver in which only low levels were significant and also the overall chi-squared value for 1970 in the weaver did not show any statistical difference.

The main difference between the two studies is that Haigh Holm closely examined the difference in degree of polygyny in two different nesting habitats, cattails and bulrushes. She found that there were differences in polygyny levels with cattail territory-holding males having more females than bulrush males. Haigh Holm claims that in 1967 twice as many chicks were fledged from cattails per female than in bulrushes per female. However I have tested her data again in the same manner and find that her data for this year is <u>not significantly different</u> from the expected values. (chi-squared value 2.9;$p < .05$, not significant). She seems to have made some error in her calculation.

In conclusion, in terms of the adaptive value of mating at different harem levels, in an established polygynous system, it is suggested that it is clearly to the advantage of the male to be polygynous. It is also to the advantage of the female to be non-monogamous although both my work and that of Haigh Holm show that the disadvantage only becomes apparent in poor breeding seasons. How these findings affect the possible evolution of polygyny will be discussed in Section 14.

Harem Size	1	2	3	4	5	6
No of Females	7	30	42	28	25	6
Observed No of Chicks Fledged	3	21	34	25	31	11
Expected No (E)	6.37	27.3	38.2	25.48	22.75	5.46
Difference (D)	3.37	6.3	4.2	0.48	8.25	5.54
$\frac{D^2}{E}$	3.78	1.89	0.52	0.01	2.19	2.79

TABLE 13 : 10 Breeding Success of the Redwing *Agelaius phoeniceus* - showing the chi-squared values. Original data from Haigh Holm (1973)

13.5 Choice of Male

To compare the characteristics of different males, the activity budgets of several individuals were recorded. In each case three males were selected, usually the same ones, and every 15 secs., the activity of each male was classified according to 12 categories as described in Section 12.

The results are given in Table 13 : 11. The various categories have been described in detail in Section 12. For each observation the time of day, date and for each male, in brackets, the number of occupied nests and minimum harem size over the whole season, are given.

The chief problem in Table 13 : 11 is that the differences in degree of polygyny between the males observed is very small. This part of the study would have been much more effective if males with more highly differing polygyny had been selected. A second fault is that the data is not well-spread, observations chiefly being taken very early in the season and towards the end. However certain trends are still detectable.

The first point is that male UI for the first part of the study consistently is absent from the colony more than the other two. Throughout the observations, with two exceptions, WR/AB is present on his territory more than either of the other two. WR/AB is the most successful male of the three. It should also be noticed that both DGR/AW and WR/AB

TABLE 13 : 11 (Part I)

	A	B	D	F	H	K	M	P	S	T	V	Y
1000 Hrs, 24.7.70												
UI (12/6)	234											
DGR/AW (8/5)	136	66	7				7		13	2	1	
WR/AB (14/6)	205	5	5				1		12	3		
1445: 30.7.70												
UI (12/6)	169	8	1				3		3	4		
DGR/AW (8/5)	77	63	5	1			9		12	1	21	
WR/AB (14/6)	88		10						77	1		
08.30; 31.7.70												
UI (12/6)	149	42	5						8	4		
DGR/AW (8/5)	45	122	5		2		12		4	7	8	
WR/AB (14/6)	66	39	4		2		5		101	1		
1140; 6.8.70												
UI (12/6)	204	4	4				1		8	2		
DGR/AW (8/5)	133	44	23	2			5	1	5	7	2	
WR/AB (14/6)	34	36	32	6			4	3	90	9	2	
1340; 11.8.70												
UI (12/6)	235	3	4						5	4		
DGR/AW (8/5)	167	34	9	2			7		32	9		
WR/AB (14/6)	125	41	11	6			1		63	7	5	

A = Absent, B = Build, D = Display, F = Fight, H = Supplant, K = Chicks, M = Nest, P = Preen, S = Sit, T = Tail, V = Steal, Y = Tree.

	A	B	D	F	H	K	M	P	S	T	V	Y
1730 20.8.70												
UI (12/6)	25	12	66	8			1		35	1		
DGR/AW (8/5)	15	4	90	12					27	1		
WR/AB (14/6)	3	11	80	10					35			
1745 8.10.70												
UI (12/6)	80	27	9	3			3	7	61	1		
		+ 3 cop										
RDG/RW	87	89	17						9			
WR/AB (14/6)	32	15	50	5				13	51			
1700 21.10.70												
UI (6/5)	98	11	18	6	1			7	151	4		
DGR/AW (8/5)	131	118	20		2		9		11	1		
WR/AB (14/6)	52	99	51	7	3		5	16	50			
0800 26.10.70												
UI (6/5)	106	100	11		1		1	9	50	5		
RDG/AW (8/5)	66	86	90	1	4		10		22	2		
WR/AB (14/6)	54	53	35	1	2		1	23	110	4		
1500 5.11.70												
UI (6/5)	139		8		4	1		6	108	5		
RDG/AW (8/5)	142		2						16	2		117
WR/AB (14/6)	67		22		7	8		4	166	3		

TABLE 13 : 11 (Part II) Comparison of the activity budgets of three individual males.

indulge in nest-stealing mostly from UI. It is clear that UI's comparative success both in mates obtained and number of nests occupied, conflicts with its apparent frequent absence from the colony. It would be expected that there would be a direct correlation between presence in the colony and success. It is suggested that part of this anomaly is due to activity at UI's nests being about one week to 10 days behind the other two. UI's first egg was not laid until about 20.8.70. There would therefore seem to be little significance in its early absence, this being mainly due to not having started nesting.

