

Breeding behaviour of the Red Bishop (*Euplectes orix*): a synthesis and new observations

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This paper gives an overview of important aspects of breeding behaviour in the Red Bishop (*Euplectes orix*), a weaverbird with a wide distribution in Africa south of the Sahara. Territorial and courtship behaviour of males in nuptial plumage as well as behaviour of immature males and females is described in detail. Pre- and post-nuptial moult, nesting sites and nests, eggs and egg-laying, rearing of nestlings, and interactions with other bird species are also described. This review thus provides a comprehensive account of Red Bishop natural history and may serve as basis for studies on sexual selection and life history evolution in this sexually dimorphic and highly polygynous species. In addition, several new observations and data are presented that were obtained during a 6-year study on a colony of individually marked Red Bishops in the Addo Elephant National Park in the Eastern Cape, South Africa. Nest heights above water or ground ranged from 20 cm to 210 cm, with a median height of 100 cm. The time delay between nest building and nest acceptance ranged from 1 to 58 days, with 8.6 % of all nests being accepted more than two weeks after the nest was built. However, in most cases (76%) the time span between nest construction and first egg laid did not exceed one week, with the median being 4 days. Intraspecific nest parasitism accounted for 6.5 % of all eggs laid. Return rates of adult Red Bishops were found to be 23.7 % after one year, 11.4 % after two years, and 5.8 % or less after three and more years, with return rates of males being significantly higher than that of females. Furthermore, territorial males had significantly higher return rates than non-territorial males. The recruitment rate of young was found to be 14.9 %.

Keywords: Red Bishop (*Euplectes orix*), weaverbird, natural history, reproductive behaviour.

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Introduction

The Red Bishop (*Euplectes orix*) is a sexually dimorphic and highly polygynous weaverbird (Ploceidae), common in southern Africa. It differs from other weaverbirds of the genus *Euplectes* not only in that it usually breeds in colonies, but also because its mating pattern with apparently random female settlement (as reported by FRIEDL & KLUMP 2000, LAWES et al. 2002) is in contrast to demonstrated strong sexual selection on male morphology and behaviour in several closely related *Euplectes* species (e.g. ANDERSSON 1982, 1992, SAVALLI 1994, PRYKE et al. 2001). Despite recent interest in sexual selection in the Red Bishop (e.g. FRIEDL & KLUMP 1999, 2002, LAWES et al. 2002), surprisingly little has been published on its breeding behaviour since the early observations of SKEAD (1956), EMLEN (1957) and CRAIG (1974, 1980). In this paper, I review important aspects of breeding behaviour in *Euplectes orix*. In addition, I present several new observations and data obtained during a 6-year study on a colony of individually marked Red Bishops in the Addo Elephant National Park in the Eastern Cape, South Africa. This includes data on aggressive interactions with other weaverbirds, nest heights, time delays between nest building and nest acceptance, intraspecific nest parasitism, return rates of adults and recruitment rates of nestlings.

Methods

I studied breeding behaviour of Red Bishops at a breeding colony in the Addo Elephant National Park in the Eastern Cape, South Africa (33°26'S; 25°45'E) for six consecutive breeding seasons (1993/94 to 1998/99). The study was conducted under licence from the Provincial Administration of the Cape of Good Hope, Chief Directorate Nature and Environmental Conservation (Licence numbers: 625/93, 653/94, 144/95, 92/96, 1/97) and with permission from the South African National Parks Board.

The breeding site was a small dam (approximately 250 m²) surrounded by an inner belt of Bullrushes (*Typha capensis*) and an outer belt of Common Reeds (*Phragmites australis*). Throughout the study, I searched daily for new nests built by territorial males in breeding plumage. In the breeding season 1993/94 I marked every nest containing eggs with yellow plastic tags attached to reed or bullrush stems close to the nest. In addition, I tagged most of the empty nests. In the breeding seasons 1994/95 to 1998/99 all nests built by territorial males in breeding plumage were tagged regardless of whether they were later accepted by females or not. Nests built by non-territorial immature males were not marked, since females never accept nests from subadult males (SKEAD 1956). In the seasons 1994/95, 1995/96 and 1996/97 I measured nest height above surface level (ground or water) to the nearest 10 cm for all nests recorded.

In the breeding seasons 1993/94 to 1996/97 I checked every nest daily to collect data on laying dates of the eggs, clutch size, hatching dates, number of hatchlings and number of fledglings for all breeding attempts that were observed within the colony. In the seasons 1997/98 and 1998/99 nestchecks were conducted every second day. In total, 963 breeding attempts were recorded during the six study seasons. The nestchecks did not seem to affect the birds, since females resumed incubation of eggs or feeding of chicks as short as 10 min after nest inspection.

Adult red bishops were caught either with mist nets or with a walk-in trap baited with commercially available mixed bird seeds. Each individual was ringed with a unique combination of four color rings and a numbered stainless-steel ring provided by the South African Bird Ringing Unit. Nestlings were ringed when about 10 days old. During the six study seasons a total of 803 adults and 753 nestlings was individually marked.

Whenever data are presented obtained from the Red Bishop colony in the Addo Elephant National Park, they represent data obtained for all six study seasons unless indicated otherwise.

