

BREEDING BEHAVIOUR AND POLYGyny IN THE

RED BISHOP BIRD

Euplectes orix (L).

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INTRODUCTION.

The red bishop bird, Euplectes orix, is a widespread and locally abundant member of the weaver family, the Ploceidae. It is found over most of Southern Africa, and as far north as Uganda in the Eastern savannah belt. Large flocks may be found in association with other seedeaters, and the breeding colonies in reeds or tall grass in marshy areas may contain from five to several thousand birds. Recently it has also been recorded as nesting in standing crops in some areas.

The adult birds are sparrow-sized, 12-15 cm in length and weighing 20-30 gm. The wing-length in the males ranges from 70-83 mm, and in females from 64-72 mm. Mackworth-Praed and Grant (1962) mention that birds from the Cape are larger, and that there appears to be a decrease in size of birds further north; measurements taken in this study seem to confirm this. During most of the year, both sexes are a mottled light brown colour, with a pale streak above the eye, and the underside pale to almost white, with darker streaks. However, at the beginning of the breeding season the adult males moult into their striking nuptial plumage: the abdomen and face mask are black, while the crown, throat, breast, rump, upper and under tail coverts are scarlet. The mantle feathers are tawny, but the wings and tail remain brown. The bill colour also changes from flesh-coloured to black.

Hall and Moreau (1970), whose nomenclature is used for all the passerine species mentioned, regard three species Euplectes orix, franciscus and nigroventris as comprising the "orix superspecies". All three retain the brown wings and tail in the male breeding dress, but show variations in the extent of the red and black plumage. There is no apparent overlap in their ranges, or any evidence of inter-breeding. Two further species, E. hordeaceus and E. gierowii, differ in that the wings and tail of the male are also black during the breeding season. Although slightly larger, their plumage is in other respects very similar, and these five species are termed a "species group".

There is surprisingly little published information on any of these species. Lack (1935) first described territorial behaviour and polygyny in Euplectes hordeaceus, and later Moreau and Moreau (1938) and Fuggles-Couchman (1942)

compared the ecology of E. hordeaceus and E. nigroventris. Skead (1956) produced a valuable basic study of E. orix, and showed it to be polygynous. Emlen (1957) made observations on several Euplectes species in Rhodesia, but the species orix and hordeaceus are confused in his paper, and it is not always clear which he is referring to. Later studies dealing with E. orix by Brooke (1964), Schmidt (1968) and Woodall (1971) are primarily concerned with clutch size, breeding seasons and nesting success, rather than behaviour. However, Crook (1962, 1963, 1964) has produced an important series of papers comprising a comparative study of behaviour in the entire weaver family. He refers mostly to the genus Euplectes, but also quotes observations on individual species, including E. orix. Collias and Collias (1964) have described nest-building behaviour in the weavers, but also mainly at the generic level.

Polygyny is of very limited occurrence in birds, only being found in 2% of the species for which adequate data is available (Lack 1968). Several authors have provided theoretical explanations for its development (Orians 1969; Crook 1963, 1965), but more comparative field studies are required. The various Euplectes species seem a most suitable group for investigation of this phenomenon, and the object of the present study was to examine the behaviour of the male Euplectes orix in relation to its polygynous habit. It is hoped to extend this work to a comparative study of other Euplectes species, and comparisons are made where data is available.

METHODS.

The birds were observed from hides placed at the edge of the colonies, so as to command the entire nesting area. Consequently, small compact colonies were selected. Each nest was numbered with a 4 cm X 7 cm metal plate, with a black number painted on a white background. These numbers were wired to reeds so that as far as possible they could be read from the hide through 12 X 40 binoculars. The birds completely removed the paint from one numberplate, and initially inspected them carefully on approaching the nests. However, they were soon accepted and ignored. The nests were inspected every three days, or more often when changes in their contents seemed likely. Every nest laid in was regarded as a mate acquired by the territory holder.

As it was important to have individually identifiable males, coloured leg rings were used for marking. The birds were caught by means of four-shelf, 3 cm mesh mist nets, set up either at the breeding colony, or where the flocks were feeding. Netting was done almost entirely by day, as there was the risk of keeping the females off the eggs at night, and the colony sites made netting in the dark extremely difficult - at one place the nets were usually erected over the water. Day-light netting had the disadvantage that the birds could see and thus often avoid the nets. Strong winds also limited catching time.

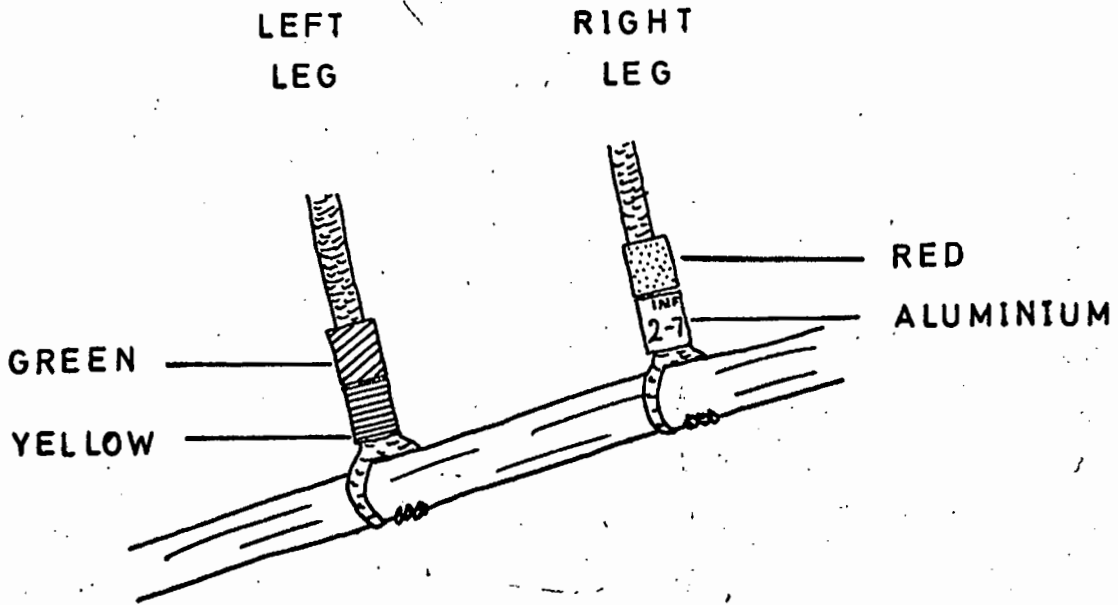
A total of 274 birds were caught and marked. All received a standard 3 mm aluminium ring issued by the NUBRA, on the right leg. Females and immature males are both brown plumaged, distinguishable in the hand by size measurements, but virtually impossible to tell apart in the field. Consequently females were fitted with a white ring on the right leg, in addition to the aluminium ring, while immature males were fitted with a white ring on the left leg. Males each received an individual combination of colour rings, using one or two on the left leg, and one above or below the aluminium ring on the right leg. Each colour was assigned a number, and the combination read from left to right and top to bottom on each leg. The system is illustrated in Figure 1.

The marked birds comprised 62 males, 60 immature males, and 152 females. However, these numbers proved to be quite

The colour-ringing system used
for Euplectes orix males.

FIGURE 1.

FIGURE 1



ALUMINIUM = 1

GREEN = 4

RED = 6

YELLOW = 7

MALE IS "4761"

inadequate, as only six of the colour-marked males were territory-holders in the colonies under observation, while the total number of marked birds sighted was only fifteen. It is clear that an intensive advance marking program would be needed to produce an appreciable number of identifiable birds. Nevertheless, with the numbered nests it was usually possible to distinguish the territory-holders, and later behavioural clues aided sexing "browns" in the field.

During over a hundred hours of intensive observation, forty-eight one-hour periods were spent monitoring the activities of single colour-marked males. The observations were recorded on a cassette tape-recorder, and later transcribed to prepared form-sheets, showing the frequency and duration of all activities during the observation period. These observations covered all periods from sunrise to last light, and form the source of the quantitative data presented.

Still photographs were taken with a 35 mm single lens reflex camera, fitted with a 500 mm lens. The hides were not well positioned for photography, being sited to survey the maximum area, but adequate material on which to base drawings of the displays was obtained. Cine photography was not used, owing to the author's total lack of experience in this field, and the limited time available.

THE STUDY AREAS.

The observations were made principally on the farm "Klawervlei" at Faure about 40 km from Cape Town, between late July and the beginning of December 1972. Over the period 7-21 December further observations were made on a colony at the farm "Thorngrove", 27 km north of Bloemfontein. This colony was visited again from 5-7 January 1973, and the final series of observations were made at "Gartmore Farm", 19 km north of Howick, Natal, from 9-26 January. These three localities will be described below, to show the different conditions prevailing in the male's territories.

(a) Klawervlei.

Breeding on this farm commenced during July, and the first eggs were found on the 9th of July. The main dam, covering an area of about 10,000 sq metres, was bordered by extensive patches of Typha capensis and Phragmites communis, in which there were at least five distinct colonies. Single males were also to be found in clumps of Cyperus congestus. An abandoned quarry about 1 km from the dam also contained a small group of breeding males, nesting in Phragmites communis. Initial observations were made at several locations, so as to become familiar with the behaviour of the males. Certain of the colonies commenced their breeding cycle later than the others, and one of these was selected for continuous observation.

The colony was located in Phragmites communis at the south-east corner of the dam. This particular patch of reeds was about 20 m long by 4 m wide, running from north to south. At the northern end it was completely exposed, while at the southern tip a narrow channel separated it from a patch of Typha in which there was a second colony. The water depth ranged from $\frac{1}{2}$ -1 metre at the deepest part, while the reeds stood up to 1.5 m above the water.

Ten males, of whom three were colour-marked, held territories in the colony. The precise size of the territories could not be determined, but none exceeded 8 sq m, and several were clearly smaller. All the nests were numbered, and it could be established which nests belonged to a particular male. Their nesting success is summarised in Table 1 below.

A fourth colour-marked male was seen twice, apparently occupying a territory in the northern section of the colony. However, he subsequently disappeared from the colony. It is possible that some of the nests ascribed to males C and D may have been taken over from this male after he left the area.

TABLE 1.

Male	No. nests	No. laid in	No. eggs	Chicks reared
A	8	5	14	8
B	9	3	8	1
C	14	7	22	9
D	11	3	12	6
E	12	4	9	0
F	7	2	7	3
G	8	5	12	5
H	3	0	0	0
I	15	1	2	0
J	6	2	5	0
Total	93	32	91	32

By the 2nd of December the colony was deserted, one nest with two chicks having been abandoned. Males caught at this time were starting to moult out of breeding plumage, and the testes had regressed almost completely. Females also showed ovaries greatly reduced in size.

(b) Thorngrove.

Here the nesting habitat was confined to small, often widely separated clumps of Phragmites communis fringing the Modder River. Dense thornbrush covered the banks, usually right down to the reeds, making access extremely difficult.

The colony observed lay in a thin strip of Phragmites communis, about 12 m long and no more than 1 m wide, with the reeds standing at the foot of a steep bank. Owing to the low level of water in the river, the reeds were on the very edge of the water, with the nests nearly 2 m above water level. Five males were holding territories here, spaced out in a straight line. The nest situation is summarised in Table 2.

TABLE 2.

Male	No. nests	No. laid in	No. eggs	Chicks reared
K	2	1	2	1
L	2	0	0	0
M	3	0	0	0
N	4	2	5	0
O	2	0	0	0
Total	13	3	7	1

As compared with Klawervlei there were very few nests per male. However, no building activity had been seen in December, but on 5th and 6th January two males started building new nest frames, and it is possible that a second cycle of breeding activity was about to begin. The smaller size of the territories may have been an additional factor, the largest being only 4 sq m, but male N had four nests in an area of no more than 2 sq m.

(c) Gartmore.

The Karkloof River forms a series of ox-bows, most of which are now partly or completely isolated from the main stream. Several small colonies were to be found in these ox-bows, either in Phragmites communis or Cyperus congestus. The area under observation was a band of Cyperus congestus, about 20 m long and 1.5 m wide, in the curve of an ox-bow. The water was about 0.8 m deep throughout.

Initially three males, two of them colour-marked, were holding territories and a fourth appeared to be trying to establish himself at the fringe of the group. The nest situation is shown in Table 3.

TABLE 3.

Male	No. nests	No. laid in	No. eggs	Chicks reared
P	4	1	2	0
Q	3	1	1	0
R	2	0	0	0
Total	9	2	3	0

However, within the first few days of observation the other males left, leaving male Q in sole possession of the entire area. He then treated the whole colony as

his territory, and it was to be regretted that observations could not have been continued, to see how long this situation persisted. As a male moulting out of the breeding plumage was seen later, it is possible that the major breeding cycle was over, with only scattered groups or single males continuing activity. Nest inspection of the colonies at Midmar Dam confirmed this impression, as chicks had already left many nests, while more recent ones contained fresh clutches of eggs.

THE BEHAVIOUR OF THE MALE.

Since the adult males spent most of their time on the territories and could be distinguished individually, quantitative records of their behaviour could be made. The proportion of time which males devoted to various behaviour patterns is shown in Table 4, and references to this table will be made in the descriptions following. The four males were all colour-marked birds, which were monitored for one-hour periods, as mentioned earlier. Records very early in the season and very late, after breeding activity had ceased on their territories, were excluded from the table. Males E and F were neighbours at the Klawervlei colony, while males M and Q were at Thorngrove and Gartmore respectively.

The conspicuous nature of the male's red and black plumage is enhanced by erecting the feathers to a varying degree in the different displays. The terms used to describe the state of the plumage are taken from Morris (1956) following his definitions:

- Sleeked - the feathers are tightly depressed against the body.
- Relaxed - the feathers are in the normal position.
- Fluffed - the feathers are partly erected, enlarging the apparent size of the body, and giving it a smooth rounded appearance.
- Ruffled - the feathers are fully erected, so that their ends do not touch, producing a ragged broken outline.

(a) The calls and their context.

Euplectes orix has no song in the accepted sense of the word, and its vocalisation accords with Crook's (1969) description of "a series of machine-like repetitive sounds". However, he admits that little attention has been paid to their calls, and deals with the entire genus Euplectes in a single paragraph.

As there is no established nomenclature, simple descriptive names will be given to the calls encountered, and these will be used throughout this account.

Chipping: this is a shrill, metallic note repeated by the male as a series of regular "chip-chip" 's. It is

TABLE 4.