The second main indicator of polygynous prowess would be expected to be the amount of displaying by the males. Male WR/AB scores a total display count of 300 compared to 268 for DGR/AW. The difference is therefore not marked but then nor is the polygyny degree. Taking only two dates of UI, 20.8.70 and 8.10.70, - the UI from 21.10.70 onwards is a different bird with lower success rates - the comparative display score against WR/AB is 75 : 130. Although the sample is small, it seems that the difference is greater than would be expected if display length was important to polygyny success.

In most of the other activity categories, the activities are not performed often enough for useful comparisons to be made. This includes aggressive behaviour where WR/AB over the whole season scores 33 for supplants and 28 for tail-flick displays compared to 18 and 32 for DGR/AW. This would suggest that WR/AB is marginally more aggressive than DGR/AW, but this point is rather inconclusive as the sample sizes are small.

Another important behaviour pattern may be the amount of time a male spends in the territory especially towards the end of the season. As pointed out the male's presence may "reassure" the female and indicate that there is no danger so that the female can continue rearing the chicks without having to watch for possible danger. Once again it seems that WR/AB spends more time in his territory towards the end of the season, his score being 377 for the last four observation periods, compared to 370 for UI and only 58 for RDG/AW.

In the original tables 13 : 2 to 13 : 5, the physical dimensions of each male, where these were available, are given. Since social hierarchies are often dependent on size, it might be expected that larger and heavier males would be dominant in the colony and therefore acquire more females. Taking Table 13 : 3 as an example, it is clear that the dimensions as given are not related to polygyny success since the smallest dimensions belong to the most successful males. But the dimensions of WDG/ALG were recorded in the previous season, when, in this case, the bird was in subadult plumage. They are therefore not relevant to its success in the 1969 season. The dimensions of those males taken in 1969 show very little variation around the mean, ± 2 gms in weight and ± 1.5 mm. in wing length. The same pattern is repeated in the other years of the study. Furthermore in studies of hierarchy in captive birds, no correlation between physical dimensions and social position could be detected (see Section 12). It seems therefore that in wild populations exemplified at the study colony, the physical dimensions of individual males are not closely correlated to their polygyny success.

In conclusion, the unsatisfactory choice of males means that there is little good evidence of how the characteristics of individual males affects female choice. It is suggested that the important activities are a) non-absenteeism b) high display rate c) high aggression levels d) prolonged presence in the colony which really is part of a). One aspect not tested at all by this method is nest-building ability. In the course of early pair-bond formation, the female often enters the nest and can be seen pushing vigorously at the nest walls. This suggests that this behaviour functions to test the strength of the prospective nest. If the nest does not withstand the test, the female presumably looks for another nest and therefore another male. I would therefore add e) nest-building ability to the above characteristics. It is realised that the evidence presented for the five characteristics is not conclusive. Efforts to establish similar correlations in other polygynous species were also not conclusive (Kok 1972 on *Quiscalus mexicanus*.)

13.6 Pair-bond Studies

In order to establish the exact nature of the pair-bond in the Cape Weaver, the relationship between a male and his females was monitored. The method used was to observe the activity of an individual male and record the time spent (in seconds) in various activities related to the nest, at each of the nests in his territory. The results are presented in the series of observations in Table 13 : 12. It can be seen at once especially in the early part of the season, that the time spent in building and displaying at the male's nest constitutes the greater percentage of his activity. In Observation 1, 100% of all the displaying time was spent at two as yet unoccupied nests.

TABLE 13 : 12 Pair bond studies - the time spent by individual males at his different nests, occupied by members of his harem. (N = New Nest, G = Initial Ring of New Nest; E = Eggs, Y = Young; O = Old Nest).

RESULTS 1

Observation: 1

Date/time (in secs) / Duration Ad. F	15. 10. 70 WY/ADG	17.20 hrs.	15 min.		
Nests	26(N)	8(3E)	86(3E)	3(3E)	25(G)
Display	293	-	-	-	50
Total 343					
Percentage	85.4	-	-	-	14.6
Building	341	-	-	-	-
Sitting	55	-	1	-	-
Territory	-	2	-	-	-
Other	-	-	-	-	-
Total	689	2	1	-	50
Grand Total 742					
Percentage	92.8	.4	.1	-	6.7
F visits	-	-	-	1	-
F/M copulations	-	-	-	-	-

Observation 2/.............

Observation: 2

Date/Time/Duration 15.10.70 5.30 p.m. 1 hour
Ad. M WR/AB

Nests	19A (o)	19B(N)	12(2E)	18(3E)	22B (3E)	49(1Y)	65(2Y)	82(3E)	112(N)	64(G)
Display	15	384	5	1	-	-	3	-	5	-
Total 413										
Percentage	3.6	93	1.2	.2	-	-	.9%		1.2	
Building	-	80	-	-	-	-	-	-	-	-
Sitting	180	415	2	2	-	-	-	-	4	-
Territory	-	-	-	-	-	-	-	-	-	-
Other (Tearing down nest)	330		-	-	-	-	-	-	-	-
Total	525	879	7	3	-	-	3	-	9	
Grand Total: 1426										
Percentage	36.8	61.6	.5	.2			.2		.7	
F visits			3	1	1	7	8		4	1
F/M copulations									1	