Acknowledgements

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Species description and distribution

The Red Bishop belongs to the family of the weaverbirds (Ploceidae), which comprises sparrows, weavers, bishops and widows. This species has a wide distribution in Africa south of the Sahara and is a very common resident throughout most of Southern Africa except the central Kalahari basin and northwestern Namibia. The breeding males of this highly sexual dimorphic species have a black bill, forehead, face and throat; the rest of the head, breast and rump are brilliant orange-scarlet. The belly is black, the mantle orange-brown, and wings and tail are brown. Females and immatures of both sexes are boldly streaked buff and dark brown above, the underparts are white with the breast and flanks washed buff and streaked brown. Wings and tail are dark brown. They show a distinctive whitish to yellowish eyebrow stripe, and the bill is pinkish horn. In the nonbreeding season males have an eclipse plumage that resembles that of the females.

Start of the breeding season and prenuptial moult

The timing of the breeding season in the Red Bishop is usually related to rainfall. CRAIG (1982a) reported that over the whole range of the Red Bishop in Southern Africa clutches were mostly laid in, or shortly after, the rainy season. A detailed analysis of breeding activity in relation to rainfall in a Red Bishop population in the Addo Elephant National Park, Eastern Cape, South Africa, showed that poor rainfall preceding breeding delayed the start of the breeding season (FRIEDL 2002); the same was noted by Brooke (1966) studying Red Bishops in Zimbabwe and by Lawes (pers. comm.) studying Red Bishops in KwaZulu-Natal, South Africa.

In a prenuptial moult, males renew their body plumage to change from brown eclipse plumage to the colourful black and scarlet breeding plumage, whereas the remiges (flight feathers) and rectrices (tail feathers) are not replaced (CRAIG 1983). There is considerable variation between individual males in the timing and duration of the prenuptial moult, lasting between four and six weeks (BROOKE 1966, CRAIG 1982a). At the beginning of the breeding season some males may not have started with the prenuptial moult, while others show already full breeding plumage or intermediate stages. However, all adult males have a black bill from the start of the breeding season. Since the black colour of the bill has been shown to indicate full testis development in the Red Bishop (CRAIG 1975), this suggests that the males are in breeding condition even before the prenuptial moult is started.

Males moult into the colourful breeding plumage in their second year; one-year-old males retain the brown eclipse plumage and are difficult to distinguish from females in the field. Some one-year-old males, however, show signs of orange in their plumage (SKEAD 1956) and some develop a black bill late in the season (pers. obs.), suggesting that males can attain sexual maturity in their first year even though they do not acquire full nuptial plumage. During my study I observed only three cases (i.e. 5.2 %) in which males presumably ringed at one year of age returned to the study site in the following breeding season without having moulted into nuptial plumage ($n = 58$). One of these males was seen in the following season in full breeding plumage; the other two males disappeared.

Nesting sites and territory sizes

Red Bishops usually breed in colonies which are most often found in reedbeds (*Phragmites* spp.) or bullrush stands (*Typha* spp.) in marshes, dams and rivers. Sometimes they are found breeding in rank grass or sedges, and occasionally also cultivated fields or trees are used as nesting sites (CRAIG 1980, 1982b). Territory sizes of Red Bishop males breeding in reedbeds or bullrush stands range from about 2 m² to 40 m² (SKEAD 1956, CRAIG 1974, FRIEDL 1998); LAWES et al. (2002) measured 52 territories situated in reedbeds and reported a mean territory size of 6.2 m² (s.d. 3.3 m²). In other types of vegetation, however, territories might occasionally be up to about 300 m² in size (e.g., WOODALL 1971). If the territories are situated over water, the males usually drink there, but foraging always takes place away from the territory (CRAIG 1974, FRIEDL 1998).

Territorial behaviour

Red Bishop males are highly territorial during the breeding season. At the start of the breeding season, often before the prenuptial moult is completed, males occupy small territories in the reeds. Successively more and more time is spent on the territories until nest building starts. The time span between first appearance at the breeding site and start of nest building activity varies from a few days under favourable conditions to almost 4 weeks in dry seasons. After nest building has started the males spend long periods on their territories and show the full range of territorial displays and courtship behaviour. During the activity peaks early in the morning males stay in their territories 70-90 % of the time (N. GEBERZAHN and T.W. P. FRIEDL, unpublished data; LAWES, pers. comm.), while during the day the time periods spent on and off the territory are about equal in duration (CRAIG 1974). Territorial defence, courtship behaviour and nest-building behaviour taken together accounted for 25-68 % of the time on the territory when measured during the activity peaks early in the morning between 6h00 and 11h00 (N. GEBERZAHN and T.W. P. FRIEDL, unpublished data), and for 12-43 % of the time on the territory when measured over the whole day (CRAIG 1974). On very hot summer days there is almost no activity during the hottest hours from about 11.00 h to 15.00 h; most activity takes place early in the morning and only in the late afternoon the level of activity increases again. While rainfall does not seem to affect behaviour unless it is very heavy, strong wind reduces the activity level. The breeding season in the Eastern Cape of South Africa was often characterised by two distinctive breeding peaks with a period in between in which there were only few

or even no nests at all that contain nestlings or incubated eggs (FRIEDL 2002). Between the breeding peaks the general activity level was reduced and the males spent considerably less time on the territory, until good rains initiated the second breeding peak and the males started with nest-building again (FRIEDL 2002). In contrast to the Eastern Cape region of South Africa, rainfall does not seem to affect the temporal pattern of breeding activity within a season in KwaZulu-Natal (CRAIG 1982a; LAWES, pers. comm.).

