BREEDING BIOLOGY OF THE CRITICALLY ENDANGERED RUDD’S LARK HETEROMIRAFRA RUDDI: IMPLICATIONS FOR CONSERVATION

HABITAT SELECTION AND CONSERVATION OF RUDD’S LARK HETEROMIRAFRA RUDDI: A CRITICALLY ENDANGERED SOUTH AFRICAN GRASSLAND ENDEMIC

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Habitat selection and breeding biology of Rudd’s Lark

*Heteromirafra ruddi*: implications for conservation.

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Habitat selection and breeding biology of the Critically Endangered Rudd’s Lark *Heteromirafra ruddi* was studied over two breeding seasons from 2002/03 to 2003/04. This study characterizes its habitat preferences and breeding biology in a core area of its range around Wakkerstroom, Mpumulanga. Habitat characteristics were recorded at 2 km intervals throughout a 1200 km² survey area and related to the presence or absence of Rudd’s Larks during the breeding season. Nests found were monitored to determine their reproductive performance. Rudd’s Larks were confined to stone-free areas of natural grassland on flat or gently-sloping hilltop plateaus, with short (4 - 9 cm) to medium grass cover (6 - 8 cm). They avoided sites either with tall (3 -17 cm) and dense (5 - 9) grass cover or sites with areas having insufficient grass cover. Laying occurred between the last week of October and late April, with two peaks both in January and February. Nests were located between two to three grass tufts and were made entirely of old grass. Only female bird built the nest and incubated. The first egg was laid on the fourth day following the starting of building activity. A single egg was laid each day with a mean clutch size of 3.4. The mean incubation and nestling periods were 14 and 13.4 days respectively. Both the male and the female fed the nestlings, and feeding rate did not differ between the sexes during early feeding. Nestlings were mostly fed on grasshoppers. Overall survival for nest, egg and chick was higher on unburned sites than was for burned sites.
However, the daily survival estimates for nestlings were inflated for burned sites since the few nests that were found with chicks all survived. One complete breeding cycle was estimated at 47 days in the case where three chicks were fledged. Although the transect work alone supports the previous findings that birds preferred annually burned and heavily grazed sites, the results from breeding performance shows that such sites were not suitable since birds experienced low overall breeding success. Moderately to lightly grazed unburned or burned sites were suitable since birds started breeding earlier, they stayed at these sites throughout the breeding season and they had higher overall nesting success. Although it was not possible to do other important comparisons between burned and unburned sites due to small samples from burned sites, the small sample size from burned areas is further compelling evidence that such sites were not suitable. Within remaining areas of natural grassland, the biggest threat to Rudd’s Larks in the study area is loss of habitat which results from poor pasture management which leads to habitat degradation and fragmentation and modification of grasslands into either fields or housing. Based on the above, it is recommended that Rudd’s Lark and other endangered grassland birds would best be conserved under controlled mixed stocking rates of sheep and cattle with burning carried out every second year.
INTRODUCTION

Rudd’s Lark *Heteromirafraruddi* is endemic to the grassland biome of eastern South Africa, where it is localized and extremely patchily distributed (Dean & Allan 1997, Barnes 2000). Despite having a gross range of some 22 000 km², its actual area of occupancy is estimated to be less than 500 km² (BirdLife International 2000) and very small portion of this area is reserved. It is one of only two lark species worldwide to be listed as Critically Endangered (BirdLife International 2000), due to ongoing habitat loss and the perception that it at the start of a precipitous population decrease (Barnes 2000, BirdLife International 2000, Allan 2001). The main causes of habitat loss are afforestation, agricultural intensification and/or poor pasture management (Barnes 2000). Habitat loss and degradation are considered major causes of avian species decline (Lens *et al.* 2001). Although Rudd’s Lark has been listed as threatened in all three South African Red Data Books on birds (e.g. Siegfried *et al.* 1979, Brooke 1984, Barnes 2000), little research has been undertaken on the species. This species is under considerable threat as it inhabits the least protected and most threatened biome in southern Africa (Barnes 2000). Conservation of Rudd’s Lark and its habitat is considered a priority by BirdLife South Africa and the IUCN (e.g. Harrison *et al.* 1997, BirdLife International, 2000; Barnes 2000).