	Male E	Male F	Male M	Male Q
Minutes on territory	546	431	299	329
Activity: % time	17.7	44.6	25.3	35.6
Building: % activity	34.8	22.2	5.7	43.7
Chipping: % activity	0.3	52.0	7.5	0.3
Preening: % activity	not recorded		33.9	5.2
Display: % activity	56.3	23.3	35.2	36.5
Sizzling: % activity	17.5	13.5	19.6	4.5
% display	31.1	54.8	55.6	12.4
Rattling: % activity	24.5	5.5	15.5	20.3
% display	43.5	25.8	44.0	55.6
Swivelling: % activity	12.0	3.6	0.0	8.0
% display	21.4	16.0	0.0	22.0
Bumble-fly: % activity	2.3	0.7	0.1	3.7
% display	4.0	3.3	0.4	10.0
Defence: % activity	8.6	2.5	17.7	14.3
Pursuits: % activity	0.8	0.2	0.5	12.5
% defence	9.4	8.0	2.9	87.4
Threats: % activity	not recorded		17.2	1.8
% defence	not recorded		97.1	12.6
Fights: % activity	7.8	2.3	0.0	0.0
% defence	90.4	91.9	0.0	0.0

Time devoted by males to various activities.

primarily an alarm call, and the frequency will vary with the degree of disturbance - the usual rate is one "chip" every two seconds. Even at high frequencies there is always a distinct break between successive notes. The male calls from an exposed perch, with the body plumage sleeked and flicking the wings - the latter is clearly an intention movement of flight, and the sleeked feathers also reflect a dominant escape tendency.

When the observer entered the colony to inspect the nests, one or more males would immediately start chipping, and any females at the nests would fly off, accompanied by most of the other birds. Some males would remain within a certain distance of the intruder, changing perches frequently. Skead (1956) also described a male "flicking his wings and making the alarm note", but the boldness of the male did not always indicate the presence of chicks, as he suggested. Chipping may be given in flight as the male leaves the colony. This call is distinctly similar to alarm calls heard from the cape weaver (Ploceus capensis), the masked weaver (Ploceus velatus), and even the white-browed sparrow-weaver (Plocepasser mahali) when disturbed at the nest. It seems probable that there may be relatively little specific variation as regards this call - since mixed flocks of several species often gather for roosting and feeding, it would be advantageous to have a mutually recognisable alarm note.

Table 4 shows that male F spent more than half (52%) of his active time in chipping. His call seemed less shrill and rapid than the usual alarm note, and it was noteworthy that his neighbour, male E, took no notice and spent little time chipping himself. However, on one occasion when another male commenced chipping, E left the colony almost immediately, after showing the sleeked posture with wing-flicking. The only explanation of male F's behaviour might be that as the bird closest to the hide, he was responding to the presence of the observer, since the hide had large, open viewing panels on three sides. The records did seem to show that during successive hours of observation, the time spent in chipping decreased considerably, and it also declined in intensity during subsequent weeks of observation.

In other males, chipping was only heard for periods longer than 30 seconds when a single male was left alone on the colony, particularly early in the season.

Sizzling: this highly characteristic call is rendered by Skead (1956) as "tay zayzayzaay". It typically lasts for about 4 seconds in a single drawn-out wheeze, and is often terminated by a harsh gargling sound. Several bursts may follow one another with a maximum of 10 recorded. Very rarely in between bursts of sizzling, a few clear call notes would be uttered, sounding most like the introductory bars of a true song. However, it never developed beyond six notes, and was always succeeded by a new burst of sizzling.

When sizzling the male always had the body plumage fluffed or ruffled. In the ruffled posture, the black feathers of the chest and belly are erected at right angles to the body - seen from the side the chest shows a series of ripples, representing the successive lines of feathers (Figure 2). The back is slightly flexed, with the head drawn back and sunk onto the chest, so that the lower mandible often appears to be resting in the groove of the breast bone during calling. This dropping of the head conceals the band of red feathers across the throat, but the red head and neck feathers are erected, to form a red crescent above the black face and balloon-like body (Figure 3). Seen from the back, the red feathers are all erected into a uniform puff, with only the brown, slightly spread tail feathers for contrast. When a perched male is ruffled, the brown feathers of the primaries are almost completely hidden; when he is only fluffed, however, they are clearly visible (Figures 4a and 4b). The degree of plumage erection is quite variable in perched sizzling - at first the male may only puff the feathers, slightly disturbing the body outline; the fluffing will then continue with successive bursts.

Sizzling has been heard during the fluffed flight display described later, but this is very rare - 0.5% of 600 recorded bursts of sizzling. It is usually given while the male is perched in the reeds; Crook (1969), Emlen (1957) and Woodall (1971) all mention the "sizzling cries" which can be heard in the vicinity of a colony. Skead (1956) writes of the sizzling of the immature males,

FIGURE 2.

Ruffled male Euplectes orix;
lateral view.

About life size.

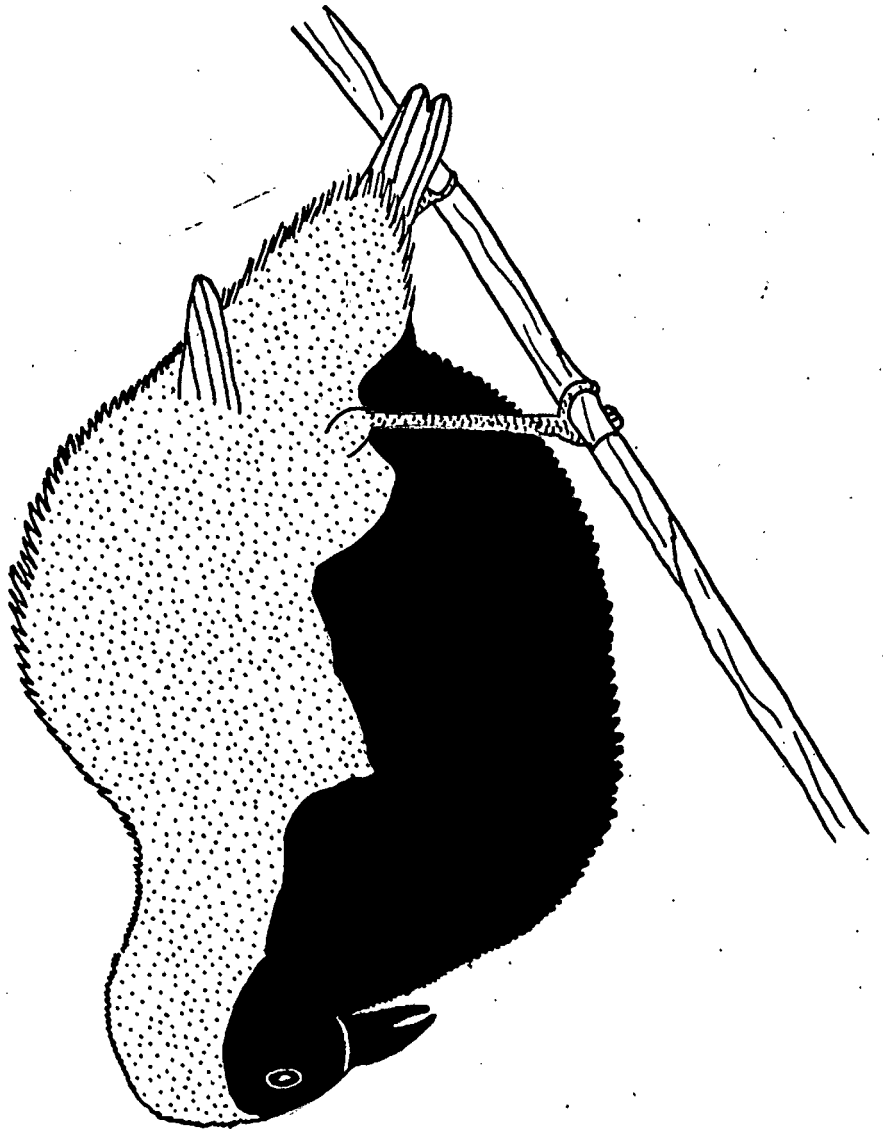


FIGURE 2

About life size.

front view.

Ruffled male Euplectes orix;

FIGURE 3.

FIGURE 3

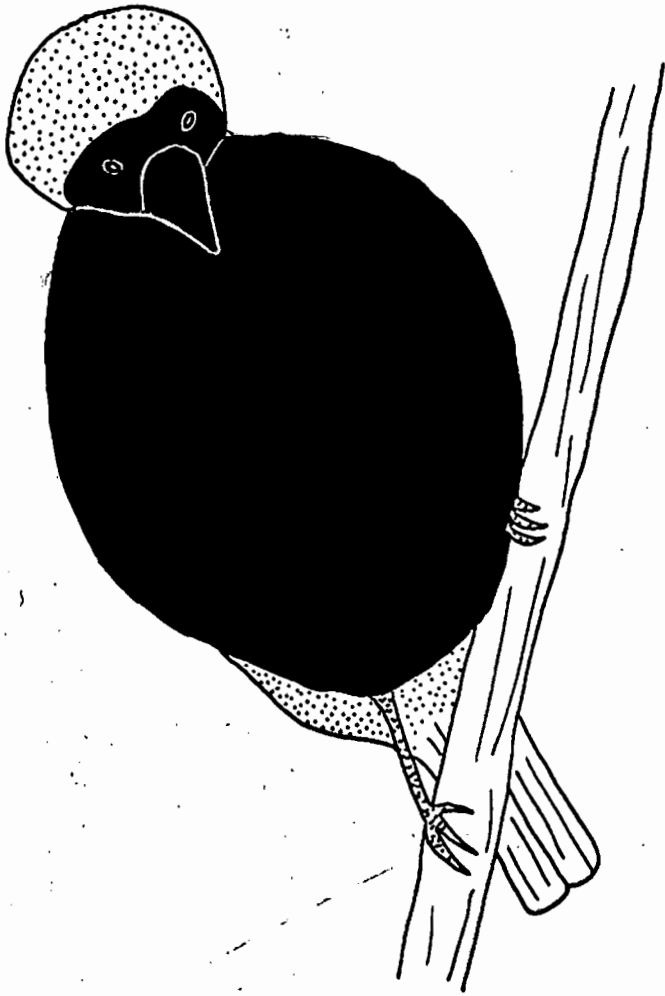


FIGURE 4.

(A) Ruffled male Euplectes orix;
rear view.

(B) Fluffed male; rear view.

Half life size.

but does not use this word in connection with the adults. However, when the bird sizzling is not visible, no difference in call can be detected.

At Klawervlei it was found that sizzling was usually given while the male was perched low in the reeds, and 68% of the bursts could in fact be associated with a specific nest on the territory. Since a male was never seen to sizzle in the vicinity of an occupied nest, it appeared that this call served to advertise the nests available to females. Sizzling at the nest was contrasted with sizzling from a conspicuous perch, which accounted for 20% of the observed bursts. The remaining 12% were given low in the reeds, but not at a specific nest.

But at Thorngrove the association was not so clear. While sizzling, the males were usually perched on reeds overhanging the river, more exposed than at Klawervlei, though still close to and level with their nests. It was thus not clear if this should be regarded as "sizzle at nest" or "sizzle from a conspicuous perch." In addition males were heard sizzling while perched in mimosa trees outside the colony, and even in trees bordering the feeding grounds. This seemed to indicate advertisement of the presence of the male, not necessarily at his nests.

Sizzling was much less frequent at Gartmore, as shown by Table 4. Here 38% of the bursts were given as the male hung below a nest which a female was inspecting. The wings were sometimes quivered, but otherwise the posture corresponded to the normal state with ruffled plumage. These bursts of sizzling sounded more laboured and drawn-out than normal, with longer intervals in between. This male also made two sizzling approaches to females prior to mounting - Woodall (1971) also records a sizzling approach before copulation. An occasional sizzle accompanied a swivelling display - these accounted for 5%, while the remaining 57% were from an exposed perch immediately above two vacant nests. Males perched in the meallie-lands were heard to sizzle on several occasions - this again could have no relation to nest or even colony location.

Nevertheless, even when the Thorngrove records are taken as representing sizzling from a conspicuous perch, 51% of recorded sizzles were at a particular vacant nest.

Rattling: this call comprises a rapid sequence of identical notes, seemingly strung together in a short phrase. It can best be rendered as "zik-zik-zik", and Skead's (1956) term "zikkering" almost certainly refers to this call. When rattling the male may adopt a fluffed posture as in sizzling, but not necessarily. The distinction is apparently that sizzling is performed after certain preparatory actions, whereas rattling is a spontaneous response to particular external stimulus situations. Thus the head is often directed towards the stimulus, and not bowed down onto the chest.

49% of all recorded rattling bursts were in response to conspecifics flying overhead, and it is the only acknowledgement given to a nesting female returning to the territory. While less than 1% of the sizzling bursts were given when the bird was not perched, rattling appears to be the flight call, 25% of rattling being while the bird was flying. A male almost invariably rattles as he lands on his territory, and may rattle as he flies off. Pursuits are often accompanied by rattling. Lack (1935) refers to a weak, metallic song of a few notes, which is uttered in flight by E. hordeaceus, but it is not clear whether this call corresponds to the rattling of E. orix. A further 10% of the rattling occurred as a prelude to bursts of sizzling - in this case the body plumage is always ruffled. Rattling seems to be an infectious call, and can often be heard spreading out in a widening circle from a single centre of activity - 16% of the cases were in response to the activity of males elsewhere on the colony. Table 4 shows that, except in the case of male F, rattling formed a major part of both display and of total activity. It may serve primarily to announce the presence of the male on his territory.