The territorial displays of Red Bishop males have been described in detail by CRAIG (1974); here I will give only a brief summary and add some of my own observations. The „chase flights“ (termed „supplant chases“ by CROOK 1964) are by far the most common form of territorial displays and always directed towards intruders to the territory. The body plumage is usually not erected (in contrast to flight displays related to courtship behaviour, see below) and the flight is rapid and direct. Since males on their territory usually dominate all other males, the intruder mostly flees, with the defending male sometimes pursuing the other bird beyond the territory boundaries. Threats, another form of territorial display, are usually seen at territory boundaries involving two neighbouring males; that is, in situations where the dominance hierarchy of the opponents is less clear than between a territory holder and an intruder. The two opposing males, situated close to the joint territory boundary, hop alternately forwards and backwards with their head feathers erected, the tail spread and the bill mostly pointed to the opponent. Usually the birds break off after a bout of mutual threatening, but sometimes they will close in and engage in physical fights, flailing their wings and pecking at each other with open bills. Occasionally they might even fall into the water during their struggles (CRAIG 1974; pers. obs.). Threats can also be observed at feeding grounds, where they usually take the form of short rushes with erected head feathers directed towards other birds feeding in the nearest vicinity. Sometimes even a short and undirected fluffing of the head feathers is enough to drive away other birds from the immediate vicinity; this is often the case when subadult males or females are involved. In contrast, when threats are directed towards other adult males in breeding plumage, longer bouts of mutual threatening and even fights might occur.

After the initial phase of territory establishment at the beginning of the breeding season, there are few changes with regard to location and ownership of territories. Intruders on territories where the owner is absent are often chased away by one of the neighbours. When a male disappears from the colony his territory is often taken over completely by one of the territory neighbours, rarely split up among two neighbours. Sometimes, however, another adult male previously without territory (i.e., a „floater“) is able to establish himself in a vacated territory. Occasionally, floaters are also able to first defend some space between two occupied territories, then slowly enlarging the area, until they have established a new territory between two already existing ones.

Red Bishop males are quite faithful not only to the breeding colony (see below), but also to the location of their territories within the breeding site. In Addo most of the territorial males that returned for another breeding season established their territory in the same area in the reeds as in the year before. Three out of five males in breeding plumage that were present at the study site in five breeding seasons, held territories in nearly the same positions within the reeds in all seasons.

Red Bishops, like other species that breed in reeds, also roost on their territory. In the evening they might be joined by large numbers of other birds, mostly bishops, widow birds and weavers, which use reedbeds as communal roosts (CRAIG 1980). In Addo these were mainly Cape Weavers (*Ploceus capensis*), Masked Weavers (*Ploceus velatus*), Spottedbacked Weavers (*Ploceus cucullatus*) and Pied Starlings (*Spreo bicolor*). At the beginning of the invasion shortly before sunset the Red Bishop males invariably try to defend their territories, but later on give up and accept other birds roosting in their territories.

Aggressive interactions with other *Ploceid* weavers are commonly observed also during the day. CRAIG (1974) reported male Red Bishops chasing Cape Weavers several times, and stated that Red Bishop males on their own territory were always dominant over the weavers. However, when

Cape Weavers breed within Red Bishop territories, there is a different outcome. While the territorial Red Bishop males can displace female Cape Weavers, they are clearly dominated by the Cape Weaver males (pers. obs.). At the Addo colony I often observed Cape Weaver males destroying Red Bishop nests, and usually the Cape Weaver males began building their own nest at or close to where the Red Bishop nest was situated before. In the 1996/97 breeding season the Cape Weaver density was at its highest, and 12.3 % of Red Bishop nests ($n = 405$) were destroyed by Cape Weavers. In most instances the nests were old and empty, but several freshly built nests were also destroyed, and in three cases the destroyed nests contained incubated eggs. The territorial Red Bishop males vigorously tried to defend their nests. Occasionally, Red Bishops nests were also destroyed by Masked Weaver males nesting in a Sweet Thorn tree (*Acacia karroo*) situated at the edge of the reedbed.

No other bishops or widow birds occurred near the Red Bishop population in Addo, but interspecific behaviour of Red Bishops towards other *Euplectes* species was often described for cases where the territories were situated close to or even overlapped with that of the Red Bishops. CRAIG (1974, 1980) gives a detailed account of such interactions, ranging from indifference to particularly aggressive encounters.

Warblers (mainly genus *Acrocephalus*) that also breed in reedbeds are completely ignored by Red Bishop males, and often the warbler nests are situated close to occupied Red Bishop nests (CRAIG 1974; pers. obs.).

Courtship behaviour

The courtship displays of the Red Bishop have received much attention by observers and have been described several times (e.g. SKEAD 1956, EMLEN 1957, CRAIG 1974); here I will summarize only the main features of these displays. On appearance of a female on the territory, the male approaches her in a conspicuous flight display with fluffed plumage and slow wingbeats, resembling puffed-out flying feather balls; CRAIG (1974) termed this flight display „bumble-flights“. The male then lands close to the female and performs a perched display, termed „swivelling“ (CRAIG 1974), which is characterised by the male hopping, sliding and swivelling over the reeds with fluffed plumage, often also swivelling around reed stems. While showing this display, the male may move alternately towards and away from the female, sometimes so close that he almost touches her. In this situation I sometimes observed a courtship display which has not yet been described before. This „swaying display“ is characterised by the male slowly swaying his body up and down with fluffed plumage while sitting in front of the female, almost in a „face to face“ position. The swivelling might be interrupted by short phases in which the male is hanging upside down below one of his nests with fluffed plumage but without wing movements.