Understanding how Rudd’s Larks respond to different land-use practices is central to planning for its long-term conservation management. Hockey *et al.* (1988) found that Rudd’s Larks prefer moderate to heavily grazed grasslands with tussocks no higher than 70 cm. This preferred habitat is thought to have been maintained by large herds of ungulate herbivores in the pre-agricultural past. Today, however, most highland grasslands are used for livestock production (Tarboton 1997), often accompanied by frequent heavy grazing, burning and cultivation of sundry pasture grasses. This leads to habitat fragmentation and changes in
vegetation height, density and, over longer periods, changes in species composition (Jansen et al. 1999). Rudd’s Larks appear to be incapable of adapting to the changes in vegetation height and density.

Fire is one of the most ubiquitous agents of disturbance in natural systems and influences the evolution of many organisms, yet its role remains contentious and continues to be one of oldest and most important topics of debate among ecosystem managers (Scholes & Walker 1993, Mills 2004). Farmers in the study area burn immediately after the onset of summer rains and use it to control ticks and disease, improve forage for grazing, remove accumulated litter, and regenerate new grass. Although the optimal burning frequency is supposed to vary according to the rate of litter accumulation (Stuart-Hill and Mentis 1982), most farmers in South Africa’s high altitude grasslands burn their pastures annually, or more frequently, irrespective of litter accumulation (Tainton 1999, Muchai 2002).

There is evidence that the flora of the eastern escarpment of Mpumalanga Province must have been a long-standing component of the Afromontane vegetation mosaic and not a secondary, fire-maintained vegetation type (Matthew et al. 1993, Jansen et al. 1999). In a recent study Jansen et al. 1999, found out that populations of grassland birds in a study area are negatively impacted by management involving annual burning and high stock rates on a landscape scale. Although periodic fire and grazing have been used extensively as management tools since the 1930s (Mentis & Bigalke 1981, Macdonald 1989), the ecological effects of these on the reproduction of birds in South African grasslands remain poorly understood (Muchai 2002). In a more recent study Muchai 2002, found out that the compound effects of annual burning which is often accompanied by heavy grazing impact negatively on nesting success of most ground nesting birds in the study area.
If Rudd’s Lark is to be properly conserved, it is important to identify its fine-scale habitat requirements and the land use practices responsible for maintaining such habitats. Hockey et al. (1988) reported its broad-scale habitat preferences, whereas Allan (2001) reported its basic biology in an area of high relative density around Wakkerstroom, Mpumulanga Province. This paper reports the fine-scale distribution and breeding performance of Rudd’s Larks in a core area of its range related to local habitat characteristics and discusses imminent threats and their management implications.
MATERIAL & METHODS

Study site

The study was conducted in high altitude grassland around Wakkerstroom on the border between Mpumalanga and KwaZulu-Natal (Fig. 1), where Rudd’s Larks occur at relatively high densities (Hockey, et al. 1988, Allan, 2001). This area corresponds to types 54 and 57 velds described by Acocks (1953): Turf Highveld sourveld transition and North-Eastern Sandy Highveld. Low and Rabelo (1996), merged the two types into one category, number 38, as moist Sandy Highveld Grassveld.

Roads were used to define the boundaries of the study area, a polygon of ca. 1200 km² with corners at 27°12’ 58.2”S 29°53’ 3.5”E, 27°03’ 10.2”S 30°05’ 19.3”E, 27°32’ 11.2”S 30°14’ 05”E and 27°24’ 20.3”S 30°18’ 40.0”E. Random transects were undertaken every 2 km along a network of some 200 km of roads within this area (Tarboton 1998). Positions of each transect were recorded with a hand-held GPS, and Rudd’s Larks were searched for and habitat characteristics recorded. At each site, the side of the road deemed most likely to support larks was sampled, based on the assumption that Rudd’s Larks avoid modified grasslands and tall stands of grass (Hockey et al. 1988). Where there was no difference in habitat on either side of the road, the side with the best light was chosen. Rudd’s Larks have never been recorded in croplands or ploughed lands, and so no sampling was conducted in these habitats.

Bird searches and vegetation sampling

Rudd’s Lark is inconspicuous when not singing (e.g. Hockey et al. 1988). Surveys to record the presence of larks were conducted once singing had commenced at sites where Rudd’s Larks are known to occur. Searches for birds were undertaken between 6:00 h and 10:00 h.
However, bird searches were sometimes carried beyond 11:00 h on cloudy days since birds were observed to call beyond 10:00 h on cool cloudy days. At every sample point, a 1 km transect was walked perpendicular to the road into the veld, scanning the area and listening for displaying birds.