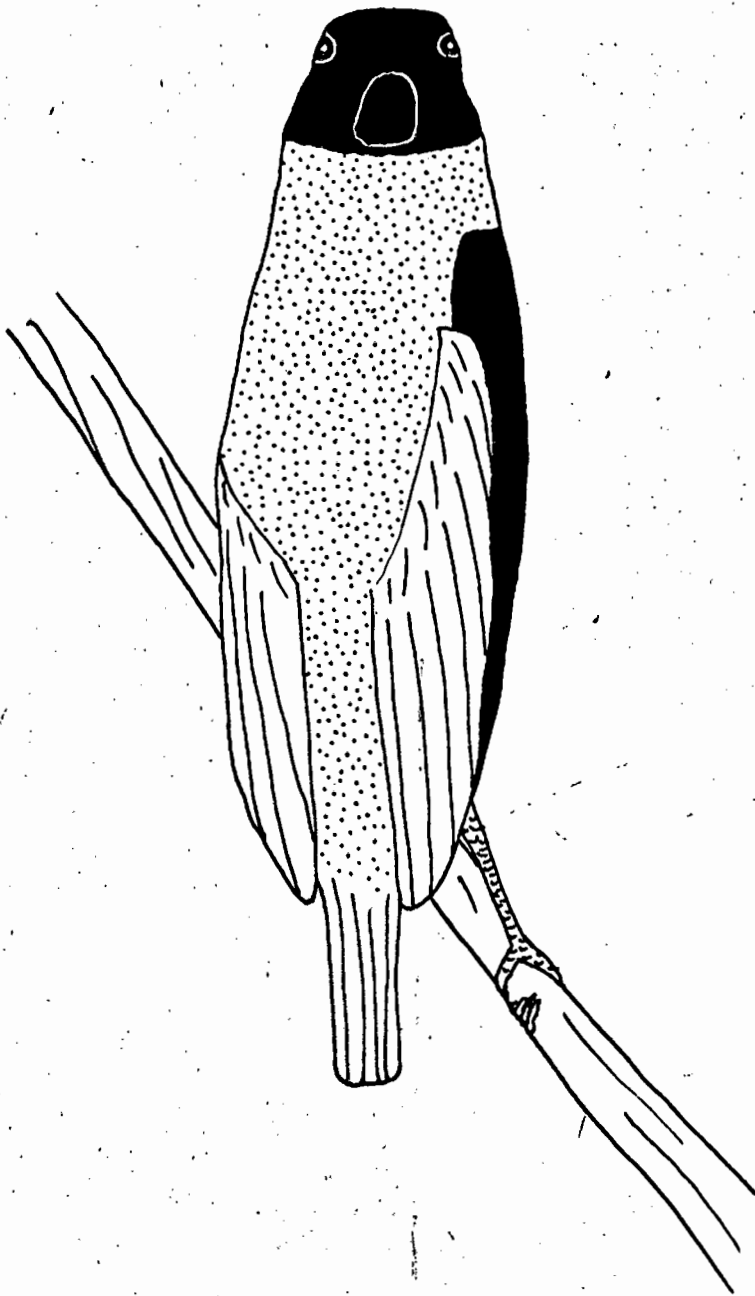
Late in the season at Klawervlei as activity declined, a "piping" call was commonly heard. This was a weak, rather plaintive single note, uttered at short intervals. The call was given in contexts where rattling would have been expected, and the tentative conclusion is that piping represented a residual response to stimulus situations, which were no longer strong enough to elicit rattling. This seemed to be confirmed by the few records of piping at Thorngrove and Gartmore, when it was given

FIGURE 5.

Sleeked male Euplectes orix;
rear view, with head turned.

About life size.

FIGURE 5



to conspecifics flying very high over the colony, thus attracting much less attention than the usual low-flying birds.

Woodall (1971) mentions that adults caught in mist nets gave a harsh "hssk", and bit painfully. Both statements can be confirmed - this call can best be termed a squawk. A similar harsh squawk, very weaver-like, was heard on three occasions in the field; once as a male bishop pursued an intruding male, and twice when a male displaced a bronze mannikin (Lonchura cucullata) from his territory. Its significance is obscure at present.

In E. hordeaceus Lack (1935) refers to a characteristic twittering call, used by the male only when one of his mates returned to the territory. No such call was recorded in the present study, and Skead (1956) also states that he found no equivalent call in E. orix. Emlen (1957) refers to "very high and thin rustling or sizzling sounds" in the Euplectes species, but his Table 1 c of the typical song patterns in terms such as "tzik³" or "ffff" has no explanation in the text or indication of the context in which they are uttered.

(b) The display postures.

As can be seen from Table 4, the calls sizzling and rattling together formed the major part of display in all four males. This implies that vocalisation may play a far more important role in the breeding behaviour of E. orix than has been assumed by previous authors. The non-vocal displays are very simple in form, though visually striking.

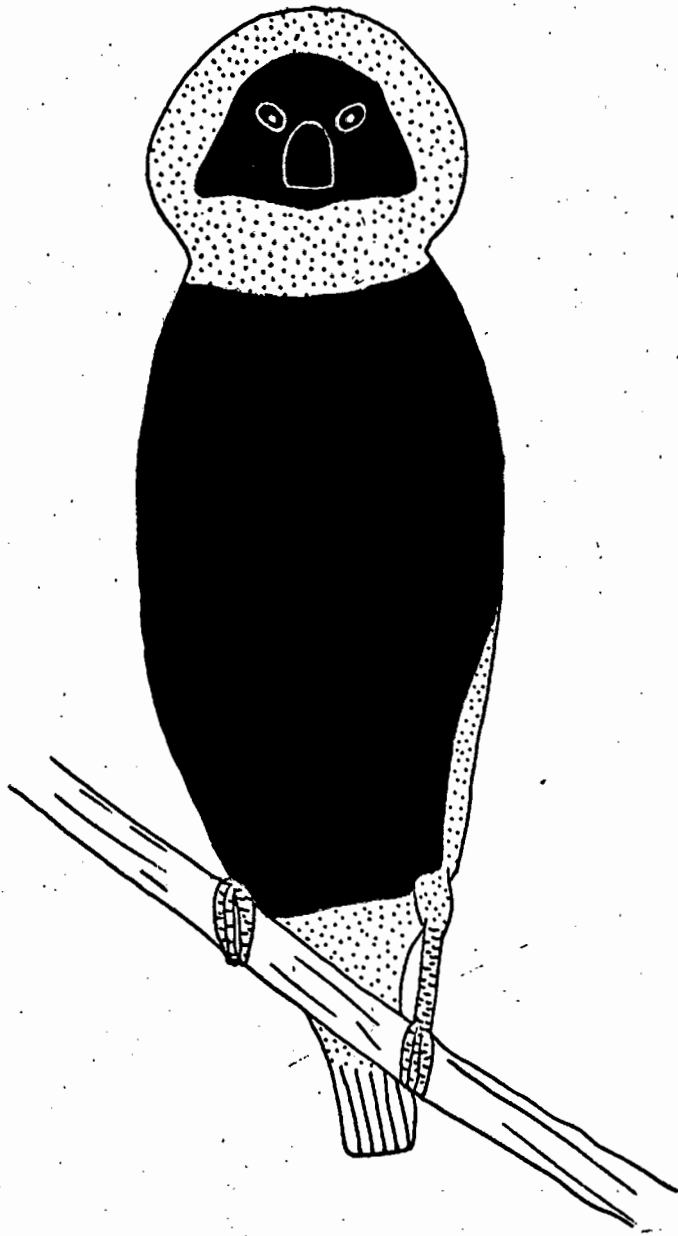
The threat posture of E. orix is well described by Emlen (1957) and is of Crook (1964)'s head forward threat type. The body is slightly crouched, with the neck stretched forwards and upwards, and the bill directed towards the opponent. The body plumage is relaxed, but the red feathers of the back may be fluffed so as to partly cover the primaries, and the tail may be partially spread. The red feathers of head and neck are flared into a striking ruff, so that from the front one receives the impression of a large red circle surrounding the small central black face mask. Gill (1959) has a vivid description of the threat, specially mentioning "a triangular black face framed in glowing scarlet". (see Figure 6). Skead (1956) makes no mention of this posture, and Lack (1935) describes

FIGURE 6.

Male Euplectes orix threatening;
front view.

About life size.

FIGURE 6



a very different display in E. hordeaceus. Here neighbouring males moved up^{and} down parallel to the border, with the chest puffed out, making short flights to the border but not across it.

Swivelling: this^{is} the perched courtship display, in which the male hops, glides and swivels over the reeds in the vicinity of a brown. The plumage is ruffled, with the beak depressed into the throat. A continuous, distinctive form of the rattling call accompanies the display; instead of being given in short phrases it now occurs in long, unbroken spells. The male may move either towards or away from the brown as he passes across the reed stems, and in swivelling will often have his back to the other bird. Up and down pumping movements of the body were seen only twice, and are not usual for E. orix as is implied by Crook (1964). Both Skead (1956) and Emlen (1957) comment on the swaying or swivelling movement of the body as characteristic. The duration of the observed displays ranged from 5 seconds to 2 minutes 50 seconds, with a mean value of 16 seconds. By far the greater part of these displays was directed to a brown on the territory, as shown by the figures below.

TABLE 5.

	Brown on terr.	Brown on neighbour's	Other
Number	94	15	2
% total	84.9	13.5	1.6

Bumble-flying: this is the most conspicuous of all E. orix displays and has been described by all three authors (Skead 1956; Emlen 1957; Crook 1964), and for E. hordeaceus by Lack (1935). The body plumage is ruffled, with the head held forwards while the wings beat slowly, so that the bird seems to buzz along in a manner reminiscent of a bumble-bee. The flight is level and not bouncing up and down, as is the case in some other species (Emlen 1957, and personal observations). As noted by Skead, wing-claps may be audible at close quarters - however, as these almost always occur as the bird comes in to land, it seems that they are associated with the braking action of the wings, and do not form a special part

of the display. Once a male flew back and forth in front of a nest which a brown had entered, with continual wing-clapping. In this instance each flight covered no more than 0.8 m, requiring extreme slowing of the wing beat, and this was the only time that sustained wing-clapping was encountered.

Although bumble-flying forms less than 4% of a male's activity and no more than 10% of display (Table 4), it has been discussed at length by the previous authors. While perched in the reeds of the colony, a male is often quite well hidden, but when he rises above the reeds in bumble-flight he immediately becomes obvious, even to an observer some distance away. Thus the impression is created of males frequently rising up in bumble-flights, for no apparent reason. However, unless individual males are being observed on their territories, the context of the flights may be overlooked. The circumstances of the bumble-flights providing the figures in Table 4 are summarised below.

TABLE 6.

	Number	% total	Cumulative %
Approaching brown	42	33.1	33.1
Preceding swivel	36	28.3	61.4
Following swivel	24	18.9	80.3
Pursuing male	7	5.5	85.8
Returning to terr.	5	3.9	89.7
To border of terr.	4	3.2	92.9
Approaching other spp.	2	1.6	94.5
Undetermined	7	5.5	100.0
Total:	127		

It can be seen that a large proportion of the flights (47%) can be directly associated with the swivelling display. This relationship is also clearly shown in Table 4 if the percentages for swivelling and bumble-flying are compared for individual males. It should be noted that, since these figures represent length of time, the values for swivelling are much larger, because these displays may last for a minute or more, while the bumble-flights never exceeded 9 seconds in duration and averaged only 4.

Flights "approaching brown" include all the fluffed pursuits of browns, since careful observation of these led to two conclusions: (1) in the absence of any clear behavioural clues, males were no better able to distinguish females and immature males than the human observer; (2) a bumble-flying approach showed the intention of the male to proceed with courtship. This interpretation was supported by the fact that three bumble-flying approaches to birds known by the observer to be immature males, abruptly changed to sleeked pursuits as the male reached them.

On two occasions such approach flights were followed by sizzling only, at which the brown flew off - it is possible that mounting attempts would have followed, had the birds remained. The approach would become a fluffed "supplant chase" if the brown flew off before the male had landed. A male might thus make several bumble-flights after a retreating brown, if it remained within his territory, before he was able to commence perched courtship. Approach flights and flights preceding the swivelling displays together form 61% of the total - bumble-flights following swivelling would then be considered further approaches, with the intention of continuing display. On this basis, 80% of all the bumble-flights were approaches to browns, with the intention of courtship.

Bumble-flights in pursuit of a male are not easily explained, unless a male excited to display may, in the absence of the correct partner, respond to another male conspecific by the approach flight. No pattern is evident in these few instances, and at present there is insufficient information on this point.

A male returning to his territory after a pursuit might make a brief bumble-flight across it, rattling. But as these flights were not above the level of the reeds, they could only be visible to the male's immediate neighbours. A few flights were also made to the border - these were always during display activity by the neighbour, and might represent approach flights which were not followed through, owing to the inhibition against crossing the border when the neighbour was present.

Two flights were directed to other species on the male's territory - one to a pair of cape reed warblers

(Acrocephalus gracilirostris) and the other to a half-collared kingfisher (Alcedo semitorquata). There could hardly have been any intention of courtship, but nor was there any follow-through pursuit, with the male bishop being completely ignored by the other birds.

Only 5.5% of the flights were for no reason which was apparent to the observer, but these were all during periods of activity elsewhere on the colony, and may have been caused by the stimulation of other male displays. It has already been mentioned that localised bursts of activity seemed to influence the other males in the colony.

Both Emlen (1957) and Crook (1964) write at length about "undirected flight displays" in the genus Euplectes. Emlen describes these as "performed as likely as not in the absence of other birds of either sex, the most common and showy of all displays". Reference to Table 4 shows that for individual males, flights are far from common, and form a very minor part of display. Moreover, Table 6 shows that close on 90% of these flights are directed towards another bird within the male's territory - there is thus no justification for terming them undirected in the case of Euplectes orix. Crook also conveys the impression that a male will fly back and forth at random until a "female" enters his territory, when he will either attack or court. This author refers consistently to "females", but gives no indication as to whether he could in fact distinguish females and immature males in the field. The results of mist netting at breeding colonies throughout the day, indicate that perhaps $\frac{1}{3}$ of the browns visiting the colony are in fact immature males, while observations on marked birds show that the males do not always discriminate.

Truly undirected display flights would represent a considerable waste of energy, and it would clearly be an advantage for the male to produce display flights only at appropriate times, when potential mates are in the vicinity. Crook (1964) also admits that selection seems to have limited such displays to certain releasing situations. It also appears that too much stress is laid on the concealed situation of the nest - in E. orix the nests are easily seen, and the browns visiting the colony show no sign of needing to be directed to the nests by the males. Since

the males leave the territory to feed with the flocks, they are not isolated from the other birds, and it does not seem necessary for special advertisement displays to announce their whereabouts. A male bishop in normal flight is conspicuous over a considerable distance, and it has been noticed that little groups of browns often accompany males returning to their territories. Merely by flocking with males in breeding condition they will be led to the colony.

Lack (1935) describes E. hordeaceus as performing a slow, flopping display flight from a higher perch to a lower one, calling in flight. E. orix was heard to sizzle while bumble-flying on three occasions, but the flight itself was normally silent, with rattling at take-off and landing. Of the other species encountered during this study, E. axillaris and ardens were only heard calling while perched, but E. afer may sizzle in flight. At Klawervlei a male E. capensis held a territory just inland of the colony under observation, and he appeared to have regular perches between which he made fluffed display flights, sometimes accompanied by a "churring" call. It was not clear if these flights were associated with the arrival of birds on the territory, since the whole area was not in view. Similarly at Gartmore male E. axillaris and ardens had territories in the vicinity of the hide, and were seen flying to particular perches in the area. Owing to the position of the hide, it was again not possible to watch their territories, but in view of the findings on E. orix these flights should not be classed as undirected without further information.

(c) Territorial behaviour.

Early in the season, a male will start frequenting a particular area of reeds, from which he will displace all subsequent visitors. Initially little time is spent on the territory, until nest-building commences. Only when nests are present does the male spend long periods on the colony and show the full range of displays. The perched displays have only been seen performed by nest-owning males.