The male performs these courtship displays until the female either flies off or permits copulation, indicated by wing and tail quivering, the typical copulation solicitation display shown by female passerines. I never observed copulations without a preceding copulation solicitation display by the female, and if a male tried to mount without being solicited by the female, she repulsed him with vigorous pecks (CRAIG 1974, FRIEDL & KLUMP 1999). Often several copulations follow in short succession, with the actual mountings lasting only a few seconds each. A female usually permits the territory owner to copulate with her only after she has accepted one of his nests (CRAIG 1974; pers. obs.). However, females also copulate with males other than their social mate („extra-pair copulations“). This was confirmed by an analysis of genetic parentage for 432 nestlings from 187 broods reared in the Red Bishop colony in the Addo Elephant National Park: 76 nestlings (i.e., 17.6 %) were „extra-pair young“ (i.e. young not sired by the owner of the territory that contained the nest from which they fledged) and these „extra-pair young“ were found in 57 (30.5 %) of all broods investigated (FRIEDL & KLUMP 1999).

Male courtship behaviour might not only be directed towards females, but also towards subadult „brown“ males (CRAIG 1974; pers. obs.). This seems to happen when the subadults land-

ing on a territory do not show any behaviour that could identify them as males. I have sometimes seen bumble-flight approaches directed towards subadult males suddenly switching to a chase flight with flattened feathers; similar observations have been reported by SKEAD (1956) and CRAIG (1974). However, I never observed an adult territorial male performing a swivelling display towards subadult males, indicating that the males are able to distinguish between subadult males and females at short distances.

A male will court a female on his territory and try to initiate copulations during the whole egg-laying period, afterwards he will usually ignore her and court other females. Red Bishops are polygynous and may have several females during the course of the breeding season; at Addo the most successful male mated with as many as 18 females in one season (FRIEDL & KLUMP 1999). The main determinant of male reproductive success was found to be the number of nests built, with males building many nests having a higher reproductive success than males building only few nests (FRIEDL & KLUMP 1999). The number of nests built accounted for 53 % to 86 % of the total variation in reproductive success between males, while the male morphological characteristics wing length, tarsus length, and body weight were found to be of no importance (FRIEDL & KLUMP 1999). Likewise, LAWES et al. (2002) reported that the number of nests built by the males but not territory size or display behaviour significantly influenced male reproductive success in a Red Bishop colony studied in KwaZulu-Natal, South Africa.

Female breeding behaviour

In contrast to males, females are capable of breeding in their first year, although not all of them actually do (pers. obs.). At the beginning of the breeding season, females arrive at the breeding site usually about one to two weeks after the first males. They start to move around in the colony, either alone or in small groups, visiting the different territories, while being courted or chased by males most of the time. However, a detailed analysis of female settlement patterns revealed that females mostly settle randomly with respect to the number of available nests within a territory. This means that every nest has the same probability of being chosen by a female independently of whether this nest belongs to a territory with few or with many nests (FRIEDL & KLUMP 2000). However, freshly built nests had a higher probability of being chosen by a female than old nests (HANSEN 2001; METZ et al. 2003). After a female accepts a nest and copulates several times with the territory owner, she begins lining the nest, mostly with soft grass flowers. Lining will continue during most of the incubation period. Egg-laying commences soon after nest acceptance (see below). Before and during the egg-laying period the female often initiates copulations with the territory owner by performing the copulation-solicitation display described above. After the egg-laying phase the female is usually ignored by the male.

Egg laying and breeding activity in the Red Bishop is clearly related to rainfall. CRAIG (1982a) found that a high amount of rainfall during the year preceding the breeding season corresponded to high breeding activity within that season. In seasons with poor rainfall, breeding activity as measured in terms of the total number of nests built and total number of eggs laid during a breeding season is reduced considerably (FRIEDL 2002). A detailed study on the temporal pattern of rainfall and breeding activity within breeding seasons at the colony in Addo revealed that peaks in egg-laying usually follow 10 to 20 days after peaks in rainfall; the total number of eggs laid during a peak corresponded to the amount of rainfall in the preceding rainfall peak (FRIEDL 2002).

Females are solely responsible for incubation and raising young. A detailed analysis of female nest attentiveness during the incubation period revealed that females spent on average 40 % of the time in the nest incubating eggs and visited the nest on average 6.5 times per hour, with clutch size having no significant effect on both the proportion of time spent in the nest and the number of visits per hour (SLOTOW et al. 1995). In addition to feeding and brooding young, the female also removes fecal pellets and broken egg shells from newly hatched eggs, while unhatched eggs usually remain in the nest. The female defends the immediate vicinity of the nest throughout incubation and

nestling period and is often particularly aggressive towards other females inspecting the nest, probably to prevent intraspecific brood parasitism. In contrast, females that have their own nest in the same territory are usually tolerated. During the night the females often stay in their nests.

At the Addo colony, 19.7 % (23 out of 117) of the individually marked breeding females started two breeding attempts within one breeding season and in 7 cases (30.4 %) both attempts were successful in producing fledglings (see FRIEDL & KLUMP 2000). In some instances females started with a second clutch about one week after chicks from the first brood had left the nest. These females were still observed feeding the fledglings while at the same time incubating their second clutch. Some females produced a replacement clutch after the eggs from their first clutches disappeared, probably through predation. The replacement clutch can be produced as soon as 10 days after the start of the first clutch. Females never used the same nest for the replacement clutches; in fact, often these replacement clutches were laid in a different territory. Two females started three breeding attempts within a season, and one female was observed to start a fourth breeding attempt within a single season (FRIEDL & KLUMP 2000).