Observation : 3

Date/Time/Duration 21.10.71 4.00 p.m. 1 hour
Ad. M WR/AB

Nests	82(G)	19(NC)	18C(3Y)	12(3E)	141(N)	112(SE)	65(1Y)
Display	-	416	7	11	20	10	-
Total: 464							
Percentage	-	89.6	1.5	2.4	4.3	2.2	-
Building	-	967	-	-	10	-	-
Sitting	4	185	3	1	17	3	-
Territory	-	-	-	-	-	-	-
Other	-	-	-	-	-	-	-
Total	4	1568	10	12	47	13	-
Grand Total: 1654							
Percentage	0.3	94.8	0.6	0.7	2.8	0.8	
M visits	-	2	3	7	1	7	1
F/M copulation	-	-	-	-	-	-	-

Observation: 4

Date/Time/Duration 22.10.70 8.30 a.m. 1 hour

Ad. M WR/AB

Nests	19(N)	112(SE)	141(NC)	82(G)	12(3E)	18(G)
Display	125	13	-	-	-	-
Total: 138						
Percentage	90.6	9.4	-	-	-	-
Building	1225	-	-	-	-	-
Sitting	250	5	-	5	-	-
Territory	-	-	-	5	-	-
Other	-	-	-	-	-	-
Total	1600	18	-	10	-	-
Grand Total 1628						
Percentage	98.3	1.1	-	.6	-	-
M visits	-	5	-	-	1	1
M/F copulation	-	-	-	-	-	-

Observation: 5

Date/Time/Duration 27.10.70 9.00 a.m. 1 hour
Ad. M UI

	89(1Y2E)	N	81(2Y)	62(1YR)	113(2E)	21(G)
Display(s)	-	272	3	-	-	14
Total : 289	-					
Percentage	-	94.1	1	-	-	4.9
Building	-	998	-	-	-	220
Sitting	-	90	-	3	-	59
Territory	-	-	-	-	-	
Other	-	-	-	-	-	
Total	-	1360	3	3	-	293
Grand Total: 1659	- -					
Percentage	-	82	.2	.2	-	17.6
Male Visits	2	4	4	3	4	-
F/M copulations	-	-	-	-	-	-

Observation : 6

Date/Time/Duration Ad. M	3.11.70 WR/AB	4.30 p.m.	1 hour				
Nests	19(G)	112(3Y)	141(C)	82(G)	12(3E)	13(2Y)	36(NC)
Display(s)	2	-	-	-	-	24	140
Total : 166							
Percentage	1.2%	-	-	-	-	14.4	84.4
Building							45
Sitting	11	5	8	10	-	342	15
Territory	2	-	-	-	2	-	-
Other (Feeding chicks)	-	-	-	-	-	40	-
Total: 646	15	5	8	10	2	406	200
Grand Total							
Percentage	2.3	.8	1.2	1.6	.4	62.8	30.9
Male visits	-	6	-	-	3	10	1
M/F copulations	-	-	-	-	-	-	-

Observation: 7

Date/Time/Duration	9.11.70	6.15 p.m.	1 hour	
Ad. M	WR/AB			

Nests	18e(G)	112(2Y N2)	141(G)	13(2YR)	82(G)	36(C)
Display(s)	-	10	-	-	3	10
Total : 23						
Percentage	-	43.5	-	-	13	43.5
Building						
Sitting						10
Territory	3		2			
Other (feeding chicks)		25				
Total:	3	35	2	-	3	20
Grand Total: 63						
Percentage	4.8	55.5	3.2	-	4.8	31.7
Male visits	-	8	-	7	-	1
M/F copulations	-	-	-	-	-	-

92.8% of all activity was concentrated on the one new, complete nest. Observation 2, of larger duration, shows a similar but less extreme picture with 93% of displaying concentrated on one nest. It is important to note that half of the occupied, active nests also received some attention though comparatively very little. This provides evidence that the pair-bond between the male and the females occupying these nests was still extant. A similar situation is shown in Observation 3, where 3/4 occupied nests received some attention consisting mainly of short displays presumably uttered by the male on the arrival or departure of the relevant female. The other main activity was sitting close to or on top of these nests, showing that the male is at least active occasionally in the parts of his territory away from his newest nest. Observation 6, shows that up to 14% of the total displaying time can occur at a nest advanced enough to contain chicks. In each set of data it is clear that there are a number of occupied nests which during the period of observation received no attention at all. But it is suggested that given long enough periods of observation, some evidence of attention would have been obtained. The amount of communication between male and female also appeared to depend on what stage in the nest cycle the female had reached and how often she visited the nest. The communication tended to take place when the male happened to be near the occupied nest when the female either arrived or departed. This often prompted the male to give a short display song and the female, a brief wing/tail quiver.

The above indicates that the male retains at least a very low level pair-bond with all the females which are active in the territory at one time. Once a female's breeding is complete, presumably the pair-bond is broken. Therefore at any one time the male Cape Weaver exhibits simultaneous polygyny. But considering the whole season, there may be old females departing and new females arriving which do not overlap one another and in this sense, successive polygyny is exhibited. In conclusion, it is unlikely that the Cape Weaver differs from other highly polygynous ploceids in that it has both simultaneous and successive polygyny, and Lack (1968) and Crook (1964) oversimplified matters by considering that only successive polygyny occurs in weavers.