Subsequent to the bird survey, each site was revisited in the afternoon of the same day to record habitat characteristics, once early in the breeding season (20 November 2002 to 10 January 2003) and then again later in the breeding season (10 January to 6 March 2003), to quantify changes in vegetation structure during the growing season. Land use of each site in terms of grazing and burning were noted and topographic features of each transect were characterized. It was easy to infer whether the site had been burned (based on presence or absence of burned grass stubs) during the recent dry season, and the grazing pressure was scored as none, light or heavy, based on grass height and cropped grass tussocks. Transects with an inclination of < 10° were described as flat or gently sloping, 10-30° as shallow sloping, and >30° as steep. Flat sites were further categorized as either valley bottoms and lowlands or hilltops and plateaus.

Ground cover, vegetation composition and density were estimated using 30 x 30 cm quadrats. Two random quadrats (selected by throwing the quadrat) were sampled every 100 m along the transect. For each quadrat, nine points 15 cm apart were sampled, recording the type of cover (grass, bare ground, forbs, stones and dead vegetation). Vegetation height was measured to the nearest 1 cm at the four corners of the quadrat. To have a comprehensive coverage of sites supporting Rudd’s Larks, vegetation sampling was conducted inside territories of displaying birds. Once a territory had been identified (mapped as described by Bibby et al. 1992), cover and vegetation height were measured in 10 random quadrats within a 100 m radius of the
territory’s centre. Territory sampling was done at the same times as the transect vegetation sampling. And some of territories represented the actual nests.

Nest finding and monitoring

Relatively little effort was devoted to finding nests in the first year when attention was focused on habitat selection. The second breeding season was dedicated to finding new sites with Rudd’s Lark, finding nests and monitoring them.

All sites where Rudd’s Lark was present in the previous year, and other new sites suspected to have Rudd’s Lark were visited on a regular basis to look for Rudd’s Lark. If birds were found, the number of individuals present was estimated based on the number of displaying males and nests were searched for. Nests were found by direct observation of adult birds, either carrying nesting material or food for nestlings, or by observing incubating females flying into or leaving the nest.

For each nest found, latitude and longitude were recorded using a portable Global Positioning System (GPS). Egg length and diameter was measured to the nearest 0.1 mm with vernier calipers. If grass was tall, each nest was marked for relocation by tying a knot on grass 10 m away from nest. If the grass was short, a clump of forbs was laid down on the ground facing the direction of the nest.

Nests were revisited at intervals of 2-3 days to determine nest outcome. Nests were monitored until chicks left the nest and where possible chicks were followed after they fledged to determine post fledgling parental attendance. Precautionary measures were taken to minimize human-induced mortality during nest monitoring as outlined in Martin et al. (1993). Pairs
were also followed to determine when they re-nested following a successful or failed nesting attempt.

Some researchers have estimated provisioning rates by observing the birds from a distance and counting the number of trips made to the nest or by measuring the time interval between visits (e.g. Nolan, 2001). Food being fed to chicks was observed using binoculars from a distance of ca. 20 m away from the nest, but only grasshoppers were positively identified and therefore prey were intercepted in five nests by placing a ring of a thin copper wire around all chicks’ necks in the nest. Intercepted food was immediately preserved in 10% ethanol. Food interception was done only on chicks that were older than 8 days old.

Because the species shows no obvious sexual dimorphism, birds were labeled 1 and 2 as they brought nesting material or food to the nest. However, the bird that later sang and displayed was considered the male and was allocated the proper number (1 or 2). In the case where only one bird was found either building, incubating or feeding, it was assumed to be the female if it never displayed and sang throughout the duration of the observations. Furthermore, mist nets were set up ca. 5 m in front of selected nests during the last week of chick feeding to catch adult birds. All birds caught were ringed before they were released. Parental role during incubation and chick provisioning was observed over 1-2 h periods in eight and five nests respectively.