Nests

The nest is initially woven by the male. It is a thin-walled upright oval about 11 to 14 cm high with a porched side-top entrance. Nest dimensions obtained by WOODALL (1971) on a Red Bishop colony in Zimbabwe were 108 to 140 mm (average 123 mm) for nest height, 60 to 97 mm (average 78 mm) for nest width, and 60 to 83 mm (average 73 mm) for nest depth. The nest is made of thin strips of reed and bullrush leaves or fine strips of grass. Material may be torn off the leaves of reeds or bullrushes within the territory, but is also collected from reed patches further away in the colony (pers. obs.). Nests are usually attached to upright reed, bullrush or grass stems at about 100 to 200 cm above water or ground level (MACLEAN 1993). In Addo, nest heights ranged from 20 to 210 cm above water or ground level ($n = 980$ nests; nest heights recorded in the seasons 1994/95 to 1996/97 only), with a median nest height of 100 cm and 91.6 % of all nests being built between 50 and 160 cm high (see Fig. 1). The distribution of nest heights was significantly different from a normal dis-

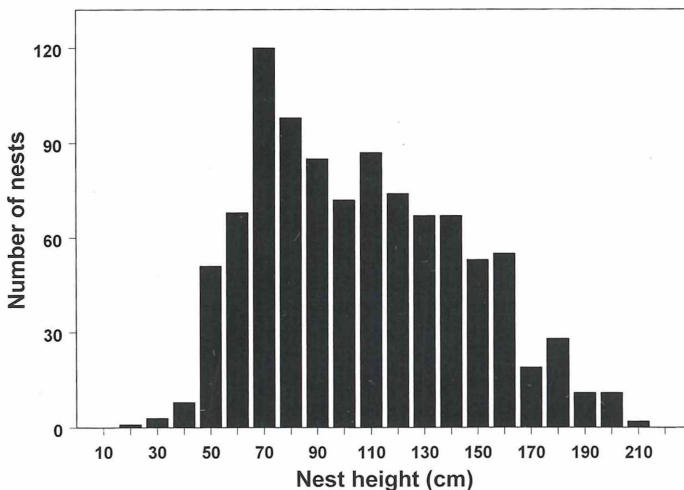


Fig. 1: Nest heights of Red Bishop nests in the Addo Elephant National Park, South Africa (breeding seasons 1994/95 to 1996/97, $n = 980$ nests). – Nesthöhen von Oryxwebernestern im Addo Elephant National Park, Südafrika (Brutsaisons 1994/95 bis 1996/97, $n = 980$ Nester).

tribution (Kolmogorov-Smirnov test, $p < 0.001$). FERGUSON (1994a) reported that in a population near Pretoria, South Africa, areas with tall, dense and thick reeds were preferred for nest placement and showed the highest nest densities. In Addo, where the breeding site was a small dam with an inner belt of Bullrushes (*Typha capensis*) and an outer belt of Common Reeds (*Phragmites australis*) surrounding it, there was a clear preference for the Bullrushes as nesting sites. Only when all the suitable territories in the inner Bullrush belt were occupied, did the males start to establish territories in the outer reed areas.

A detailed description of nest-construction behaviour by Red Bishops is given by SKEAD (1956). Briefly, the male first constructs an upright circle attached to reed, bullrush or grass stems, which later forms the entrance, and then proceeds back and downwards to form the complete upright oval nest shape. The nest structure is rather wide-meshed at the beginning, but subsequently the males (to a varying degree) incorporate more material to thicken the nest structure. However, the final lining resulting in a strong and non-transparent nest structure is mostly done by the female (see above). WOODALL (1971) analysed one nest in detail and found that it consisted of 340 strands of *Phragmites communis* and of 1440 grass heads. Nest construction usually takes about two to three days, but occasionally, especially after rainfall, males can build a complete nest within one day. Males construct several nests within their territories, and often territories contain nests with eggs and chicks as well as empty nests at the same time. At Addo one male built five nests within seven days after exceptionally good rain in November 1996. This male built a total of 28 nests during the course of the breeding season (FRIEDL & KLUMP 1999), the highest number reported for Red Bishops so far. However, not every nest built is accepted by a female, resulting in most territories containing one or more empty nests of different ages. In Addo, on average 47.5 % of all nests built within a season were accepted by females (range 35.5 % – 59.1 % for the five study seasons from 1994/95 to 1998/99; in the season 1993/94 not all nests built were recorded, see methods), with differences among seasons being significant (Chi-square test: $\chi^2_4 = 36.8$, $p < 0.001$). „Leaf-stripping“ (SKEAD 1956), that is tearing off the top of the reed and bullrush stems close to the nest by the territorial male, is regularly observed in the Red Bishop; however, the function of this behaviour is unclear.

In contrast to many *Ploceus* species, in which nest destruction by the territorial male is often observed (e.g. JACOBS et al. 1978), male Red Bishops never destroy their nests. In fact, sometimes they even repair nests that have been damaged by predators, heavy storms, or movement of the reeds (WOODALL 1971; pers. obs.). The reason for this behaviour seems to be that in the Red Bishop even quite old nests are sometimes accepted by females, provided that they are in good condition. This is in contrast to several *Ploceus* species in which only fresh and green nests are accepted by females (e.g. JACOBS et al. 1978). In Addo, 36 out of a total of 419 nests for which exact dates on nest building and nest acceptance (day of first egg) were available (i.e. 8.6%) were accepted more than two weeks after being built, and 8 nests (1.9%) were even accepted more than 4 weeks after being built (see Fig. 2). The longest time span between nest building and nest acceptance observed was 58 days. However, in most cases (76%) the time span between nest construction and first egg laid did not exceed one week, with the median being 4 days (see Figure 2). In six nests a second clutch was laid after the first clutch had disappeared before hatching (probably through predation), and in four of these cases the second breeding attempt was successful in raising young. Mean time span between first and second acceptance of these nests was 17 days (range 11 to 39 days). In one nest a second clutch was laid after a successful first breeding attempt; the time span between first and second acceptance was 37 days and the second breeding attempt failed (eggs disappeared probably through predation).