Lack (1935) records that the males of Euplectes hordeaceus seldom left their territories, and then only for a few minutes to drink. Feeding was apparently done

on the territory. In the E. orix colonies studied the males could drink on the territory, but all feeding was done away from the colony. Thus territorial behaviour concerns the nesting area alone, and has no relation to food requirements. Skead (1956) found a similar situation, although his birds also had to leave their territory to drink, and to bathe. He did not time their absences, but with the marked males this was possible, and their attendance on the territory is summarised below.

TABLE 7.

Male	Average no. visits/hr	Mean time (minutes)	Average no. absences/hr	Mean time (minutes)
E	2	15.2 (1 - 52)	2	8.4 (1 - 36)
F	3	13.5 (1 - 35)	2	8.6 (1 - 25)
M	2	18.7 (1 - 60)	1	20.0 (1 - 50)
Q	3	14.3 (1 - 45)	3	4.8 (1 - 34)
Means	2.5	15.4	2	10.4

There is surprisingly little individual variation in these figures, despite the different conditions in the three colonies. These observations covered all one-hour periods between 0500 hours and 1800 hours; as there was an uneven spread over the thirteen hours, the data cannot yet be effectively correlated with the time of day. However, substituting hours of day in place of "male" in the above table caused little overall deviation from these figures. The longest recorded absence was three hours, while the longest unbroken visit lasted an hour and a half. It seems that the general pattern of attendance shown by Table 7 is of an alternation of periods on the territory, followed by slightly shorter periods off the colony.

Table 4 reveals that in all cases less than 20% of the male's active time is devoted to territorial defence; it is always much less than for display and, except in the case of male M, also less than the time spent building the nests.

The male defends his territory chiefly by pursuit flights, or supplant chases as they are termed by Crook (1964), or by threat displays which under certain circumstances may pass into actual fighting. The colony members generally respect the territorial boundaries, and among males a distinction can be drawn between "intruders", who are non-members of the colony, and "trespassers", who are members of the colony not on their own territory.

Pursuit flights may be bumble-flights of the form already described, but more often the body plumage is relaxed, and the flight is rapid. As implied by Crook's term, the object is evidently to "supplant" a stranger landing on the territory. The defending male may then occupy the perch the intruder has vacated, or may follow the other bird further. This may lead to more territorial infringements, with other males either joining in the pursuit, or driving the pursuer back to his own territory. The details of 158 observed pursuits are summarised in the table below.

TABLE 8.

Bird chased	No.	% fluffed	% relaxed	% of total
male	20	35	65	12.7
imm. male	9	67	33	5.7
brown	129	17	83	81.6
Total	158	22	78	100

"Brown" is a blanket term, including all birds whose sex could not be established. The high percentage of fluffed pursuits of immature males is misleading due to the small number which could be distinguished; in most cases this sexing was based on the previous behaviour of the bird concerned. It is clear from Table 8 that pursuit flights are usually in the relaxed plumage state.

The significance of the fluffed flights has been discussed already, as it is likely that the original motivation of these flights was courtship rather than territorial defence. This leaves the problem of the fluffed pursuits of males. Again the actual number involved is small, and in some cases the male was already fluffed in a display posture when he became aware of the intruder. Skead (1956) describes how a male with feathers erect will suddenly flatten them and dash at a brown - this has

also been noted, and implies a contrast between the fluffed display posture and the relaxed aggressive display. Lack (1935) states that males would actually rise to meet an intruder overflying, and might physically buffet the bird in pursuit. As already mentioned, E. orix normally rattles when conspecifics overfly, and will not pursue unless the bird attempts to land on the colony. No physical contact was seen in the air. Lack also records that all the browns, bar the male's own mates, were chased out; this was certainly not the case with E. orix, but as Lack's observations were late in the season it is possible that courtship was virtually over.

Intruders are readily recognised by the extreme sleeking of their body plumage, which makes them obvious to the observer and perhaps also to other males. This sleeking is most marked in the head region, with the result that, from the front, the head appears completely black above the red collar of the throat (Figure 5). If the intruder lands on the territory of a male absent from the colony, the first neighbouring male to notice him will immediately chase him off. Thus all the males, in addition to defending their own territories, will defend the colony as a whole from non-resident males. C. Elliott (1973) has observed similar defence of an area larger than the individual territory in the cape weaver, Ploceus capensis, but it is not mentioned by any other authors. Towards the end of the season as the males spend less time on the colony, this response fades and the males will ignore any intruder unless on their own territory.

Trespassers, in contrast, have the plumage relaxed or fluffed and never sleeked in the manner of intruders. They may enter a neighbour's territory in his absence to collect nesting material or inspect his nests, but never steal material from any nests, as is the case in some of the weavers (Collias and Collias 1959; Elliott 1973). Sometimes in pursuing a brown a male will cross the border, in which case he is chased back to his own territory by the owner, but if his neighbour is off the colony he may continue to display off his territory. Most often, however, he will stop sharply at the border. Trespassers are always ignored by other members of the colony, until they approach an occupied territory.

Should a male fail to return to the colony, the neighbouring males will extend their territories to include his area. As this was seen only twice, it cannot be said if the territory is usually split up among several males or taken over complete by a single male. At Klawervlei, male F left the breeding area permanently well before the others, and it was noted that one of his neighbours began spending long periods on F's territory and finally defended it as his own. This was also seen in the case of male Q, who took over the territories of two other birds which had left the colony.

The territory of a single male, as described, did not normally exceed 8 sq metres, which accords well with the 10 sq yards estimated by Shead (1956). In both cases the male could reach his boundaries in a short dash, and did not need to make extended pursuits, except to displace an intruder elsewhere on the colony. Thus Table 4 shows that males E, F and M all spent less than 1% of their active time in pursuit flights, while pursuits formed less than 10% of territorial defence. However, male Q who had taken over an area of 30 sq metres, spent 12.5% of his time in pursuits, and they constituted nearly 87% of his defence. It would seem advantageous for the male to have a smaller territory, as even though male Q did not spend less time in display than the others, he on several occasions interrupted displays to pursue a bird landing elsewhere on the territory.

Territorial behaviour in E. hordeaceus is not really comparable, since Lack (1935), and Moreau and Moreau (1938) recorded territories ranging in size from 400 to 1,400 sq yards. Fuggles-Couchman (1943) found territories of 490 to 870 sq yards for E. hordeaceus, and 120 to 510 sq yards for E. nigroventris. In the case of the latter Moreau and Moreau found that territory size varies according to the vegetation, and the smallest were found in Phragmites, where they ranged from 9 to 120 sq yards. Emlen (1957) lists territory sizes ranging from 0.1 to 0.5 acres for E. orix and hordeaceus, but these figures can certainly not apply to the former. The territories of other Euplectes species are certainly larger than those of E. orix, but no comparative figures are available for the areas where these observations were made.

Although birds on strange territory never offered any resistance to the territory holder and were always supplanted, as mentioned in both Lack (1935) and Skead (1956) in three cases a supplant chase by the male failed to displace a bird perched on his territory. He then perched nearby and adopted the threat posture, at which the intruder took flight.

Apart from one threat to an immature male, all threat displays were directed at other adult males, and the commonest type was a bout of mutual threatening between neighbours at the border of their territories. The form which this takes is the "aggressive dance without song bows or stretches" described by Crook (1964). Yet he lists this display as lacking in E. orix and all other Euplectes species studied - it can only be concluded that his information on this genus is very far from complete.

When threatening, the opposing males approach the border, hopping alternately towards and away from one another, in the threat posture. The contest is always completely silent. Often the males will merely posture, but at times they will close and lunge at one another, pecking with open bills. Wing-flipping is common. On two occasions males with bills interlocked, wings flailing, and claws scrabbling were seen to fall into the water in their struggles. Elliott (1973) has seen fights in the cape weaver, Ploceus capensis, end in this way.

Actual fighting was only seen at the Klawervlei colony. Unfortunately it initially obscured the importance of threats without any physical contact, so that these were first recorded later in the study. Skead (1956) remarks that "Fights were rare" but thus implies that he did observe fighting. It seemed that the factor determining whether or not threats would pass into fighting was the proximity of nests to the territorial border. At Klawervlei opposing males had nests almost on their common border, virtually within bill-reach of one another. It was always at these points that fighting occurred, while elsewhere on the border the males would merely exchange threats. Table 4 shows that about 90% of E and F's defence consisted of fighting, but this percentage would definitely have been lower had threats been included in the records.

Male M at Thorngrove spent 17% of his time in threat displays - here there was little territorial defence against intruding birds, and the threats were almost all between neighbours. Several times when the colony was quiet, male M would adopt the threat posture and proceed to his border, whereupon the neighbouring bird would follow suit and an "aggressive dance" would take place. The threat display was never seen performed "in vacuo", and only once did male N fail to respond. Male Q had no neighbours from an early stage, and his threats were all directed at intruding conspecifics. In both cases, the nests of neighbouring males were well back from the border, and no fighting was seen.

Emlen (1957) indicates that threat was found to be similar in all Euplectes species observed, and it would certainly be surprising should E. hordeaceus differ from E. orix in this respect as Lack's (1935) observations suggest. Emlen, however, writes of these displays "Their form is such as to primarily emphasize features of size, shape and blackness rather than distinctive species characters." This statement cannot be accepted, as the contrasting red and black plumage of E. orix is highlighted in this display. Moreover, the position of the body effectively obscures the size and shape of the opponent, as seen by the bird receiving the threat. It is likely that a more critical study of the plumage features most prominent in this display will show that its appearance is in fact highly characteristic of the species - and elsewhere in his paper Emlen provides evidence that this is so.

(d) Nest-building.

Nest-building by E. orix has been described by Skead (1956), Crook (1963) and Collias and Collias (1964). The form of the nest is shown in Figure 7. Construction commences with an upright ring between two reed stalks, and the body of the nest is then built downwards and outwards from this. As will be described later, the lining is done by the female, but the later extension of the entrance of the nest into a projecting hood, which Skead ascribes to the female, is at least in some cases added by the male.

At the Thorngrove colony Phragmites leaf-blades were the only building material available, and the masked weavers, Ploceus velatus, also collected their nesting material

FIGURE 7.

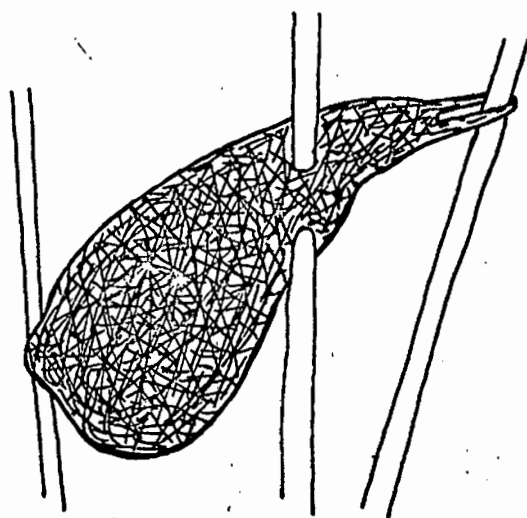
Nest of Euplectes orix:

(A) Lateral view.

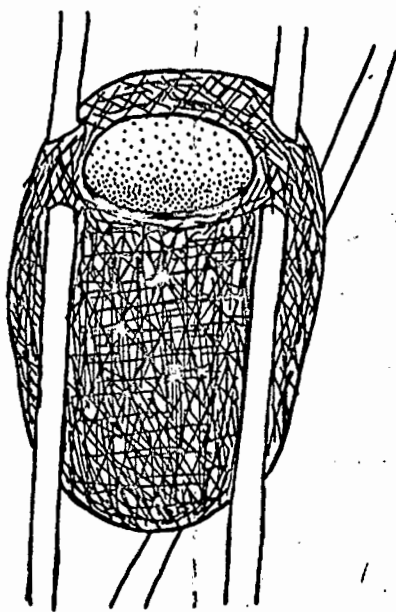
(B) Front view.

One quarter life size.

FIGURE 7



(A)



(B)

on the bishop colony. However, at Klawervlei some unidentified grasses growing outside the colony in a male E. capensis territory were also used. Here it appeared that the E. orix males nesting in the patches of Typha collected all their building material from this area of grass, and often four or more could be seen there at a time. Birds carrying long grass strips regularly flew over the colony under observation without landing there. Of the birds breeding in Phragmites, some collected all their material outside the colony, while others used only Phragmites strips, and in a few cases both sources were used in one nest. Male F built his first nest entirely of Phragmites collected on his territory, but later built another solely from grass collected off the colony. The males at Gartmore were only seen to use grasses collected in the vicinity, as the Cyperus leaf blades were evidently too tough.

Of 108 spells of building in five different males, the duration ranged from 15 seconds to 7 minutes, with an average of 1 minute 18 seconds. During one hour of observation the maximum number of building spells recorded was 16, totalling 15 minutes 50 seconds. Tables 4, 9 and 10 show that building makes a very significant contribution to the activity of the males. There is no demolition of nests and re-use of the material as is found in some weavers such as Ploceus cucullatus (Collias and Collias 1959), nor stealing of material from other nests as has been recorded in several species of Ploceus. (Crook 1960; Collias and Collias 1959; Elliott 1973.)

Nests may be built at irregular intervals for as long as the male remains on the territory, and new nests are built even though vacant nests are still available. The extreme example of this was male I at Klawervlei, who had built 15 nests before one was accepted by a female. At this colony on average 34% of the nests on a male's territory were accepted by females. In two cases males commenced building at a time when there were no occupied nests on their territories, while two others started new nests while a female was laying in one of their other nests. Thus it does not seem that either the presence or absence of mates need serve as a stimulus for nest-building. The experimental work of Collias et al (1971b) shows a correlation between the number of nests built and the number

of females in the colony for Ploceus cucullatus - under natural conditions the frequency with which females visit the territory may be an important factor in stimulating nest-building.

Leaf-stripping was seen occasionally, but showed no particular pattern - Skead (1956) regarded it as almost "recreational". It is almost certainly an incomplete performance of the normal behaviour for collecting nesting material, since the leaf is grasped in the bill close to the stem, but instead of a thin strip being torn off towards the tip, a large piece or the whole leaf is broken off and dropped. Collias and Collias (1964) suggest that this habit may make it easier to see the approach of hawks or to watch for potential mates. They do not mention ever seeing hawks at a colony, however, and no aerial predators were seen in this study or by other observers. The leaf-stripping behaviour appears too unsystematic to serve any special function in E. orix.

(e) Courtship.

There is not any very elaborate courtship performance, but any brown, which may be regarded as a potential mate, landing on the territory, is received by bumble-flights and swivelling displays.

The swivelling display was seen performed to both immature males and females (colour-marked birds), and there was no indication of any "selection" of a partner. In several cases a female feeding chicks at a nest near the border of the territory would repeatedly evoke swivelling displays from the neighbouring male, although she was no longer eligible as a mate. At the Klawervlei colony there was a point where the territories of four males adjoined, and when a brown perched there all four might approach, swivelling, but remaining within their own territories. In one case the bird "serenaded" was a ringed immature male.