In order to identify and quantify causes of mortality at nests several authors (Moors, 1983; Major, 1991; Pasitschniak-Arts and Messier 1995, Brown et al. 1998) used techniques such as signs at nests, imprints on plasticine, clay or wax. Whenever a nest failed, the surrounding area was examined for evidence of possible predators. The identity of predators was inferred
as follows: If the nest was intact following predation, this was ascribed to either a snake or mice. If eggs were gnawed and ground or partially broken this was ascribed to mice. If the nest was found intact sometimes with tiny pieces of egg shells either inside or within 0.5 m away from the nest, this was ascribed to snake. On a recent study on Great Tit *Parus major* and Blue Tit *P. caeruleus*, Sorace *et al.* (2000), observed that snakes swallow the nests contents whole and leave the nest intact and undisturbed. Where nests were torn up, these were probably destroyed by Yellow Mongoose *Cynictis penicillata* or Suricates *Suricatta suricatta*. A nest was considered trampled if it was found pushed down into the soil, additional signs of animal hoofs were searched for. Some birds did not remove failed eggs from nests following hatching. These eggs were left with the chicks in the nest for several days, and then later were taken out and broken to determine whether hatching failure was caused by infertility or embryonic death.

In order to verify further who the main predators were, artificial eggs were placed in the nests that were found still intact following predation of eggs. These eggs were made with plasticine and sometimes mixed with Long-tailed Widow *Euplectus progne* eggs that had been filled with candle wax. If subsequent visits showed them to have been predated, tooth marks were examined to determine the identity of the predator. Chicks were assumed to have left the nest successfully if they were at least more than 11 days old and if there were fresh faecal sacs around the nest entrance. Other indicators were; a well flattened and undisturbed nest lining with feather scale present and adults carrying food or giving alarm call nearby.

**Statistical analysis**

Non-parametric tests were performed to compare differences in six measured variables between the two surveys, and to compare parameters between sites with and without Rudd’s
Larks. The primer statistical software package (PRIMER 5 for windows v5.2) was used to relate habitat variables and land physical features to the presence and absence of Rudd’s Lark. PRIMER is increasingly used to relate bird species to habitat types (e.g. Jansen & Robertson, 2001, Froneman et al. 2001). SIMPLER (similarity percentage analysis) procedure was used to identify habitat variables contributing most to the Bray-Curtis similarity between grouped transects (Clarke 1993). The presence or absence of birds was incorporated into the model as a factor. Subsequently, hierarchical cluster analysis and non-metric multi dimensional scaling (NMDS), based on Bray-Curtis similarity in PRIMER were used for classification and ordination of transects (Clarke & Warwick 1994). NMDS has the advantage of robustness being more sensitive to outliers and preserves the rank order of inter-samples distance, as opposed to the linear relationship of classical scaling, such as principal components analysis or correspondence analysis (Colloca et al. 2003). Randomization tests were performed to test for the observed differences between transects with and without Rudd’s Larks.

An ANOVA was used to compare amount of time each individual spend sitting on the nest during incubation. Student t-tests were used to compare an amount of time birds spent incubating during early (4th – 8th day of incubation) and late (11th – 13th). This same test was used to test for differences between clutch sizes from burned and unburned areas. An egg volume index (= length x breadth\(^2\)) was calculated as a measure of egg size. Egg volume was compared between burned and unburned sites and between early (Oct-Jan) and late (Feb-April) clutches using one-way ANOVA. Significant differences were also tested using One-way ANOVA between first, second and third repeat clutches. The incubation period was determined from successful clutches located during the laying period and nestling period was determined from nests whose hatching date was known. For nests found either during incubation or nestling period, possible nest initiation date was estimated by back-dating from
the day on which eggs hatched or the day on which chicks fledged. A one-way ANOVA was further used to examine the relative contributions of the sexes during chick provisioning and rearing.

Nest success data were analyzed using the Mayfield method (e.g. Mayfield 1961 & 1975) as described in Krebs (1999). Daily survival rate were done separately for nest both during incubation (14 days) and nestling and for individual eggs during incubation and individual chick during nestling (14 days). Only nests visited more than once were included in the analysis. If the precise day of failure or hatching was not known, the midpoint between the two visits either side of the event was taken.

RESULTS

A total of 103 random transects were conducted throughout the study area. Rudd’s Larks were recorded at 13 sites during the initial survey and 9 during the second survey, of which two were sites where birds had not been recorded during the initial survey. The six sites where birds disappeared between surveys were visited several times to confirm that they had moved away from these sites. Because of the low overall encounter rate (13% in the first survey and 8.7% during the second survey), the sample of sites suitable for Rudd’s Larks was augmented by surveys conducted in 69 breeding territories in the first survey and 67 territories during the second survey.