Eggs and incubation

Eggs are usually laid on successive days early in the morning (CRAIG 1982b; LAWES & KIRKMAN 1996; pers. obs.). The eggs are mostly immaculate and greenish blue in colour, but rarely faintly

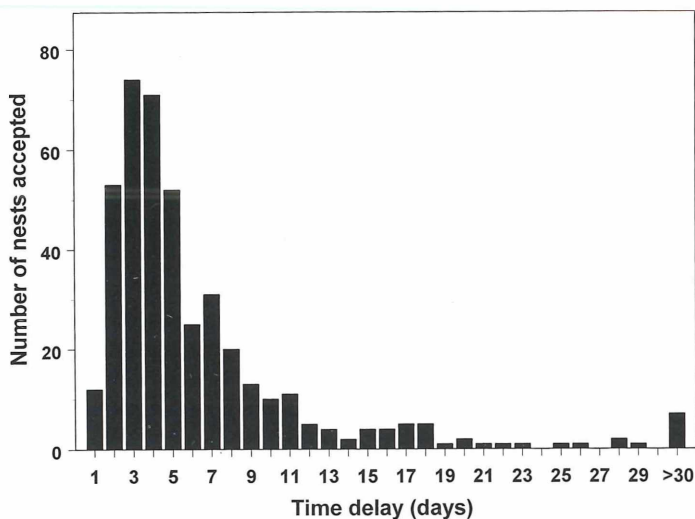


Fig. 2: Time delay between nest building and nest acceptance (day of first egg) in a Red Bishop colony in the Addo Elephant National Park, South Africa (breeding seasons 1994/95 to 1996/97, $n = 419$ nests). – Zeitspanne zwischen der Fertigstellung von Nestern und ihrer Akzeptanz (Tag an dem das erste Ei gelegt wurde) in einer Brutkolonie von Oryxwebern im Addo Elephant National Park, Südafrika (Brutsaisons 1994/95 bis 1996/97, $n = 419$ Nester).

spotted black or dark brown. Red Bishop eggs lightly spotted with black were also noted by WOODALL (1971). Average egg size is 19.2×14.1 mm (range $14.6\text{--}21.6 \times 11.8\text{--}15.7$ mm) and clutch size ranges from 2 to 5 eggs, with the modal size being three eggs (MACLEAN 1993). Mean clutch size from 670 clutches produced in Addo over the four breeding seasons 1993/94 to 1996/97 was 2.97 ± 0.60 eggs (FRIEDL & KLUMP 2000), with 1 one-egg clutch, 119 two-egg clutches, 454 three-egg clutches, 89 four-egg clutches and 7 five-egg clutches. Clutch sizes differed significantly among seasons and average clutch sizes were related to the amount of rainfall during the breeding season, with a larger average clutch size in seasons with a higher amount of rainfall (FRIEDL 2002). In Addo I observed only one case in which a female laid a one-egg clutch and incubated it, however, the egg did not hatch. Single-egg clutches that were incubated were also reported by CRAIG (1982a) and LAWES (pers. comm.). If an egg disappears from a full clutch during the incubation period, the female often continues to incubate the remaining eggs. Incubation is done by the female alone and the incubation period is usually 12 to 14 days (MACLEAN 1993, pers. obs.). Females with clutches containing more than two eggs often start incubation with the penultimate egg, resulting in the last laid egg hatching one or sometimes even two days later than the other ones (SKEAD 1956, pers. obs.).

Nestlings and fledglings

Hatching occurs after an incubation period of 12 to 14 days (see above). Chicks are fed and brooded by the female only. While adults are almost exclusively granivorous, chicks are fed a mixture of seeds and animal material, mainly insects and spiders (SKEAD 1956, pers. obs.). Depending on brood size and temperature the chicks leave the nest after 12 to 15 days, with chicks from smaller broods and chicks reared in periods of higher ambient temperatures tending to leave the nest earlier

than chicks from larger broods or chicks reared under more unfavourable weather conditions. When disturbed, chicks might jump out of the nest when only 11 days old. During the first week after leaving the nest (i.e., until they are able to fly) the fledglings stay in close proximity of the nest where they are fed by the female. Thereafter they become more mobile and often try to follow the female. Fledglings are fed for approximately two weeks; thereafter the female gradually decreases her feeding efforts and the fledglings start foraging by themselves. I frequently saw fledglings begging from males, but usually they were ignored and sometimes the males even showed aggressive behaviour towards them. In three instances, however, I observed a male feeding fledglings that had hatched on his territory.