Initially the swivelling display, as described, is an apparently random movement in the vicinity of the brown. However, if the bird remains perched on the territory, the male increasingly directs the display towards the brown and the nest. It is difficult to establish which is in fact the focal point of the display, since a brown visiting the territory will move towards a nest of its own accord -

it does not appear that the male uses swivelling to "herd" the brown towards the nest. In four cases at the Klawervlei colony, a male hung below the nest with plumage ruffled and wings shivering - a display common in the other weavers (Ploceus), but not hitherto recorded for the bishop (Euplectes). No call was given during this display, and the brown remained perched just outside the nest entrance. Male Q at Gartmore would regularly terminate a swivelling display by hanging below the nest sizzling, always when the brown had entered the nest. In this case the male was in the usual ruffled posture, with no noticeable wing movements. No swivelling displays were seen from male M, and swivelling was only seen twice at the Thorngrove colony. This seemed to be related to the very low frequency of visits to the colony by browns, as more display activity was later found at other colonies on the Modder and the Vaal rivers.

Copulation was seen three times, none of which was associated with a swivelling display. The male made a bumble-flying approach, landing close to the female, then sidled towards her ruffled and sizzling, with up and down pumping movements of the body. Mounting lasted five to seven seconds, with the male flailing his wings to keep his balance. The female was twice perched on a reed in the colony, not at a nest, while the third copulation took place on a fence just outside the colony. A similar description is given by Woodall (1971), and it does not appear that copulation need occur at the nest as stated by Lack (1935) and quoted by subsequent authors.

Crook (1964) records very different perched displays in E. orix, with the birds posturing with spread wings, and states that he has also seen such displays given to other males and while the male was alone on the territory. No displays to males, except for bumble-flying, were seen in the present study, but since Crook's observations were made in East Africa, it is possible that they reflect a subspecific difference between the two populations. Perched courtship was not observed in any other Euplectes species, but the descriptions of Emlen (1957), Skead (1959), and Crook (1964) bear little resemblance to the courtship of E. orix. Lack (1935) states that E. hordeaceus showed no elaborate display, with the male crouching shivering his wings and twittering to the female.

Both Emlen (1957) and Crook (1964) note that their "undirected flight displays" may terminate in a "pounce", whereupon perched courtship is assumed. Since this pounce merely consists of the bird dropping down into the reeds and landing, it seems scarcely necessary to separate it from the remainder of the flight. Crook regards this "pounce" as being homologous with the song approach of the other species of weaver which he deals with. However, following the argument against the concept of undirected flight displays presented above, it is proposed that the entire bumble-flying approach of the male Euplectes orix can be regarded as equivalent to the song approaches found in many Ploceus species.

(f) Seasonal changes in behaviour.

In a study of the red-winged blackbird (Agelaius phoeniceus), a territorial and polygynous Icterid in North America, Peek (1971) found seasonal changes in the behaviour of the males, correlated with changes in the difficulty which the male experienced in maintaining his territory. There was a major shift around the time of pair formation, with the early emphasis on intraspecific territorial defence changing to interspecific defence and protection of the nest, females and young.

In the case of Euplectes orix, interspecific territorial defence was a very minor component of behaviour throughout the season. Since success in colour-marking territory holders was not achieved immediately, individual records are not available for the entire season. However, Tables 9 and 10 summarise the proportion of time spent by males E and F in various activities from the time they were marked until they left the Klawervlei colony.

There is little apparent correspondence in the weekly figures, but owing to the long periods spent in nest-building as compared with other activities, peaks in activity are in both cases associated with nest-building. This did not appear to be restricted to any particular period; in other males building continued until shortly before the colony was finally abandoned.

For male F, chipping was initially the major component of activity, but then declined before abruptly ceasing. Display then became the chief activity, with sizzling the most common form, while rattling increased in importance

TABLE 9.

Male F.

	Week 1	Week 2	Week 3	Week 4
Total activity: % time	54.4	20.8	27.3	15.6
Building: % activity	27.9	0.0	0.0	0.0
Chipping: % activity	52.1	40.1	36.8	0.0
Display: % activity	17.9	55.9	58.6	88.0
Sizzling: % activity	9.9	30.2	25.5	51.1
% display	55.1	54.1	43.5	58.1
Rattling: % activity	2.9	16.4	20.1	31.7
% display	16.5	29.4	34.2	36.0
Swivelling: % activity	3.3	8.3	12.5	5.2
% display	18.6	14.9	21.4	5.9
Bumble-fly: % activity	0.6	0.2	0.6	0.0
% display	3.6	2.4	1.1	0.0
Defence: % activity	2.2	4.1	4.6	12.0
Pursuits: % activity	0.2	0.6	0.3	1.7
% defence	7.8	14.3	9.5	16.7
Fights: % activity	2.0	3.5	4.3	10.3
% defence	92.2	85.7	90.5	83.3
Nests with eggs	1	1	1	0
Number of eggs	4	4	4	0
Nests with chicks	1	1	0	0
Number of chicks	3	3	0	0

Variations in activity during the
observation period.

TABLE 10.

Male E.

	Week 1	Week 2	Week 3	Week 4	Week 5
Total activity: % time	10.9	25.3	13.1	31.6	11.5
Building: % activity	0.0	54.5	12.5	54.3	0.0
Chipping: % activity	0.0	0.7	0.7	0.0	0.0
Display: % activity	78.9	38.1	83.1	45.1	100.0
Sizzling: % activity	18.4	12.8	23.2	23.2	26.1
% display	23.3	33.6	27.9	51.4	26.1
Rattling: % activity	28.9	18.9	39.9	17.2	30.5
% display	36.7	49.7	47.0	38.2	30.5
Swivelling: % activity	27.4	5.2	17.8	2.1	44.5
% display	34.7	13.6	21.6	4.7	44.5
Bumble-fly: % activity	3.3	1.2	2.2	2.6	0.0
% display	4.2	3.1	2.6	5.7	0.0
Defence: % activity	21.1	6.7	3.7	0.5	0.0
Pursuits: % activity	1.4	0.5	1.2	0.5	0.0
% defence	7.0	7.0	33.3	100.0	0.0
Fights: % activity	19.7	6.2	2.5	0.0	0.0
% defence	93.0	93.0	66.7	0.0	0.0
Nests with eggs	3	1	1	0	0
Number of eggs	4	1	1	0	0
Nests with chicks	0	0	0	0	0

Variations in activity during the
observation period.

as bumble-flying declined and swivelling fluctuated. Surprisingly, defence rose to a peak after there were no more occupied nests on the territory, with pursuits becoming more frequent than fighting. Male F left the colony during week 4, and was not seen again. Week 1 was not the first week of breeding; since the chicks had hatched at the beginning of that week, the eggs must have been laid about thirteen days earlier.

Male E showed a more consistent pattern. Defence declined rapidly, and in the final two weeks no territorial defence was recorded. Pursuits decreased less rapidly than fights, though their contribution to overall activity was never very large. Display fluctuated apparently in association with building, until it was the only activity recorded, rattling being the chief and ultimately the only component. The peaks in sizzling appeared to be correlated with nest-building, but swivelling varied erratically, with a maximum value late in the season. Bumble-flying was infrequent, then ceased completely. Male E left the colony in week 6. During this week the only activity recorded was rattling, which occupied 5.3% of the male's time. Again week 1 was not the first week of breeding.

Many more quantitative records are required before individual variations cease to obscure any possible pattern. Had threats been recorded throughout, territorial defence might have shown a very different cycle. One male had three females all feeding chicks on his territory, and it was noticed that as soon as a female returned, he would proceed to his borders and patrol in the threat posture. This suggests that conditions on the male's own territory may be more important than an overall seasonal cycle, but at present this can only be speculation.

THE BEHAVIOUR OF BROWNS AND FEMALES.

Although in the hand the female appears somewhat paler than the immature male, no consistent plumage character could be found which would aid sexing in the field. Only marked birds or birds lining nests and feeding chicks could be assumed to be female.

Especially early in the season, small groups of the browns would often accompany males returning to the colony, and even later on only females feeding chicks regularly returned to the colony singly. This would be expected in a bird which apparently has a strong flocking instinct, and even the territory-holding males tended to leave and return in small groups. Emlen (1957) noted that the response of browns to one another was to flock together regardless of species. It was suggested earlier that this flocking instinct probably serves to bring birds to the breeding colony.

A brown landing in a male's territory is always sleeked and silent, flicking the wings as if about to fly off. It will leave immediately if pursued, and a bumble-flying approach by the male may be continued as a fluffed pursuit, but if he proceeds with a swivelling display, the brown shows no response other than avoiding actual contact. This lack of any positive reaction probably explains why both females and immature males may be courted.

It appears that the brown always tries to approach a nest, though it may be prevented from doing so by its evident desire not to come too close to the male. But since the male often moves away during display, the brown usually has the opportunity to hop to a nest. The inspection may be very brief, but on one occasion in the presence of the male, a brown spent four minutes at a nest; it entered six times, climbed on top pecking at the structure with its bill, then examined the label and tugged at the underside of the nest. (However, this nest was not laid in until two months later, so the inspection apparently proved unsatisfactory.) Often if the male was close to the nest, the brown would remain inside until he had moved further off, and retreat into the nest again if he swivelled towards it as the brown was emerging.

Copulation can only take place once the female has accepted a nest and is spending more time on the territory.

There is no solicitation by the female, and she may even peck at the male as he mounts. Lining of the nest may start before the first eggs are laid and continue during laying, but it is very variable in degree and some nests are scarcely lined at all. As noted by Skead (1956), soft seed-heads of Eragrostis are chiefly used, but the fluff of Typha seed-heads is also common. Once a female has started laying, the male on whose territory she is usually takes no further notice of her, though his neighbours continue to respond to her arrival with courtship displays. This change in the behaviour of the male may be very marked, and is then a clear indication that mating has taken place and laying has commenced. On one day a brown was repeatedly displayed to by a male as she visited a particular nest, which proved to be empty. The following morning the male ignored a brown which landed in front of him and proceeded to this nest - an inspection showed that the first egg had been laid. Yet, another male was twice seen to swivel to a female feeding chicks on his territory - but when he approached her at the nest, she repulsed him, pecking vigorously. Thereafter he ignored her, and this behaviour was evidently unusual. Skead also writes "When females come flying straight to their nests they are usually unmolested".

Observation of marked nests very close to the hide, which later hatched, confirms Skead's impression that consistent brooding in the daytime is not usual. Incubation lasted 12 - 13 days, and the egg-shells were removed from the nest while unhatched eggs were not. Clutch sizes are recorded in Appendix 2. Visits of females to the nests were recorded during the one-hour periods monitoring the territory-holding male. When feeding the chicks a female may come to the nest up to nine times an hour, and spend as much as thirteen minutes at a time there, although the average of 59 visits by 4 females was only 3.1 minutes. The maximum time in the hour spent at the nest was 25 minutes. In about a quarter of the cases insect food was visible in the female's bill - dragonflies were common, and caterpillars were also noted. No spiders were seen brought in as food. Females were several times seen regurgitating a white mush, which was then fed to the chicks. This was sometimes regurgitated by birds caught in the mist nets, and when examined in dissected specimens it

proved to be composed of partly digested seed. Skead found that seeds formed the major component of stomach contents of nestlings from the first day onwards, and Reed (1968) found a seed mixture in the stomachs of Diederik cuckoo (Chrysococcyx caprius) chicks from E. orix nests. Thus it seems that a seed diet is commenced immediately, only supplemented by insects. Faecal sacs were removed from the nest at the rate of one or two per hour (nest of three chicks) and carried out of the colony. It is not known how far away they are dropped. However, perhaps as the nestlings grow larger, not all faeces are removed, since after the chicks have left a nest a hard platform of guano can be found in the bottom.

Females seem to ignore territorial boundaries when leaving or returning to the nest, and as noted by both Lack (1935) and Skead (1956) they frequently intrude on the territories of neighbouring males. On three occasions two females returned to neighbouring nests simultaneously, and brisk scuffles with harsh squawks ensued. This was the only time that females were heard to make any sound.

From the eleventh day onwards the young may leave the nest. At both Klawervlei and Thorngrove ringed fledglings were seen perched in the reeds for two to three days after leaving the nest. They were ignored by the males, even when one approached a male with beak agape and wings shivering, in the begging posture. The female continues to feed the young for a period - Skead was not able to discover for how long. A roosting flock caught in mist nets at the end of the breeding season in the Cape contained about 30% juveniles, so that the fledglings must join the flocks as soon as they are flying strongly enough.

Both browns and males show the same grooming and comfort behaviour. Wing stretching, scratching the head with the foot, and ruffling of the feathers (distinct from the sustained ruffled posture) are all common. Bill-wipes are performed very frequently when a bird has just returned to the colony, and almost certainly serve to remove food particles from the beak in this case. Typically, the bill is wiped rapidly three times, on alternate sides. In the male this may also occur in displacement contexts, when the bird is restless and about to leave the colony. One male, after a spell of nest-building, would dip his bill in the water and then wipe it repeatedly.

Early in the morning all birds on the colony select exposed reed-tops to perch on, and ruffle their feathers in the first rays of the sun. Preening is then the first activity of the day. At least in the case of the male, preening may occupy quite long periods, and probably increases considerably towards the end of the season with the onset of the post-nuptial moult. Unfortunately comparative figures were not recorded, but this was the impression gained in observation. Since the females spent less time perched on the colony, they appeared to preen less often, but observations away from the colony are also required. Bathing was not observed at the colonies, although the males often climbed down to water level to drink. When the fighting males fell into the water, they spent about twenty minutes preening and drying out their feathers before indulging in any other activity.

THE BEHAVIOUR OF THE IMMATURE MALES.

Throughout the breeding season birds in brown plumage but of a size equal to that of breeding males, and demonstrably male on dissection, are to be found in the flocks. They are also frequent visitors to the breeding colonies, where they may inspect nests and even be courted by swivelling displays. It is generally accepted that in E. orix, as in many other Ploceidae, the males do not come into breeding condition and adopt nuptial plumage until their second year (McLachlan and Liversidge 1958; Mackworth-Praed and Grant 1962). The testes of dissected specimens were never larger than 1.5 mm and clearly inactive - those of breeding males are up to 15 mm in length.

No systematic observations were made of immature males, and they were only watched when they visited the breeding colonies. In the presence of adult males they were given no opportunity to display, being either pursued or courted, and soon displaced from the colony. However, as already described, the Gartmore colony had only one resident male, and when he was off the territory the area was undefended. At these times several immature males would land on the nesting area and "hold court" until the adult male chased them off on his return. Most of the information on the immatures was obtained during these periods.