SECTION 14. DISCUSSION

14 : 1 Introduction

Although almost every aspect of the biology of the Cape Weaver has been covered by the preceding sections, the primary aim of the study has been to throw some light on the problem of the evolution of polygyny. As shown in a number of other studies on polygynous species and in discourses on the evolution of mating systems, there appear to be several situations present in a bird's biology which are prerequisites for the evolution of polygyny. There are also a number of adaptations which tend to develop as a consequence of polygyny being established as the normal mating system. Comparative studies of families in which both monogamous and polygynous species occur, have led to a number of generalisations as to the factors operating at the two levels described above. It is chiefly these theories and how the Cape Weaver results fit into them, which will be examined in this final section.

14.2 Sex Ratio

Evidence has been given (Section 6) which shows that in the Cape Weaver, polygyny is not the product of an abnormal sex ratio at the nestling stage producing an excess of females. At fledging the sex ratio was equal, with a tendency for more males to be fledged and the ratio in adults also slightly favoured males. At the same time, the mean breeding sex ratio over the four year study was found to be 3.06 : 1 in favour of females. The discrepancy between the ratios was due to two factors. One was that males do not breed until their second breeding season while females breed in their first season. The other was that a number of adult males do not breed despite being in full breeding plumage. Assuming a starting theoretical population of 50 males and 50 females, it was shown in Table 8 : 4, how deferred maturity would produce a 3 : 1 breeding ratio favouring females. The closeness of this predicted ratio to the observed one of 3.06.1, does not mean that deferred maturity was solely responsible for the female excess in the breeding ratio. The observation of non-breeding males in full plumage supports the idea that two factors must be considered, deferred maturity and the exclusion of some adult males.

14.3 Deferred Maturity

In Section 8, it was pointed out that deferred maturity was a misnomer and that deferred adult plumage would be the more correct term since subadult males were likely to be sexually mature at least towards the end of their first season. The chief proposal was that deferred maturity was a direct result of the highly exaggerated level of competition for mates which occurs in polygynous species. Because of the high competition, it was vital for the male to have practice both at territorial holding and at nest-building as well. The supporting evidence from Collias and Collias (1964) was cited where it was shown that birds experimentally deprived of nest practice often failed completely to build nests in subsequent seasons. Although the weavers are unusual in building relatively complex nests compared to the Icterids, nest complexity cannot be used as an argument for a general theory of polygyny since a number of species can build apparently complex nests at the end of their first year. But the territory argument does hold for all species since only in polygynous species will competition for mates be so severe. The hypothesis put forward was that if young males adopted full plumage in their first season, they would still be unable to practise because of the high aggression-provoking aspect of the full plumage. The retention of subadult plumage would produce less aggression from territory-holders and therefore allow the young males to practise nest-building and territorial activities on the periphery of the colony.

It will be noticed that the above contends that deferred maturity in the Cape Weaver is a result of polygyny rather than a factor tending to produce polygyny. As far as it is known, all polygynous birds exhibit deferred maturity. On the other hand, it could be pointed out that deferred maturity has also evolved in a number of species which are not remotely polygynous, like the albatrosses and other sea-birds. As Lack (1968) says, the great majority of these are non-passerines and are exceedingly long-lived, so that the failure to breed in the first few years of life will not be of great consequence. Also in such cases, maturity is usually equally deferred in both sexes.

The incidence of deferred maturity in passerines does not seem to have been established. It is generally accepted that most breed in the first year after fledging.
One example of deferred maturity is given by the European Starling Sturnus vulgaris, where males breed at two years old and females at one.

Young males, however, do not have a distinctive subadult plumage. The female Starling suffers much heavier mortality (70% : 39%) than the male in their first year (Coulson 1960 in Lack 1968) which results in there being an excess of males. This in turn will produce high competition for mates among males, similar to that in the Cape Weaver. It is not clear whether the male Starlings all breed only in their second year or if some manage to breed in their first year, as would seem more likely. It is interesting to note that polygyny has been recorded in the Starling (Kessel 1950) though it is uncommon. Where it does occur, inter-male competition would be further increased.

It can be concluded that deferred maturity will tend to arise in situations where competition for mates is severe and this is especially so for polygyny. Since deferred maturity is the product of polygyny rather than vice-versa, it cannot be said to have contributed to the latter's evolution.

14.4 Male Exclusion

The second aspect of the imbalanced breeding ratio is that of male exclusion. The exclusion of some adult male Cape Weavers from breeding, as evidenced by males in full breeding plumage being present in roosting flocks, appears to operate at two levels. First, as a result of competition, such males fail to gain or maintain territories within the centres of colonies. They either manage to construct nests only at the colony periphery or away from the colony or possibly they do not build nests at all. Second, even when they do construct nests, the females do not select them as mates.

It seems to be a characteristic of colonies that there are good parts and bad parts with the centre generally being the most advantageous and the edges being the most vulnerable or unsuccessful (cf. Coulson 1968). This property of colonies revolves around their function as anti-predator and food-finding adaptations. In weavers Collias and Collias (1969) have shown that colony size is also important in attracting females, the larger the colony, proportionately more the number of females attracted.
Therefore as a result of normal competition between colony members, some Cape Weavers become pushed out of the colony centre or sometimes totally out of the colony.
In a monogamous species, this would only result in lower success in the peripheral regions of the colony, because some females probably young or inexperienced would be forced to accept them in order to reproduce at all.
In the Cape Weaver and other polygynous species an alternative is available and that is not to breed at all with peripheral males, but to select a male in the centre of the colony. This behaviour is specific to polygyny although it would still seem more to result from polygyny than to be a factor tending to produce it. Thus a female would not choose to mate with an already paired male, unless there was an advantage in doing so. If a female could not raise as many offspring by taking this action as she would in the original monogamous one, then polygamy would not have evolved.