Behaviour of one-year-old males

Nest building behaviour by immature („brown“) males was first described by SKEAD (1956). At his study site near King William's Town, South Africa, the immature males formed own colonies away from the main breeding colony. At Addo, the immature males frequented areas in the same reedbed where the territories of the adult males in nuptial plumage were situated. However, they were usually restricted to patches with low reed densities and not allowed in the bullrushes, the preferred nesting habitat of the adult males (see above). In the following, I will term these areas, where the immature males showed their nest-building behaviour, the „youngster's playground“. Nests built by immatures were untidy, out of shape and often unfinished. They were usually built in close proximity to each other and often several nests were attached to the same reed stems, so that late in the season, in some years, the „youngster's playground“ was characterised by a high density of nests in all stages of construction. Sometimes several immature males worked successively on one nest. Occasionally, immature males built single nests in other areas of the reedbed not occupied by adult males. In three instances, however, one-year old males were able to establish and defend a territory in the bullrushes amongst adult males in breeding plumage. All three cases involved one-year-old males with a black bill (indicating sexual maturity; see above); they never lasted more than a week and the nests they built within their territories were never accepted by females.

I often observed immature males showing territorial behaviour and defending the area around one of the nests against intruders. However, this behaviour usually did not last longer than a few minutes, and later the same area might be defended by another immature male. Whenever a female entered the „youngster's playground“, she was courted by one or more immature males. The courtship display was very similar to that of adult males (see above) and comprised mainly hopping, sliding and swivelling over the reeds with ruffled plumage; bumble flight approaches were only rarely seen. The females did not react to these courtship displays and I never observed a female copulating with an immature male. There were no indications of females accepting nests that were built by these immature males, since these nests were always unlined and never contained eggs.

Intra- and interspecific brood parasitism

Quite often single eggs are found in nests which are not incubated; these are possibly attempts of intraspecific brood parasitism by other females. Other examples of intraspecific brood parasitism observed at the colony in the Addo Elephant National Park are the addition of a single egg to a clutch two or more days after completion, and the appearance of two new eggs in a nest within one day. According to these criteria, 138 out of 2113 eggs laid during the breeding seasons 1993/94 to 1996/97 (6.5 %) were parasitic eggs (29 out of 647 eggs in 1993/94, 61 out of 632 eggs in 1994/95, 13 out of 240 eggs in 1995/96, 35 out of 594 eggs in 1996/97). Using similar criteria, LAWES & KIRKMAN (1996) reported that 4 out of 61 nests (i.e. 6.6 %) were parasitized by conspecifics in Red Bishop colonies in KwaZulu-Natal, South Africa. However, the attempts of intraspecific brood

parasitism were mostly unsuccessful, as revealed by paternity determination using DNA fingerprinting. Out of 177 nestlings that hatched at Addo and for which both putative parents were known, only 4 nestlings (i.e., 2.3 %) were the result of intraspecific brood parasitism (FRIEDL & KLUMP 1999).

Red Bishops are known to be a major host of the Diederik Cuckoo (*Chrysococcyx caprius*), but the amount of interspecific brood parasitism varies considerably between different populations, with parasitism rates ranging from 0 % to almost 60 % (OTTOW & DUVE 1965, REED 1968, JENSEN & VERNON 1970, FERGUSON 1994b, LAWES & KIRKMAN 1996). At Addo, only two incidences of successful interspecific brood parasitism were observed during the study period, though Diederik Cuckoos were common in the area. Whenever a cuckoo appeared in the vicinity of the colony it was harassed vigorously not only by Red Bishop males and females but also by Cape Weavers. As pointed out by FERGUSON (1994b) and LAWES & KIRKMAN (1996), the main factor determining the amount of Diederik Cuckoo brood parasitism in Red Bishop colonies seems to be the colony size, with small colonies suffering from high rates of parasitism and large colonies showing only very low degrees of parasitism or none at all, possibly due to increased overall vigilance.

Termination of breeding and postnuptial moult

After the breeding season, both sexes undergo a complete moult in which they replace their entire plumage, and juveniles have a complete post-fledging moult (CRAIG 1983). While the nuptial plumage in males is replaced by the female-like eclipse plumage within about four weeks, the primary moult lasts for 110–120 days (CRAIG & MANSON 1979a). Like the prenuptial moult, there is also considerable variation between individual males with regard to onset and duration of the postnuptial moult (CRAIG & MANSON 1979a).

Similar to the start of the breeding season, the termination of the breeding season is also influenced by rainfall, with breeding seasons lasting longer in years with good mid-seasonal rain (FRIEDL 2002). The first indication of the end of the breeding season is the termination of nest-building behaviour by the males. Gradually other activities like territorial displays and courtship behaviour decrease in frequency and the males spend less and less time on their territories. Shortly after they have started the postnuptial moult the first males leave the colony. Some of the territorial males, however, will stay longer, and these are invariably males with nests that contain incubated eggs or chicks (FRIEDL pers. obs.). Often the last males will suddenly leave the breeding colony altogether, so that the breeding site is completely deserted from one day to the next.

In the non-breeding season Red Bishops are nomadic, moving around in large flocks often together with other *Euplectes* species (CRAIG 1980), frequenting grasslands and agricultural lands. Usually they do not cover great distances; in fact, 78.7 % of all recoveries reported so far for Red Bishops were at the original capture site, and a further 19.7 % of the recoveries were within 20 km from the original capture site ($n = 1520$; SAFRING, Avian Demography Unit). The greatest distance between ringing and recovery site reported was 112 km; a record of a recovery 1215 km from the original capture site must be regarded as doubtful (D. OSCHADLEUS, pers. comm.).