Chipping was never heard from immature males and rattling was rare, but sizzling was a very common and characteristic call. This is also mentioned by Skead (1956), but he considers the sizzling of the immatures as distinct from adult calls. He states further that the call characteristic of adult courtship was not heard from immatures. Certainly at Gartmore, during the swivelling displays of immature males sizzling was usual, and the special form of rattling which accompanies this display in the adult was never given. At the other colonies where immature males had no chance to perch on a territory to display, sizzling was often heard from sites such as trees bordering on the colony area.

The immatures gave no indications of territorial behaviour, and the threat display was seen only once, when a male E. ardens landed nearby. There were often three immatures on the colony at the same time, but they did not remain in the vicinity of any particular nests - the only

"clash " occurred when one bird almost landed on top of another. There was a brief breast-to-breast scuffle, but no pursuit.

A brown landing on the colony would be approached by the nearest immature male in bumble-flight, and a swiveling display would follow if the bird remained. If the brown entered a nest, the immature would hang below the nest sizzling - it was also at Gartmore that this display was regularly performed by an adult male. Skead (1956) saw an immature hang sizzling from a fence, but did not record this display at the nest for either adults or immatures. It is likely that both females and other immature males were courted. When intruding adult males landed on the area, they ignored the immature males, which in turn ignored them. In contrast the territory holder would chase off all immatures immediately on his return.

Skead found "colonies" of nests built by immature males during the main breeding season in the Eastern Cape, but nest-building by brown-plumaged birds was seen at Klawervlei during March and April 1972 - this is well after the end of breeding in the Cape, and no immature building was seen at other times. It is, however, a regular occurrence at this time of year (N. Myburgh, pers. comm). In April browns were also seen building at Philadelphia in the Western Cape. None of the nests were complete, and in many cases only a series of rings, one above the other, was made. Crook (1964) suggests from his observations on the weavers Ploceus cucullatus and philippinus, that the immature colonies may be the site of adult breeding when the birds reach their second year. The colony observed at Klawervlei was on the site of the earlier nest-building by browns, and as this group of males started breeding later than E. orix colonies elsewhere on the farm, it is possible that these were birds breeding for the first time. Moreover, male I built two pairs of nests one above the other, in the manner one would expect if the successive rings were extended into completed nests.

Since the immature males are physically incapable of reproducing and normally have neither nest nor territory, it is surprising to what a large extent the adult displays are already shown. The maturation of these displays is clearly a subject worth detailed study.

THE NEST.

The nests appear to have a considerable attraction for all visitors to the territory. The behaviour of the browns at the nest has been discussed, and both adult and immature males have been seen nest inspecting. There are some indications that fresh nests, still green, are the most attractive, and even incomplete nest frames may be carefully examined by browns. As recorded by Skead (1956) at his colony, some nests are laid in as soon as weaving is completed, while others stand empty for some time. In one case at Klawervlei a nest was laid in over two months after it had been built. But it is perhaps significant that after male Q had taken over all the nests at Gartmore, he added fresh material to a nest completed by male P, and frequently displayed to browns at that nest.

Male trespassers may also examine the nests on their neighbour's territory. While male F was building, he several times crossed over into male E's territory while E was absent, and entered the newest nest two or three times before returning to his own partly-finished structure. In some other Ploceidae such as Ploceus velatus, it is said that certain nests are used only for roosting (McLachlan and Liversidge 1958). At all three E. orix colonies one nest on the territory often had an accumulation of droppings in the bottom, though it had never been occupied by a female, and this deposit appeared to increase during the season. This suggests that the male may use one nest for roosting, but as no night checks were made, confirmation is still required.

Figure 8 shows the number of nests per male plotted against the number of mates in each case, using the data in Tables 1, 2 and 3. Although some of the points are fairly scattered, calculation shows that there is a very significant correlation between the two parameters. Thus the more nests a male has, the more females he is likely to have, as might be expected. Individual variations between males with respect to the number of nests and the number of mates at the Klawervlei colony were not significant, but the totals involved are small for satisfactory statistical testing.

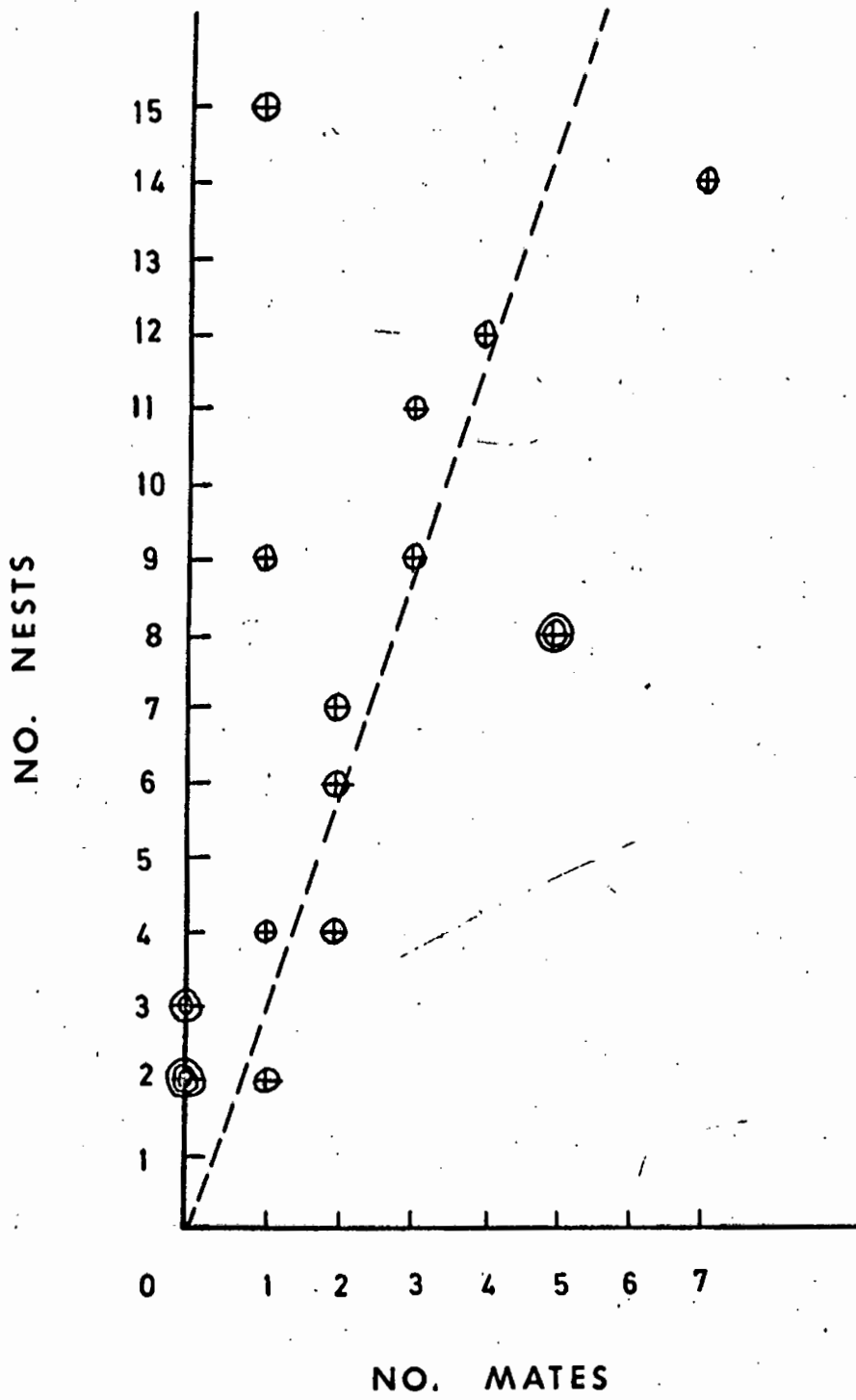
In the Klawervlei colony 15 of 91 eggs (16%) were

FIGURE 8.

Relation between the number of nests
and the number of mates in
Euplectes orix males.

Correlation coefficient $r = 0.6716$
for which $0.05 > P > 0.01$

FIGURE 8



taken by predators, from eight different nests. Two of the nests had been ripped open from the bottom, and as they were very close to the water level, the gallinule Porphyrio porphyrio was suspected. However, in the other cases the eggs disappeared without any visible damage to the nest, and often only one egg from the clutch was removed. Only once were any egg-shells found in the nest. Elliott (1973) has seen Rhabdomys pumilio jump out of Ploceus capensis nests and swim away, so it is likely that despite the apparent protection provided by the water, mice can still rob nests.

Movement of the reeds may also distort the nest, and one nest with a full clutch of three eggs was squashed like a sandwich so that no bird could enter it. In addition, if the gaps where the nest is attached to the reeds are too large, the eggs may roll out. This was seen to happen to one egg during a high wind. Thus it is proposed that to investigate factors possibly influencing female choice of a nest, each nest in a colony should be given values for features such as: stability, time elapsed since building, and accessibility to predators (height above water and distance from shore). The character of the nest may be the major factor determining the breeding success of a male.

INTERSPECIFIC RELATIONS.

Numerous other species frequented the reed areas in which the colonies were located, and some of these came into regular contact with the territory-holding males. In very few cases, however, could there be said to be any clash of interests.

Cape reed warblers (Acrocephalus gracilirostris) were extremely common at both Klawervlei and Thorngrove. They displayed, defended territories and collected food throughout the colony area, ignored by the males even when they landed on and examined the nests. A reed warbler nest at Klawervlei was situated 10 cm below a bishop nest, though no chicks were raised, while at Thorngrove two nests were found very close to bishop nests, and chicks were reared successfully by both species. The only reaction by a male E. orix was a bumble-flight towards a pair of reed warblers calling loudly on his territory, but neither party took any further notice. Le Vaillant's cisticola (Cisticola tinniens) was found at all colonies, while at Gartmore the African marsh warbler (Acrocephalus baeticatus) and the great reed warbler (Acrocephalus arundinaceus) replaced the cape reed warbler. None of these species showed any interactions with the bishops.

A bumble-flight was also seen to a half-collared kingfisher (Alcedo semitorquata) at Thorngrove; this was the only time this bird was seen. At Gartmore a malachite kingfisher (Corythornis cristata) regularly fished from the reeds of the colony without interference.

Moorhen (Gallinula chloropus) occurred in both the Klawervlei and Gartmore colonies. Elliott (1973) has observed them taking chicks and eggs from the nests of cape weavers (Ploceus capensis), but male E. orix did not react, even when the moorhen passed close to their nests. In contrast, a purple gallinule (Porphyrio porphyrio) swimming near the nests at Klawervlei was closely followed by two male bishops and a brown, chipping loudly and pecking at the bird until it left the nest area. Since some of the nests had evidently been attacked from the water, the behaviour of the birds may imply recognition of the gallinule as a potential nest predator.

The Diederik cuckoo (Chrysococcyx caprius) is a well-

documented nest parasite of E. orix (Reed 1968). None were seen or heard at Klawervlei during the observation period, and it seems probable that they arrive in the Cape too late in the season to affect bishop colonies in this area. At Thorngrove a pair of Diederiks was regularly seen on a dead tree across the river from the colony, where the male presented hairy caterpillars to his mate (up to nine caterpillars per hour on occasion). But they were never seen on the bishop colony, and no evidence of parasitism was found. In Natal Diederiks were again in evidence, and Dr. G. Maclean had found a dead Diederik chick in a E. orix nest at the Pietermaritzburg sewage farm. The Gartmore colony had a pair in attendance, usually perched on the nearby telephone wires. The male, complete with hairy caterpillar, was once caught in the mist net, while his mate perched on the pole.

Once when the male cuckoo was perched directly over the colony, male Q flew up, perched on the wire beside him, and adopted the threat posture until the cuckoo moved farther off. Later while male Q was absent, the female Diederik landed on the colony and approached a nest which had been visited by browns very frequently in the past few days, though it had not yet been laid in. A brown E. orix was also on the territory, but did nothing beyond following the cuckoo at a short distance, quite silent. Finally the female Diederik entered the nest briefly, then flew off. A few days later elsewhere on the farm, a male cape weaver (Ploceus capensis) was seen pursuing a female Diederik which had a blue egg, presumably a weaver's, in her bill.

Reed (1968) has recorded that males of E. orix will attack adult Diederik cuckoos, while Friedmann (1956) quotes an observation of E. orix males chasing a jacobin cuckoo (Clamator jacobinus), which had apparently been robbing their nests. Skead (1956) also saw Diederik cuckoos near his colonies, but found no sign of parasitism.

The relations between E. orix and other members of the Ploceidae were not consistent, but away from their territories the birds appeared to mix freely. Mist-netting on the feeding grounds at Thorngrove produced mixed catches of red bishop (E. orix), golden bishop (E. afer), and red-billed quelea (Quelea quelea). The feeding flocks

at Gartmore contained red bishop, (E. orix), red-collared widow (E. ardens), sakabula (E. progne), and pin-tailed whydah (Vidua macroura) as well as other seedeaters such as waxbills. Skead (1956, 1959) has observed similar mixed flocks of Euplectes species.

Immature males of Ploceus capensis built four nests within the Klawervlei colony, and females and breeding males also visited the area. Fluffed and normal pursuits were recorded in equal numbers, without any relation to the sex concerned, and in the colony area the weavers always gave way to E. orix males. None of these pursuits were included in the records on which Tables 4, 6, and 8 are based. Male bishops would not chase off weavers except on their own territory, and the bumble-flights may occur only when the male is in display at the time - the sample of thirteen pursuits is too small to permit of any firm conclusions.

Along the Modder River at Thorngrove the masked weaver (Ploceus velatus) was common, but it did not build in the reeds, instead suspending its nests from the weeping-willow trees. Adult males regularly visited the bishop colony to tear strips of building material from the reeds. The territory holder responded with threat displays, but never pursuit flights. This may have been due to the small size of the territories compared with those at Klawervlei. In one case, a male P. velatus returned the bishop's threat display, but then left the territory. Many of the visits were in the absence of the territory holding E. orix, and the neighbours did not defend his area against the weavers.

Mixed colonies containing several species of Euplectes as encountered by Emlen (1957), were not found, but there was some overlapping of territorial boundaries. The colony at Klawervlei bordered on the territory of a male Euplectes capensis, and many E. orix males collected their building material from the grasses in this area. On one occasion the male E. capensis made a brief fluffed flight at a male E. orix landing near him, but when this bird circled and landed farther off he did not attempt to drive it off the territory. When the E. capensis male perched very briefly on the reeds of the colony, there was no response from the E. orix males. Two browns of E. capensis

inspected a nest while the male E. orix made a bumble-flight towards them, but they flew off before any further display was shown - it is not certain if the male recognised them as being of a different species or not.