As far as the significance of the excess of females in the breeding ratio is concerned, Section 8 gives evidence for the rejection of existence of sex-linked mortality factors in the Cape Weaver. And it has been shown above that both deferred maturity and the exclusion of some adult males from breeding, appear to result from polygyny and not vice-versa.

14.5 The Question of Food

It seems to me that one of the errors in the arguments of Lack (1968) and Crook (1962, 1964) is to place too much emphasis on the idea that polygyny is closely linked with diet. Hence the generalisation that insectivorous weavers are monogamous, and graminivores, polygynous. Yet at the very time when the pair-bond is in operation, during the breeding season, the polygynous species are largely insectivorous. They often feed their chicks totally on insects or at least on insects in the first half of the nestling period. The Cape Weaver has been shown (section 6) to feed its chicks very largely on insects with a tendency to include a higher proportion of grain in the diet towards the end of the season.

It is suggested that there is no direct correlation between diet and the type of pair-bond. Diet is related only to the type of dispersion found in each species. In other words all species which feed on a diet which tends to be scattered and locally superabundant will benefit from forming flocks and collecting together in colonial breeding areas and colonial roosts. Such a theory for the function of flocking is now generally accepted (cf. Horn 1968, Zahavi 1971, Siegfried 1969). It is suggested that the insect food of forest weavers is more or less evenly spaced through the environment and that this is one of the main reasons why forest weavers nest solitarily. The reason that the Cape Weaver nests colonially is because its mainly insect diet is clumped and locally superabundant, and not evenly spaced. My evidence for this is only superficial. When watching birds feeding from the main study colony to try to get some idea of how far each female had to fly to collect food, I noticed that almost all the birds appeared to be feeding in the same area. This was a nearby lucerne field in which there was a large number of caterpillars. The majority of the colony appeared to be operating a shuttle service between this one field and their nestlings. Only the occasional female was seen to fly over this area and out of sight over the hill. It would seem that the colony is functioning in the same way as has been suggested for roosting flocks. The location of locally superabundant food is made more easy by colonial effort and there is "information transfer" back at the colony as to where the food is. Thus a female without a ready source of food will follow one which leaves the colony and flies off in a "purposeful manner". Outside the breeding season when the classification graminivore or insectivore appears to become valid, the colony remains intact and in fact may expand if the area is a roosting one as well as a breeding one. The colony will then operate in the same way for the location of locally superabundant supplies of seeds and grain.

I therefore regard diet as being directly related to the type of dispersion in the species. Only in one sense is it connected to the type of pair-bond. This concerns not the type of food but the type of dispersion of the <u>food</u>. Thus one of the fundamental necessities of polygyny is that the female must be able to raise the chicks on her own. If this is not the case, then there would be advantage neither to the female nor to the male and the system would never evolve. It is suggested that if the food is locally superabundant and colony activity locates these patches, then there will be sufficient food for the female to raise the chicks unaided. If the food is scattered and the female has to search solitarily for the food, then it is unlikely that the female will be able to raise the chicks unaided. It should be noted that it does not matter what the food is, so long as it is locally superabundant. Any classification of the ecological parameters which promote polygyny should concentrate on the type of food utilised during the breeding season, not out of it, and on how that food is distributed and acquired.

In conclusion, I suggest that the above consists of two of the fundamentals to the evolution of polygyny in passerines. The first is the development of coloniality or at least loose coloniality during the breeding season to promote the finding of food. The second is that food should be sufficiently locally abundant for the female to be able to raise the chicks unaided. It should be noted that the above does not contend that the exploitation of food sources is the only advantage in coloniality. A number of others follow, some of which are specific to weavers such as the attraction of females by the "flower effect" (Collias 1969). Anti-predator aspects are also possibly important in certain contexts and probably were important in the evolution of coloniality in the Cape Weaver.

14.6 Duration of Breeding Season

It is suggested that another factor which would promote the evolution of polygyny is for a species to have a long and drawn out breeding season. Such a situation is of course typical of temperate regions where the winter is not severe, such as in

South Africa. If the season is short and sharp with a temporary superabundance of food, there simply will not be enough time for successive polygyny to develop. Even in a species like the Cape Weaver which has both successive and simultaneous polygyny, the attraction and "settling in" of each female takes a number of days. With a short season, the opportunities for polygyny to evolve are very much reduced. I therefore disagree with Crook (1962) who envisaged the precise timing of the breeding season to peak food abundance, as being important to the development of polygyny.

One of the apparent exceptions to my proposal is the Quelea Quelea quelea where such timing does occur. The Quelea has often been suggested as an exception to the rules of polygyny since it is colonial and yet monogamous. If the above is correct, then one reason for its monongamy would be the shortness of the "life" of each colony. Alternatively, I would propose that the Quelea has a form of "partial polygyny" by forming a very temporary bond with a female and then moving on to a new area of food abundance and forming a new pair with another female. This would amount to successive polygyny but in a series of different localities following the line of the breeding migration as described by Ward (1971). Proof of such a situation would be hard to obtain because of the vast numbers of birds involved. However Ward has shown clearly that the female Quelea tends to have second or more broods, as her ovaries start to recrudesce as the nestling stage of her first brood is complete. Again because of the large flocks involved, the chances of her remating with the same male would appear to be slim. The second point that is not known in this species is whether some males have a series of females, or whether a female would mate with a previously unmated male. Ward remarks that males still had enlarged testes at the end of one breeding cycle and might have been capable of repeat breeding. Ward has also shown that there is often a considerable population of unmated males in the population.