Population biology

Return rates of adult Red Bishops ringed at the breeding colony in the Addo Elephant National Park are presented in Table 1. Overall return rates of adult Red Bishops were found to be 23.7 % after one year, 11.4 % after two years, and 5.8 % or less after three and more years (Table 1). However, overall return rates can be misleading because return rates might differ considerably between the sexes and/or between individuals of the same sex but different reproductive stages. That is indeed what I found in the Red Bishop colony studied. Return rates of adult or subadult males after one, two, three, and four years were significantly higher than the corresponding return rates of females

Table 1: Return rates of adult Red Bishops marked at the breeding colony in the Addo Elephant National Park, South Africa. – Wiederkehraten von adulten Oryxwebern in einer Brutkolonie im Addo Elephant National Park, Südafrika.

Ringed as	Individuals ringed / individuals returned (%)				
	after 1 year	after 2 years	after 3 years	after 4 years	after 5 years
Territorial males in breeding plumage	49 / 29 (59.2)	47 / 19 (40.4)	44 / 12 (27.3)	40 / 6 (15.0)	24 / 1 (4.2)
Non-territorial males in breeding plumage	111 / 26 (23.4)	106 / 9 (8.5)	92 / 3 (3.3)	72 / 3 (4.2)	46 / 2 (4.3)
One-year-old males in eclipse plumage	192 / 58 (30.2)	151 / 21 (13.9)	147 / 10 (6.8)	102 / 5 (4.9)	27 / 1 (3.7)
Females	451 / 77 (17.1)	383 / 29 (7.6)	325 / 10 (3.1)	282 / 4 (1.4)	140 / 3 (2.1)
All adults	803 / 190 (23.7)	687 / 78 (11.4)	608 / 35 (5.8)	496 / 18 (3.6)	237 / 7 (3.0)

(Chi-square test, all $p < 0.005$). Recovery data from the South African Bird Ringing Unit analysed by CRAIG & MANSON (1979b) and CRAIG (1982c) indicated no differential mortality of Red Bishop females compared to males; thus the low return rates of females found in my study might rather be due to a lower degree of breeding site fidelity of females compared to males.

Significant differences in return rates were found not only between males and females, but also among males in different reproductive stages. Males ringed as territory owner in full breeding plumage showed significantly higher return rates after one, two, and three years than both non-territorial males in full breeding plumage (floaters) and one-year-old males in eclipse plumage (Chi-square test, all $p < 0.001$; see Table 1). The difference in return rates after four years approached significance (Chi-square test, $p = 0.055$). No significant differences with regard to return rates were found between non-territorial males in full breeding plumage and one-year-old males in eclipse plumage (Chi-square test, all $p > 0.1$; see Table 1). The data presented here are the first data on return rates of territorial versus non-territorial Red Bishop males; therefore it remains to be shown whether the pattern of return rates reported here represents a general pattern for Red Bishops. The recruitment rate of nestlings was found to be 14.9% (112 out of 753 individuals marked as nestlings); this low recruitment of nestlings is probably due to a higher mortality in the first year compared to subsequent years (CRAIG & MANSON 1979b).

Zusammenfassung

Der Oryxweber (*Euplectes orix*) ist eine im südlichen Afrika weit verbreitete sexuell dimorphe, polygyne und in Kolonien brütende Webervogelart, welche in den letzten Jahren mehrfach Objekt von Untersuchungen zur sexuellen Selektion gewesen ist. Eine zusammenfassende aktuelle Übersicht von grundlegenden Aspekten zur Brutbiologie und Fortpflanzungsverhalten dieser Art fehlt jedoch. Die vorliegende Übersichtsarbeit soll diese Lücke schließen, indem wichtige Aspekte des Fortpflanzungsverhaltens der Oryxweber im Detail vorgestellt und beschrieben werden. Dies beinhaltet das Territorial- und Balzverhalten von adulten ♂ im Brutkleid sowie das Verhalten von ♀ und einjährigen noch nicht geschlechtsreifen ♂. Weiterhin werden Mauser, Nester und Nestbau, Eier, Aufzucht von Jungen und Interaktionen mit anderen Vögeln genau beschrieben. Zusätzlich zur Zusammenfassung schon bekannter Daten zur Brutbiologie des Oryxwebers werden eine Vielzahl neuer Beobachtungen und Daten präsentiert, welche im Rahmen einer 6-Jahres-Studie an einer Oryxweberkolonie im Addo Elephant National Park, Südafrika, erhoben worden sind. Die Nester wurden zwischen 20 cm und 210 cm über Grund oder Wasser gebaut, wobei der Median 100 cm betrug. Die Zeitspanne zwischen der

Fertigstellung eines Nests durch ein ♂ und seiner Akzeptanz durch ein ♀ betrug zwischen 1 Tag und 58 Tagen, wobei 8,6 % aller Nester mehr als zwei Wochen nach ihrer Fertigstellung akzeptiert wurden. In den meisten Fällen (76 %) betrug die Zeitspanne jedoch weniger als eine Woche (Median 4 Tage). 6,5 % aller Eier wurden von ♀ in fremde Nester gelegt; es handelt sich hierbei also um versuchten intraspezifischen Brutparasitismus. Die Wiederkehrate für adulte Oryxweber betrug 23,7% nach dem ersten Jahr, 11,4 % nach dem zweiten Jahr, und 5,8 % und weniger nach drei oder mehr Jahren. Die Wiederkehraten von ♂ waren dabei signifikant höher als die der ♀; zudem waren die Wiederkehraten von territorialen ♂ signifikant höher als die von nicht-territorialen ♂. Die Rekrutierungsrate von im Nestlingsstadium beringten Oryxwebern betrug 14,9 %.

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