The red-shouldered widow (Euplectes axillaris) covered part of the E. orix colony at Gartmore in his flights, but no encounters between the two species were seen. Skead (1959) states that the male E. axillaris may "escort" other species passing through his territory, and that this was seen in the case of E. orix. A red-collared widow (E. ardens) was ignored by E. orix males when flying over their territory, but was twice seen to displace male red bishops from the grassland area of his territory. Woodall (1971) notes that the only interspecific encounters which he witnessed were between these last two species, with E. ardens usually proving dominant. In East Africa on the other hand, Fuggles-Couchman (1943) found that the two species E. hordeaceus and E. nigroventris defended their territories against each other, but both tolerated E. ardens within their territories. Emlen (1957) states that the males of five Euplectes species appeared to defend their territories successfully against all intruders, regardless of species.

At Gartmore a female thick-billed weaver (Amblyospiza albifrons) inspected several nests in the male's absence, but was later seen bathing on the territory within half a metre of the male E. orix, who took no notice. Two bronze mannikins, (Lonchura cucullata) were driven off, however. As already described, the male did not employ the threat posture, but flew at both birds unfluffed, giving a harsh and uncharacteristic squawk. This mannikin is recorded as using the old nests of other weavers (Friedmann, 1950; McLachlan and Liversidge 1958), so that its interest in the male's may not have been entirely innocent. More observations are needed, but some specific recognition by the male E. orix is implied.

On the last evening of observation at Thorngrove, a pair of cape white-eyes (Zosterops pallida) was seen repeatedly entering a E. orix nest, carrying white matter in their bills. The territory-holder was perched nearby, but paid no attention to their activities. A later inspection showed that the nest, which had been unlined in

the morning, was now partly lined with scraps of wool. Subsequently in Natal Dr. G. Maclean found a E. orix nest containing two pure white eggs. A pair of white-eyes was seen in the vicinity and the eggs were of the right size, but the nest could unfortunately not be observed up until hatching. Following these tantalisingly incomplete observations, N. Myburgh (personal communication) reported that he had seen three cases where Ploceus capensis nests were used by white-eyes - a second nest was built within the weaver's frame, and young were reared successfully. Thus in Zosterops pallida, E. orix may have a totally unexpected nest parasite!

It appears that male E. orix will show aggressive responses towards competitors for territory and nest-building material, and also to certain parasites and predators. Other species are generally ignored -except, perhaps, when they overstep the "individual distance" of the bishop. The findings of Emlen (1957) suggest that the males do not discriminate between the browns of different Euplectes species, and specific recognition by the females is a point requiring detailed investigation.

DISCUSSION.

The breeding areas of E. orix have been described as "colonies" throughout this account. Lack (1968) refers to the Euplectes species as breeding in "neighbourhoods" and not in vegetation over water. But he cites no measurements of territory size for E. orix when describing territories "so small that the birds have been termed colonial". Species breeding in grassland, such as E. axillaris certainly have widely scattered territories, and the variations in territory size are probably best explained by Crook (1965) as dispersal in relation to predation - thus colonial concentrations in Euplectines are only possible in protected situations such as reed clumps surrounded by water. Regarding a definition of a colony, Horn (1970) distinguishes between passive concentrations of birds in the most favourable localities, and clumping due to an aggregating tendency in the birds themselves. Since E. orix feeds and roosts in flocks during the non-breeding season, nests in close association with other conspecifics, and continues to feed in flocks during the breeding season, it can justifiably be regarded as colonial.

At Midmar Dam (Natal) there were several large colonies of E. orix in clumps of Phragmites on dry land, but in an area that would be underwater when the dam was full - these were the only "dry" colonies encountered. At Klawervlei a few isolated clumps of Cyperus congestus formed the territories of single males, while at Gartmore male Q later became a solitary territory holder. Most of the colonies in the study areas were, however, considerably larger than those under observation, and it will be necessary to compare the behaviour of males in a large colony with the results described here, in respect of factors such as percentage of time spent in activity, and the frequency of display. The concept of social stimulation in colonial breeding has recently received support from field studies of North American Icterids (Horn 1970), and experimental work on Ploceus cucullatus by Collias and others (1971 a & b). E. orix seems to be a suitable subject for similar investigations. It is also likely that a larger colony is more efficient in attracting mates than a smaller one - Collias and Collias (1969) found that the

breeding colonies of P. cucullatus with ten males or fewer had a significantly lower proportion of resident females than did larger colonies. This would follow if, as was suggested for E. orix, females are led to the colony by flocking with males returning from the feeding grounds - the fewer males there are flying in a particular direction, the fewer females are likely to be drawn to follow them.

Since the pioneer studies of Howard (1920), territorial behaviour has been described in a great variety of forms among birds (Hinde 1956 has many examples). However, as discussed by Brown (1964), the type of territorial behaviour shown by a species depends on the requirements for which competition exists, and the degree to which the individual can practicably defend them. In E. orix the food sources are exploited by numerous species, and are clearly indefensible, so that territorial behaviour is limited to the defence of an area in which nests can be built. If there is direct competition for nest sites and building material, this may involve interspecific territorial defence as described by other authors, but there was no clear indication of this in the areas studied.

It is difficult to assess the extent to which E. orix males may be prevented from breeding by being unable to obtain a territory. While in some species the removal of a territory-holding male will lead to his replacement (Crook 1965), in the three observed cases of males disappearing from the colony, their neighbours took over their territories in addition to their own. At Gartmore where male Q had an abnormally extended area to defend, intruding males were frequent visitors, but none attempted to establish themselves. Nor did an intruder ever attempt to oppose a territory holder, so that the defeat and eviction of a resident by an outsider is improbable - the reaction of other males to an intruder on their neighbour's territory would preclude his success. At the Klawervlei colony several non-resident males were colour-marked, and two of these were later seen as intruders on the colony. This implies either that males resident in a particular colony may visit other colonies in passing, or that some males remain "intruders" throughout the season, without being able to establish themselves as members of any colony. Since the early occupation of a territory seems to

be important, this "rule of precedence" may exclude late-maturing males from the colonies. These males might establish territories, as there is usually plenty of unoccupied nesting habitat in the area, but with a reduced chance of securing a mate owing to them not being associated with other males. The ideal study situation would evidently be a colour-marked population with the various colonies under simultaneous observation.

The differences in degree of erection of the plumage, and the marked differences in the resulting display of colours in the male suggests very strongly that this may serve to signal the motivation of the male. In the threat display the male always faces his opponent, to whom the plumage of his back is probably invisible. The features displayed are the black face mask with its complete red ruff, and the black chest (Figure 6). In the sleeked posture, in contrast, no red is visible above the head, while the band across the throat is made more pronounced by the stretching of the neck (Figure 5). During the swivelling display, the body plumage is ruffled and the male may turn away from the brown, so that the red feathers of the back are displayed, while the threatening elements of the head and bill are averted (Figure 4 a). From the front, the red feathers above the head are erected, but since the bill is depressed onto the chest, the band under the throat is completely obscured (Figure 3). On the few occasions when a male swivelling to a brown suddenly changed to the threat posture and chased the bird off his territory, it could be clearly seen how the body feathers were relaxed, while those of the head remained erected as the bill was raised and pointed at the other bird, thus exposing the red band on the throat.

The threat displays of the male E. orix show an obvious compromise between attack and escape elements: the wing and tail flipping with the relaxed body plumage show readiness for flight, while the erected head feathers, with the bill directed continually at the opponent indicate attack. The conflict is emphasised by the alternate hops towards and away from the opponent. It is perhaps also significant that both the threat and sleeked (or submissive) postures share the displaying of a broad red collar below the head. The degree of sleeking of the plumage

of a threatening male probably serves as a measure of the strength of the escape drive. The function of the colours could be tested by dyeing the red areas of the plumage black or vice versa, and then observing the reactions of the other males. Smith (1972) has obtained very interesting results by using this method on the North American Icterid Agelaius phoeniceus.

It was mentioned earlier how one male regularly proceeded to the border in the threat posture after one of his females had returned to a nest on his territory. This may in fact not represent defence of the mate and nest, but may be a redirected activity on the removal of the external stimulus, as described by Tinbergen (1952). Here the stimulus is a brown landing on the territory close to the male, which he would normally respond to by either threat or courtship. But the bird then enters a nest, thus effectively removing the stimulus. Consequently the male redirects his activity towards his neighbour, and initiates a bout of mutual threatening at the territorial boundary.

Crook (1964) regards the bumble-flying displays of Euplectes species as having "the appearance of an aerial tail-depressed threat", and writes further "It seems an original attack-escape conflict posture has been selected for its signal value in attracting females." However, it was proposed in an earlier section that bumble-flying in E. orix is normally released by a brown landing on the territory, and should be regarded as an approach preceding courtship rather than as a means of attraction. The tail is certainly depressed in flight, but this should rather be considered in conjunction with the retarded wing beats as necessary for the slow, level flight. A pure tail-depressed threat has not been seen in E. orix, and even during threat displays the tail is rarely lowered. The ruffling of the body plumage is also in marked contrast to any attack-escape conflict posture. The most obvious feature of the bumble-flight is that it is the exact opposite of the rapid, unruffled pursuit flight used in territorial defence. The male ruffles his plumage before he takes off - that is he adopts the posture of perched courtship. He then flies slowly towards the brown, so that he can at any moment land and commence swivelling -

the entire bumble-flight resembles most closely the final "landing approach" of normal flight. The ruffled plumage will emphasise the specific plumage characters of the male, and thus signal both "species" and "non-aggressive intent".

For a brown landing in the territory, there is again a conflict between advance and retreat. The sleeked body plumage with wing and tail flicking shows the desire to flee, but the bird nevertheless tries to move deeper into the territory and approach a nest. It is probably the relaxed plumage and direct flight that enables a male to recognise a mate returning to a nest on the territory, and consequently not display to her. Since the female has not been seen to respond to the male by any form of display, it is likely that the situation in the bishop falls into the second category of pre-coition displays mentioned by Tinbergen (1952) - where there is a tendency to keep away from the partner as well as the tendency to draw together, due to the normal avoidance of bodily contact with other individuals. During the swivelling display it is quite clear that the brown withdraws when the male approaches too closely, while the male moves both towards and away from the bird being courted. Only later will the male be permitted to come really close, and it is only then that the up-and-down pumping movements of the body (intention movements of mounting) are shown. Yet even at this stage the female may fly off, and her acceptance is purely passive; there is no reciprocal movement towards the male. The female needs to become habituated to the presence of the male so as to permit his approach, and she must be sufficiently sexually motivated to allow the final act of mating.

COMPARISON WITH ICTERIDS.

The close parallels between members of the American Icterid genera Agelaius and Xanthocephalus and the African Ploceid genus Euplectes form a fine example of convergent evolution (Lack 1968). The North American Icterid species have been studied in some detail, and the recent review by Orians and Christman (1968), on which the following account is based, is the best source of information.

The tricoloured blackbird (Agelaius tricolor) may breed in colonies of as many as 200,000 nests, and small territories are defended briefly. Many matings may be monogamous, and this species seems to resemble Quelea quelea of the Ploceidae, rather than any Euplectes species. However, the red-winged blackbird, Agelaius phoeniceus, which has a striking physical resemblance to Euplectes axillaris, nests in grass or reed beds in which the nest is suspended, and usually has two to four mates. It may breed in colonies like E. orix, in small groups or even solitarily; territory size ranges from 50 to 2,750 sq m. The female both builds the nest and feeds the young, but the male may also feed the fledglings. Xanthocephalus xanthocephalus, the yellow-headed blackbird, has a smaller territory, but the male may have up to six mates, although he helps in feeding the young.

The male A. phoeniceus has a display termed "flight song"; the body plumage is erected with the epaulets particularly conspicuous, while the tail is spread and lowered and the wings beat slowly, almost at stalling speed. The song is given in flight. X. xanthocephalus males have a similar display, but the bird is silent. In both cases the display is elicited by another male flying over, the arrival of a female, or the display of a territorial neighbour. Euplectes orix is normally silent in flight, but E. afer has been heard to sizzle while bumble-flying, and E. capensis also has a flight call for its fluffed flights. E. axillaris has a soft trilling song in flight, rendered by Skead (1959) as "tseek, wirra; wirra". Thus in both form and context (cf. Table 6) the flight song is very like the bumble-flight of E. orix and the other species. Although the male blackbird does not build the nest, the flight song display may terminate in a "nest-site display",

which suggests a further parallel to the swivelling display of E. orix.

In the head forward threat of A. phoeniceus the epaulets are displayed, but the authors note that no contour feathers are conspicuously erected. No description is given for X. xanthocephalus whose head plumage bears more resemblance to that of E. orix in pattern. The bill-up territorial boundary display of A. phoeniceus and A. tricolor is similar to the threat of E. orix, but there is no erection of head plumage and the head is pointed almost vertically upwards. X. xanthocephalus males apparently tend to face away from one another during boundary displays - this may be a form of "head-flagging", but has not been seen in the bishops.

The song spread display is similar in the males of all three Icterid species: the tail is lowered and spread, while the head is thrust forward and the body feathers fluffed or ruffled according to the degree of intensity of the display. This is evidently similar to the sizzling posture of E. orix, and it is also often given in the absence of any bird to which it might be directed; in the case of A. tricolor "well down in the vegetation where the bird is visible only to other birds above him and to his immediate neighbours" (Orians and Christman 1968). This description could just as well refer to a male of E. orix sizzling in the vicinity of a nest. The song spread may also grade into a precopulatory display - and in E. orix sizzling is evidently a part of the approach for copulation.

Other displays of the blackbirds such as sexual chasing, solicitation by the female and mutual post-copulatory displays appear to have no counterparts in the behavioural repertoire of E. orix. It is noticeable that the female blackbird plays a far more active role than the female bishop, even to the extent of threatening intruding males and defending the territory against neighbouring females. The major difference between the Icterids and the Ploceids is that in the case of the former, the female builds the nest. It may be suggested that the behavioural exchanges between the male and female blackbirds are important, as there is some co-operation between the two sexes in rearing the young, and because the female needs to build a

nest on the territory before she can commence laying the eggs. In contrast the male E. orix provides the nest, and the female need have no further contact with the male after mating - this may have led to a reduction in the variety of displays.

It is of note that two unrelated groups of birds on different continents, but with very similar ecological requirements, should both have polygynous mating systems and show similar patterns of breeding behaviour. This implies that polygyny is an adaptation favoured by certain environmental conditions, and that in similar habitats a limited range of behaviour patterns will prove to be adaptive. It is to be hoped that further studies of the Euplectes species, in particular of E. axillaris as the physical "double" of A. phoeniceus, will enable a more detailed comparison with the American work, which could then provide fundamental information on the evolution of polygyny.

POLYGYNY IN Euplectes orix.