In conclusion, it can be said that although the Quelea presents problems, further information could show that it is not as exceptional to the above proposals as has been thought.

14.7 The Nest

Another possible pressure which may promote the development of polygyny is the building of the nest by the male. The female only assists in preparing the nest-lining. This means that the pair-bond between the two birds need not be very strong since it only has to endure at a high level for a very few days. In many passerines, the building of the nest is a combined operation necessitating a strong pair-bond over an extended period. Any tendency for the male to take over the nest-building operations will reduce the necessity of a close pair-bond and increase the potential for polygyny.

14.8 The Question of Chick Raising

It has been suggested that one of the prerequisites of the evolution of polygyny is the development of coloniality and it has also been shown how this may enable the female to raise her chicks unaided. Given an original situation in which the Cape Weaver had developed coloniality in its tree and reed colonies but remained still monogamous, one can speculate as to the process by which the switch to polygyny took place.

As Lack (1968) points out, for the female to carry out incubation and to rear the chicks on her own is quite common for monogamous species. He does not specify which species he has in mind. In South Africa, there are a number of species in which incubation is solely carried out by the female, such as the Nectariniidae (Skead 1967).
In Section 6, it was pointed out that in a number of studies of South African passerines, the males carried out only 25% or less of the nestling feeding duties (Broekhuysen 1958, 1959 and 1963). Seel (1970) showed how the male House Sparrow Passer domesticus began to decrease his participation in nestling feeding in the second half of the nestling period. It is not clear what promotes the development of this intermediate stage. Perhaps it is connected with the male having to spend more time in territorial defence, song-post singing and keeping watch for predators, which tends to make him take less than a 50% share in raising the chicks.

It should also be noted that the Cape Weaver has not reached the stage where the male takes no part in the feeding of the chicks at all. It was shown that the male often can make a considerable contribution to the feeding of the chicks, but that he tended to do so only late in the season, presumably when the chances of attracting another mate were becoming reduced. However, for most of the nests in his territory, his participation in the actual rearing is negligible.
It is suggested that in the original situation, the development of coloniality will have increased the potential of disturbance by conspecifics through the territorial intrusion. Therefore the male weaver would have had to spend more time in territorial defence, than in a dispersed territory system.

This would result in the male taking less part in the feeding of the chicks, and more time in defending the territory against the numerous comings and goings of a colony. However, the crux of the matter is that the male would not take a smaller part in the rearing of the chicks than he was able, if this resulted in a lower success rate in the number of chicks raised. At this point in the proposed evolutionary sequence, there is no element of choice. There is no alternative between monogamy and polygyny. The situation is still normal monogamy. If the female raises less offspring with less help from the male than is his ability, then this would be equally detrimental to both sexes and the tendency would be selected out.

Since it is apparently not uncommon for females to do the lion's share of the rearing of the nestlings in a number of monogamous species which are not at all colonial, one can only assume that the other activities carried out by the male, when he could otherwise be feeding the chicks, have advantages which outweigh the disadvantages of the female being the main supplier of food to the nestlings.

14.9 Female Choice

We now have a theoretical situation in which our original savannah weaver is breeding in colonies in a monogamous system, with a male mostly active in defending the territory and with reduced, but not removed, involvement in feeding chicks. The female carries out the incubation and most of the feeding. We then introduce the aspect of female mate selection. Given a colonial situation, it can be expected that the males present will vary in their attributes.

Some will be more aggressive than others and will therefore provide better defended, less disturbed territories. In the centre of the colony, food information will be more readily available. The centre of the colony will also be safer from predators. Many of these points are common to all colonies of birds regardless of the mating system. It would therefore be to the female's advantage to choose a male in the best colony position even if he was already mated. In the original situation, it would be expected that successive polygyny would be more likely to evolve rather than simultaneous polygyny, or least the male's nests would be spaced so that each nest's chick stage did not overlap with another. This would allow the male still to contribute to feeding the chicks. The fledging success would remain the same as in the monogamous situation.

It can be seen that there are two aspects to female choice suggested, one the choice of a particular male and the second the choice of a particular position in the colony, to benefit most fully from the food-finding ability of colonial activity. In the Cape Weaver, I consider that the first of these two was the more important partly because territories were so small that there could be little physical difference between one male's territory and the next. As has been mentioned, Haigh Holm (loc. cit.) found some relation between polygyny and habitat in the Redwing. It is possible that a similar situation operated in the Cape Weaver i. e. if it is advantageous for a female to select a particular habitat, say reeds instead of trees, and to try to breed in the centre of a colony, then it may be advantageous for her to mate with an already mated male in the best position rather than with an unmated male in a less good position. In different species the importance of these factors, the males "personal" attributes, the position and the habitat he defends, in female mate selection, may vary. In the Cape Weaver the first two are thought to be more important. In Icterids, it is possible that habitat is more important. In the oxyurids such as the Maccoa luck Oxyura maccoa it is also suggested that habitat is a vital factor (Siegfried pers. comm.).