Rudd’s Larks were only found on flat or gently sloping plateaus and hilltops, avoiding valley bottoms, lowlands and slopes steeper than 10° ($\chi^2_3 = 18.7, \ P < 0.001$) (table 1). This preferred habitat made up 39% of the 103 random transects, of which only 38% of this habitat was occupied. Of the 103 random transects, 69 (67%) had been burned during the winter dry
season, including all but one site where Rudd's Larks were recorded ($\chi^2 = 4.20$, P<0.05).
Within the preferred habitat mentioned above, 75% was burned. Only transect with birds was
found in 15% preferred habitat that was not burned. During the first survey, 13 transects were
scored as not grazed, 82 as lightly grazed and 8 as heavily grazed. This same number was
maintained for the second survey. In both surveys birds were found only in those transects that
were scored as lightly grazed.

SIMPLER identified grass cover, average grass height and the amount of bare ground as
contributing mostly to the Bray-Curtis (dis)similarities between sites with and without Rudd's
Larks, whereas forbs, dead matter and stones had negligible contribution. There was no
significant difference between sites with Rudd's Lark and those without Rudd's Lark during
both surveys (ANOSIM: Global R = 0.07 and Global R = 0.02 respectively) in terms of these
three variables. However, Kruskal-Wallis test showed that there was significant difference in
terms of grass cover ($H = 11.52$, df = 1, $P = 0.001$), bareground ($H = 14.44$, df = 1, $P = 0$) and
grass height ($H = 76.7$, df = 1, $P = 0$) and no significant difference between forbs ($H = 0.57$, df
= 1, $P = 0.45$), dead matter ($H = 0.39$, df = 1, $P = 0.53$) and stones ($H = 0.48$, df = 1, $P = 0.49$)
when the two surveys were compared. Taking these significant variables alone, sites with
birds had grass cover ranging from 4-8.5 during the first survey to 4.8-8.5 during the second
survey, while the bare ground ranged from 0.2-3.6 for the first survey to 0-3.6 cm during the
second survey (table 2). For sites without Rudd's Lark grass cover ranged from 3.5-9 for the
first survey to 3.33-8.83 during the second survey, bare ground ranged from 0-3.93 for the first
survey to 0-5.33 during the second survey while grass height ranged from 1.43-24.38 cm for
the first survey to 1.73-38.19 cm during the second survey.
Within the 40 suitable transects however, sites with Rudd’s Lark had grass height ranging from 2.53-9.11 cm and grass cover ranging from 4.58-8.38 cm while sites without birds had grass height ranging from 1.43-17.19 and grass cover ranging from 4.75-8.75 cm (table 3).

Of the six transects that lost birds between surveys, two exhibited a marked increase in the extent of bare ground (from 43—56% and 47-53 %), possibly due to excessive grazing. There was no obvious cause for the disappearance of birds from the other four sites. Of the two transects where birds appeared during the second survey, one probably had too little cover during the first survey (bare ground 71-29% between surveys). Botha’s Lark *Spizocorys fringillaris*, a species characteristic of more open habitats, was recorded at this site during the first survey but not subsequently.

Both cluster analysis and NMDS ordination (fig. 2a, b, c, d), based on grass cover, average grass height and bare ground indicated that Rudd’s Larks preferred sites with short to medium grass cover with medium open spaces and avoided sites with tall and thick grass cover or sites that were too bare (heavily grazed). The above pattern was also repeated for the second survey (fig. 3a, b, c & d). A further NMDS ordination of the 40 suitable transects, showed that two of the six transects that no longer had birds in them were bare during the second survey while the other four transects were still within the range of suitable habitat (in terms of the grass cover and height). Figures 4a & b shows the distribution of birds relative to grass height, grass cover and bare ground. While birds clearly avoided tall and dense grass during the second survey (fig 4b far left), some birds remained on the same site despite such sites increasingly becoming bare (fig. 4b far right).
**Nest site selection and nest building**

Eight nests were found during building phase in 2002/03 and 16 in 2003/04. Only one bird (female) built the nest. Nests were usually located between two to three grass tufts between which there was accumulation of old dry grass. The peak nest building occurred in January and February with slightly higher peak in February. Most nests came from the sites that were unburned (table 4) during 2002/04. Two of the three main sites were burned during the last week of October, when many birds were fully paired and others had possibly begun to breed. All sites except one where Rudd’s Lark was found in 2002/03 had been burned in early September that year.

Nesting started much earlier and lasted longer on unburned sites than on burned sites (fig. 5). A total of 52 nests were found on unburned sites compared to 17 on burned sites during 2003/04. There was significant difference (F$_{1,12}$, P = 0.02) between the number of nests found per month on unburned sites compared to number of nests found on burned sites.