Polygyny is rare in birds; Lack (1968) estimates that according to present knowledge, 91% of bird species are monogamous, 6% promiscuous, and only 2% polygynous. Consequently the evolution of polygyny in birds has been the subject of a number of theoretical discussions.

For polygyny to be advantageous for both sexes, the female must be able to feed the young without requiring assistance from her mate, leaving the male free to court further females. Thus in a series of papers, Crook (1962, 1963 a, 1964, 1965) treats monogamy and polygyny in the Ploceidae as adjustments in relation to the abundance and seasonal availability of food. In African savannah country there is a very marked seasonal peak in food supplies for seed-eating birds, freeing the males from the necessity for parental care, and enabling them to increase their breeding productivity by polygyny. Brooke (1964) provides evidence for the timing of breeding so as to coincide with the period of food abundance following the rains, and this situation applies to E. orix. In America, Verner and Willson (1966) also noted that thirteen of the fourteen regularly promiscuous or polygynous species bred in the marshes, prairies or savannah-like habitats, where there is a seasonal fluctuation in food supply. In Europe, however, von Haartman (1969) could find no clear correlation between the occurrence of polygyny and food supply.

While ecological conditions make polygyny possible for E. orix, the sex ratio in a breeding colony shows that not all males are breeding, since throughout the breeding season the brown plumaged males with undeveloped gonads are present. There is good evidence for most of the polygynous Ploceidae that males do not breed in their first year, whereas the females do. A study of the hormonal factors controlling maturation in these species is clearly needed. Crook (1964) proposes that this "trial year" enables the birds to gain experience in nest construction and knowledge of topography and local predation, which increases their breeding efficiency when mature. Lack (1968) rejects this argument for the Euplectes species on the grounds that they "have fairly simple nests", and thus should not need any practice. But as was described

above, the immature males of E. orix are nevertheless unable to build effective nests. Verner and Engelsen (1970) found in the polygynous long-billed marsh wren (Telmato-dytes palustris) that there were significant differences in the nest-building behaviour of bachelor males, and suggested that this reduced the success in mate attraction of first-year males. In all species where the male builds the nest, and deferred maturity is shown, the maturation of this behaviour is likely to be under direct control of the (presumably hormonal) factors determining reproductive condition. Among the Icterids the female builds the nest, but first-year males apparently do not hold territories (Orians and Christman 1968) - there is also an apparent lack of territorial behaviour in immature male E. orix, although they perform the other displays before coming into breeding plumage.

Despite the accepted influence of deferred maturity on the breeding sex ratio in E. orix, there have been repeated suggestions that the overall sex ratio is biased in favour of females. Thus Priest (1936) states without any supporting evidence that more females than males are hatched in E. orix, and Moreau and Moreau (1938) propose a genetically-based imbalance in the sex ratio of the related E. nigrifrons. Lack (1968) quotes an estimate of one male to four females in the breeding colonies, and one male to six browns in the browns in the flocks, as indicating higher mortality in the adult males of the Euplectes species. He ascribes this to their conspicuousness to predators in their nuptial plumage - immature males do not breed in their first year owing to the real danger attendant on breeding males. In their second year the males breeding for the first time then reinforce a depleted male population. However, this whole argument rests on the assumption that there is an excess of females in the species.

To investigate these assumptions, the numbers of birds caught for ringing in the present study were examined according to sex, since mist nets will obviously not bias the catches in favour of one sex. The system used for sexing the browns is described in Table 11. Table 12, in which the numbers are compared statistically, includes unpublished figures kindly provided by Mr. G.H. Wilson,

TABLE 11.

Sexing Euplectes orix by wing length.

Sex	Cape.		
	No.	Range (mm)	Mean
Male (plumage)	73	73 - 83	77
Male (dissected)	41	73 - 81	76.5
Female (dissected)	25	66 - 73	70

Any bird with a wing ≥ 73 mm was sexed as male; only one exception was found on dissection, but in doubtful cases body weight should also be considered. It is most likely that more young males with a wing length >73 were misidentified - thus a slight bias in favour of females might result.

O.F.S. and Natal.

Male (plumage)	16	70 - 80	74.5
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No specimens were taken for dissection. However, the birds were definitely smaller than in the Cape, with the browns averaging only 67.5 mm in wing length. All birds with a wing ≥ 71 mm were sexed as males; there were in fact very few birds in the ambiguous range.

Other than size, there are apparently no physical characters that can be used in sexing. Browns of the other Euplectes species caught were distinguished in the hand by a few key features:

E. axillaris always shows a cinnamon shoulder patch;

E. capensis is more darkly streaked, with a yellow wash on the shoulders and rump;

E. ardens has no streaking on the chest, which is covered by a broad buff band, clearly separated from the white of the stomach;

E. afer is smaller than the others with more delicate legs, and a very marked golden eye-stripe.

TABLE 12.

Sex ratio in Euplectes orix.

Locality	Males	Females	Total	Probability (χ^2)
Breeding colonies	103 (51 imm)	104	207	P = 1
Feeding Flocks	19 (9 imm)	48	67	0.025 > P > 0.01 significant
Roosts	119	117	236	0.95 > P > 0.90
Total	241	269	510	0.25 P 0.20
Klawervlei (G. Wilson)	295 (129 imm)	268	563	0.50 > P > 0.25
Grand total	536	537	1073	P = 1
G. Wilson (my criteria)	335 (169 imm)	228	563	P < 0.001 significant

For the statistical testing, a sex ratio of 1:1 was assumed; thus the probability shown is the probability that the figures obtained represent such a ratio. Immature males are not listed separately where totals include birds caught outside the breeding season, since they are then indistinguishable from adult males.

who ringed E. orix at Klawervlei during the breeding seasons of 1970 and 1971. The measurements which he used for separating the sexes were slightly different from those shown in Table 11; consequently his totals are listed twice, with the birds sexed by both methods. It is probable that the second figure, showing a highly significant bias in favour of males, is not correct, since the measurements of wing length by two different ringers may differ by up to 3 mm. The excess of females in the feeding flocks is not surprising, as they spend little time at the nest by day unless feeding chicks, whereas the males are spending most of their time on the territory. It is quite clear that in a population of E. orix the overall sex ratio is effectively 1 : 1. Similarly, both Zimmermann (1966) and Verner and Engelsen (1970) found an equal sex ratio despite the polygynous mating system.

It seems most likely that the primary reason for polygyny in the Euplectes species is a restriction in the available nesting sites, so that a proportion of the males can occupy all the suitable areas. The different species appear to be selective in their choice of nesting habitat, and in this regard the distance of the territory from the feeding grounds is a critical factor, in those species in which no feeding is done on the territory. Although there may be males in breeding condition which fail to gain territories, this has still to be demonstrated for E. orix.

As shown in Tables 1, 2 and 3, there was no constant number of mates per male, and unmated males were present when others had several females. The differences between individual males are not statistically significant, but it is evident that some sexual selection of males by the females is taking place - the theoretical explanations for polygyny in birds in fact assume mate selection by the females for maximal individual reproductive success (Orians 1969). Female choice may be related to features of the territory; Willson (1966) states that in the yellow-headed blackbird (Xanthocephalus xanthocephalus) females choose the territories with the most suitable nest sites, and Zimmermann (1966) says the same of the dickcissel (Spiza americana). However, in a detailed study of the long-billed marsh wren (Verner and Engelsen 1970), male pairing success could not be correlated with any

territorial parameter measured, although the nature of the territory had been thought to be the deciding factor (Verner 1964). It was also found that success in attracting females, as reflected by the song rate, was not equivalent to success in forming pair-bonds.

In the case of E. orix, the territory as such is unlikely to have any influence on female choice, since it is merely an area surrounding the completed nests. Thus mate selection by the female can be dependent on only two basic factors; the behaviour of the male, and the nature of the nest. At present there is insufficient data on the behaviour of individual males, but as this accumulates it may later be possible to compare the time spent in display during the season with the number of mates acquired. The impression gained at Klawervlei was that male I had as many visitors and displayed approximately as often as males E and F, but he was unfortunately not marked and could not be monitored satisfactorily. In a large colony the position of the male's territory, at the edge or in the centre, is another factor which may determine the number of visitors he will receive, and thus the frequency of display.

Elliott (1973) found for Ploceus capensis that more dominant neighbours might intrude on a male's territory while he was courting a female, and intervene physically. Thus the position of a male in the colony hierarchy would determine his success in acquiring mates. However, for E. orix even in the absence of the territory-holder trespassing was very rare, and a male displaying to a brown on his territory was never interrupted. The only case where territorial defence could be said to interfere with courtship was at Gartmore, where intruders sometimes landed on other parts of the colony while the lone male was swivelling, but this was not a normal situation.

Crook (1965) writes "Males that spend most time constructing nests acceptable to females and performing the attractive advertisement display are likely to acquire more mates than their companions." While it has been argued that there are no displays whose sole function is advertisement, an active colony will, through the displays of the members, "advertise" its presence over a certain range, depending on the location. Display must have an

important role in the system, but the lack of participation by the female is a most unusual feature. The behaviour of nest-inspecting females suggests very strongly that there are certain criteria which make a nest acceptable. The general trend is that the more nests a male builds, the more females he will get (Figure 8), but the exceptions imply that if a male builds a lot of inferior nests, he is not proportionately increasing his chances of getting a mate. With more data, adequate statistical testing of this point will be possible.

Although dealing chiefly with mate selection at the species level, which appears to be the chief function of the brilliant and diverse nuptial plumage, Emlen (1957) concludes that the female Euplectes responds to a "total nesting situation", including nesting habitat, the completed nest, and the attendant male. The present observations support this deduction, but allow of some further speculation regarding the interrelation of the different components. The nesting habitat will be the least important, if the female arrives at the colony by flocking with conspecifics or sighting males from a distance, rather than by searching likely areas of vegetation. An acceptable nest will then induce her to stay long enough in the territory to permit approach by the male and ultimately mating. Clearly there will be a very fine balance between the internal motivation of the female to stay, and the intimidating effect of the male's behaviour, and the reactions of the females need more detailed study.

Finally, is there any indication that polygyny does increase productivity in E. orix? The Thorngrove and the Gartmore colonies cannot be considered here, since there breeding was only observed during a part of the season. However, at Klawervlei the full cycle of breeding was followed, and despite the heavy losses of eggs, it appears that production of chicks was higher than could have been expected from a monogamous mating system. The mean clutch size was 2.8 eggs, and 10 males mated with 32 females produced 32 chicks; that is 3.2 chicks per male, and one chick reared by each breeding female. With a clutch size of this order it is unlikely that chick production could increase appreciably with all males breeding. The adult mortality shows no sign of being unusually high, and, to

date, ringing studies indicate that E. orix may be longer lived than many other small passerines - one breeding male recaptured proved to be at least eight years old. This might be expected in a bird which does not breed until its second year, and it appears that polygyny is a highly practical adaptation for this species.

SUMMARY.

The behaviour of the red bishop bird, Euplectes orix, during the breeding season is described, with emphasis on the polygynous habit of the males.

The male establishes a territory, which he defends by means of pursuits of male intruders and threat displays with occasional fighting. The male builds the nest, as many as fifteen being completed during the season. Two vocal displays, termed rattling and sizzling, are given by the male on the territory. Potential mates are approached in fluffed bumble-flights, which may be followed by the perched courtship display, swivelling. After copulation he pays little further attention to his mates. The birds feed in mixed flocks away from the territory. There are many interesting parallels with the polygynous Icterids of North America.

Male birds in their first year remain physiologically immature and retain the non-breeding plumage. They do not defend territories or build effective nests, but show many of the displays associated with adult breeding behaviour.

Females visit the territories, but show no response other than nervousness in the presence of the male. They examine the nests, line that selected, and do all the incubation and later the feeding of the chicks. Many eggs are lost or fail to hatch.

The sex ratio in the overall population of E. orix is 1:1. The delayed maturation of the males may be related to the availability of nest sites. There is no evidence of increased mortality in the males due to their conspicuousness during the breeding months, and it seems likely that the adult birds are relatively long-lived.

Polygyny allows all the available females to reproduce. Mate selection by the females may be influenced primarily by characteristics of the nest, but this is not yet proven. The system is evidently successful in maintaining the population, and thus has selective advantage for this species.

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APPENDIX 1.

Attendance of males on territory.

Hour of day	No. obs.	No. absences	Time absent	Mean duration	Mean no. absences
5 - 6	1	3	46	15.3	3
6 - 7	1	1	39	39.0	1
7 - 8	6	8	118	14.7	1.3
8 - 9	5	7	119	17.0	1.4
9 - 10	5	12	105	8.7	2.4
10 - 11	5	10	81	8.1	2.0
11 - 12	3	4	15	3.8	1.3
12 - 13	4	14	87	6.2	3.5
13 - 14	1	2	18	9.0	2.0
14 - 15	2	3	25	8.3	1.5
15 - 16	4	12	99	8.3	3
16 - 17	3	8	79	10.0	2.6
17 - 18	1	3	17	5.6	3
Total	41	87	848	154	28
Average				11.8	2.1

Hour of day	No. obs.	No. visits	Time present	Mean duration	Mean no. visits
5 - 6	1	4	14	3.5	4
6 - 7	1	1	21	21.0	1
7 - 8	6	11	242	22.0	1.8
8 - 9	5	11	181	16.5	2.2
9 - 10	5	12	175	14.5	2.4
10 - 11	5	12	219	18.3	2.4
11 - 12	3	7	162	23.1	2.3
12 - 13	4	16	153	9.6	4
13 - 14	1	2	42	21.0	2
14 - 15	2	5	95	19.0	2.5
15 - 16	4	14	141	10.0	3.5
16 - 17	3	9	141	12.6	3
17 - 18	1	4	43	10.8	4
Total	41	108	1629	201.9	35.1
Average				15.5	2.7

APPENDIX 1 (conc).

Hour of day	No. obs.	Active time	% time on ter. active
5 - 6	1	2' 02	14.3
6 - 7	1	2' 40	12.4
7 - 8	6	70' 42	29.2
8 - 9	5	37' 23	20.8
9 - 10	5	50' 10	28.6
10 - 11	5	73' 32	33.6
11 - 12	3	62' 10	38.3
12 - 13	4	54' 58	35.9
13 - 14	1	5' 36	13.3
14 - 15	2	14' 51	15.6
15 - 16	4	60' 25	42.7
16 - 17	3	22' 56	20.1
17 - 18	1	22' 56	53.3

All times are given in minutes.

APPENDIX 2.

Clutch size in Euplectes orix.

Area	No. eggs			
	1	2	3	4
Natal + O.F.S.	7 23%	16 51%	8 26%	0 0%
Cape	2 6%	6 19%	22 69%	2 6%
Total	9 14%	22 35%	30 48%	2 3%

Mean clutch size (Cape) = 2.8 eggs
 " " " (other) = 2.0 eggs