In the above manner, it is suggested that polygyny would become established. Once established, the exaggerated competition between males for females and for prime areas in the colony would produce the various adaptations to polygyny such as enhanced sexual dimorphism, deferred maturity, highly developed nest displays etcetera, as have been described in the relevant sections above.

Two points arise from the above. The first is what is the evidence that this may have been the manner in which polygyny evolved and the second is, if this is so, why are not more birds polygynous.

14.10 Evidence for Evolutionary Trend

It is suggested above that one of the factors which facilitates the development of polygyny is the existence of coloniality. Here I am taking coloniality in a broad sense which includes loose colonies and grouped territories as found respectively in Euplectes and some of the Icterids. The evidence is that all true polygynous species nest broadly colonially. The main difficulty in this interpretation is that one would expect those species which are occasionally polygynous, to show an intermediate stage in development. However this does not appear to be so. Indeed it is often difficult to understand the presence of partial polygyny in such species as the Pied Flycatcher Ficedula hypoleuca (von Haartman 1951). 13% of the females observed, were mated polygynously. The flycatcher male normally defends only the area immediately around the nest-hole, but he may defend a number of nest-holes separated by up to 500 m. The adult sex ratio is equal and there are therefore a number of unmated males. von Haartman also seemed to think that the female raised fewer chicks if she received no help from the male than if she did. It is most surprising that unmated males did not take over vacant nesting holes when the owner was defending one of the others, especially as the holes were often widely separated.

It would appear one aspect of coloniality important for the evolution of polygyny is that the nests should be close enough for one male to defend the whole area. The nesting groups of some euplectines are probably close to such a limit. von Haartman also points out that most of his records of polygyny were recorded in one area where the density of nest-boxes was particularly high. It is suggested that in the natural state of scattered nest-holes, the incidence of polygyny would be even rarer than that found by von Haartman and probably would only occur when two or more nest-holes happen to occur in a small area. von Haartman appears therefore to have reported on an artificial situation created by the high density of nest-boxes.

Another characteristic of coloniality is that it usually only occurs in species where the territory is not used for feeding. If a species does most of its feeding in the territory, this usually means that the territory must be fairly large. This in turn will tend to militate against the male being able to defend a large number of large territories all at the same time. But when conditions are unusually good, there may be enough food in one normal-sized territory for more than one female to occupy a nest. It is suggested that such conditions allow occasional polygyny to develop in such species as the Wren Troglodytes troglodytes (Armstrong 1955) and the Long-Billed Marsh Wren (Verner 1964).

Orians (1969 and 1972) places considerable emphasis on the correlation between early successional habitats particularly marshes and the evolution of polygyny. I think that by including this as one of his seven parameters promoting polygyny, Orians has taken two narrow a view of the incidence of this mating system. Basically what he has done is to consider only North America and has ignored Africa where it is well known that polygynous weavers often nest in trees and bushes.

However there does seem to be a close connection in America between marsh'nesting and polygyny. It is suggested that this has nothing to do with the food production in marshes since observation has shown that species such as the Redwing seldom feeds in the marsh in which it nests. (Haigh, Holm 1973). On the other hand, as Orians says, most of the food derives from other marshes where no nesting is taking place.

According to Haigh Holm, sometimes insect emergence occurs in some marshes and not in others. This suggests that the main function of coloniality may be the location of these locally superabundant supplies of insects emerging from the swamps. An anti-predator function may also be important. The similarity to the situation proposed for the Cape Weaver is therefore strong i.e. the existence of coloniality on the one hand and a locally superabundant food source on the other. Combined, they are likely to produce small territories within a colony and the type of food source which will make it easier for the female to feed her chicks unaided. One can well imagine that once an area where insects are emerging in big numbers is located, the female Red-wings will form the sort of shuttle-service seen in the Cape Weaver.

I also do not think that Orians' prediction that polygyny will develop when feeding areas are scattered but nesting sites are restricted, is necessarily widely applicable. This is however a contentious point and difficult to prove either way. In the Cape Weaver, the variety of nest-sites possible is such that it appears there never could be a shortage. It seems that the actual habitat is not important in the species, rather the existence of an active colony and there would seem to be nothing to stop unmated males forming colonies in the vacant habitat. Orians contends that African weavers in savannah country may have a shortage of nest sites because of a lack of available trees. In natural savannah, the number of trees is often large. Only in special conditions such as the flood plain of a large river, or where human influence has caused over-population of elephants, or high agricultural development, is there a lack of tree or reed sites available. Usually the problem in weavers is to understand why some trees are utilised and not others or why the whole of the reed-bed is not used.

Orians (1972) himself remarks that on lakes near Redwing breeding areas, there were undefended foraging areas where the birds collected their food. This would imply that there were a number of areas available for nesting which were not utilised. Lack (1968) follows Orians in thinking that restricted areas for nesting are important to the evolution of polygyny. He supports this idea by pointing out that if a territory-holding male dies or is artificially removed, it is quickly replaced. Orians (1961) found that if he shot a Redwing territory-holding male, a replacement rapidly took over the vacant territory. The Cape Weaver presumably has the same potential in that there is a large population of unmated subadult males and a smaller one of unmated fully adult males. Presumably these males initially attempt to gain territories in the densest part of an already established colony, since this is the best position for the attraction of females. Having been outcompeted by the resident males, they then either build nests on the periphery of the colony or apparently often do not breed at all. The point is that the breeding areas are not at present restricted by lack of availability, but by the behaviour of the males, although one cannot be certain what the ancestral situation was. To the human eye, it seems inexplicable that the unmated males do not all at least build nests on the colony edge, or do not start new colonies elsewhere in the apparently innumerable available sites. Such a situation was interpreted by Wynne-Edwards (1962) as being an indication of the self-regulation of the population to the advantage of the group. Apart from the fact that it is not known how such a system would function genetically, except by kin selection (Chitty 1967) the evidence both for the Cape Weaver and the Redwing is that actual number of offspring produced is already at a maximum since all females apparently breed in their first year, and females can, because of the special food source, raise their broods on their own.

It seems that there is only one explanation for this odd state of affairs and that is, that it is a result of natural variation in the breeding capabilities of individual males and in the habitat where they establish territories. Given the situation where the female is already doing most of the reproductive work, then to select the best male in the best strategic position (if the actual habitat is not important) is the overriding priority; i.e. if unmated males did move off and found another colony, then the female would still choose a male in the first colony because it would offer better facilities. In the satellite colony, a low level of aggression in the males might mean, for example, a high level of intrusion and disturbance to the female. Although selection will therefore tend to produce more and more able males, and, say, select for larger and larger colonies, there will be counter-selection whereby too-highly-aggressive males will suffer higher maturity, and the feeding efficiency of too large colonies will break down.

A number of authors has concentrated on the comparison of the actual territories of different males in terms of nest cover (Martin 1971), vegetation (Haigh Holm 1973) and amount of "edge" (Verner 1964). In the Cape Weaver, the actual males themselves were compared. Although the results were not conclusive, there did seem to be some tendency for certain aspects of the behaviour of the more successful males to be more pronounced (see Section 13). Superficially, there seemed to be no obvious differences in the territories of the males. Compared to the Icterids, the ploceid territories are usually small, and in the Cape Weaver the territory of a successful male would be within a metre or two of that of an unsuccessful one. Certainly there was no difference in constituent vegetation in such a small area. Unfortunately the degree of polygyny in other colonies particularly those in trees was not monitored. It was thought possible that the polygyny was more pronounced in reeds than trees. Orians (1969) in a general discussion of mating systems made several predictions on pressures likely to cause polygyny or on situations in which polygyny is likely to arise. Of these, the prevalence of polygyny in marshes or early successional habitats has already been mentioned. He also states that polygyny will be more likely to evolve in altricial than precocial birds. However, the above discussion has dealt primarily with evolution of polygyny in passerines, all of which are altricial. The question of restricted breeding sites has also been discussed.

Finally, Orians suggests one further pressure likely to promote polygyny. This is that polygyny should be more prevalent among species in which clutch-size is influenced by factors other than the number of offspring which the parents can support. He suggests that birds feeding on low-energy food such as pulpy fruit will have small clutches because their food is not good for egg production or for feeding chicks.
This point seems to be highly illogical. It is rather like saying that if a humming-bird eats worms, it would be able to have a larger clutch. It also implies that pulp-eaters were once insectivores and evolved pulp-eating to reduce their reproductive output.

I think there is no evidence to support the idea that such birds are not attempting to breed at the maximum rate, in line with Lack's theory of clutch-size. Orians also cites the example that in stable environments, competition for food will increase and therefore birds may have to spend a lot of time in competitive activities. He says that such a situation would mean reduced male reproductive and brood-raising activity and the potential for polygyny increased. I would strongly disagree with this point of view on the following grounds:-

a) a stable environment will mean an even distribution of food and therefore no advantage to the development of coloniality, therefore no grouping of nests and therefore make it difficult for the male to defend more than one territory.

b) a stable environment will mean that the female will have to search for food on her own and therefore will be unlikely to be able to raise the chicks on her own. Orians may well be right in proposing the above pressures as one promoting promiscuity, perhaps in response to high predation rates and the difficulty of maintaining a pair-bond in a dark and complex forest. But it would not seem to apply to the development of polygyny of the type found in weavers or icterids at all.

14.11 Conclusion

It is therefore proposed that in the Cape Weaver and generally in passerines, the most important prerequisite for the development of polygyny is the utilisation of the type of food source which promotes coloniality and gregariousness during the breeding season. Other factors promoting the development of colonies should also exist.

Perhaps one of the chief reasons for the high frequency of the occurrence of polygyny in weavers is that their nests are ideally adapted to reduce predation and can be hung in a variety of sites where they are inaccessible to most predators.

Once coloniality has developed, it may be followed by the evolution of polygyny under a variety of pressures such as:-

1. The male reducing his participation in late nest activities especially the feeding of the chicks, and increasing his part in nest-building.

2. Variation in the qualities of the habitat, in weavers particularly in the strategic position which a territory offers, in the colony.

3. Variation in the attributes of different males.

It is suggested that polygyny has not developed more often in passerines because the food situation of locally abundant insects is not often met and nor are the other factors which promote coloniality.

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MORAL OF THE STORY

"During one of the perennial discussions on divorce in the daily press, a correspondent suggested that mankind ought to be monogamous because this is nature's rule, particularly in birds. Apart from the mistaken notion that what happens in nature is necessarily the best guide to what ought to happen in man, the present survey would suggest that irregular mating habits are permissible in vegetarians" (Lack 1968)

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