**Nest structure, egg laying and incubation**

Rudd’s Lark nest consists of a cup with a roofed top (dome). The dome usually consists of old grey grass while the cup is lined with fresh dry grass. Nest dimensions were: internal diameter 6.5 cm – 8.5 cm (7.5 cm, n = 47), dome height 4 – 8 cm (5.5, n = 47), entrance height 3 – 6 cm (4.5, n = 47) and entrance lining 0 – 12 cm (1.3, n = 47). Out of the sixty-nine nests for which nest entrance orientation was noted, entrance aspects faced in virtually all directions, although there was more preference for North and South. There was no significant difference ($\chi^2_{1} = 0.087$, P = 0.1) when NE, N, NW and W (n = 41) were compared against SW, S, SE and E (n = 28).
Only one bird (female) collected nesting material and constructed a nest unaided by the male. Nest building took 2 – 4 days with a mean of 2.8 ± 0.54 days (n = 16). The first egg was laid on the fourth day after the start of nest-building. The exception was one nest found early during the 2003/04 breeding season. Although, it looked finished on the third day, the first egg was laid in it only 9 days later. Some birds added nest lining to the entrance during incubation.

Egg lying occurred from the last week of October to the first week of April. One egg was laid per day, and clutch size ranged from 2 to 4 eggs with a mean clutch size of 3.4 ± 0.4, n = 73 (table 5). Freshly laid eggs had a mean mass of 2.36g ± 0.5, n = 50.

Egg dimensions were: length 23–19 mm x 14 – 16 mm (21 x 15.2, n = 139). There was no significant difference (F_{1, 139} = 1.77, P = 0.18) between egg volume from burned sites and unburned sites, nor was there any significant differences (F_{1 - 137} = 0.12, P = 0.73) between eggs laid early (October – January) and late (February - April) in the breeding season.

For some birds, egg volume increased during repeat clutches while for other it decreased, or went up and down. There was no significant difference in egg size between the first, second and third egg clutches (F_{2, 24} = 0.83, P = 0.45) and there was no significant difference either between the first and the second clutches either (F_{1, 20} = 0.84, P = 0.44). No significant differences were found between the clutch sizes from burned and unburned areas (t_{84} = 0.47, P = 0.32) for the combined data coming from the two breeding seasons.

Incubation was observed to have started the day the third egg was laid and took 13 -15 (mean 14 ± 0.53) days (n = 15) to hatch. All eggs within a clutch hatched on the same day. Incubation behaviour was observed at 8 nests, which ranged from day 4 to 13 of incubation and
18.8 h were spent making observation on the role of the female and the male during incubation. All these nests were from unburned areas and one nest was from unburned but heavily grazed site. Only the female incubated the eggs. On average the incubation shifts were $16.1 \pm 12.4$ min (1-59 min) with no significant differences among individuals ($F_{7, 26} = 1.2, P = 0.32$) or between early and late incubation ($t_{29} 0.35, P = 0.72$). On average, 56% of the time that was spent making observations birds incubated the eggs. Periods away from nests averaged $12.4 \pm 8.5$ min (1 - 45) with no significant difference ($F_{7, 21} = 1.8, P = 0.14$) amongst individuals or between early and late incubation ($t_{17} = 1.42, P = 0.17$).

In a case where a nest failed due to predation or other factors, a replacement nest was built within two to three days and they were often built within 50 m of the old nest, the closest being about 10 m from the old nest. It was easy to monitor each pair until they re-nested since birds rarely flew out of their territories. Although only one bird was re-trapped out of nine adult birds that were ringed, breeding birds often flew with their legs hinging down so that rings were readily seen. Thirteen individual pairs were known to have made more than one breeding attempts either following unsuccessful attempts or predation. Of these, two pairs had four breeding attempts; four pairs had three breeding attempts while eight pairs had at least two breeding attempts.

**Development and Care of nestling**

A total of 9 h were spent at five nests timing individual male-female role during chick provisioning, while another 2.5 h were spent intercepting food during chick provisioning. Male to female contribution during provisioning varied between individuals within a pair and amongst the pairs, although on average a male took a lead role in provisioning the chicks while the female sometimes brooded the chicks. The interval between visits by males ranged from 2-
83 min (mean 18.6) and for the females it ranged from 2-54 min (mean 17.7). There was no significant difference ($F_{1, 41} = 0.03, P = 0.9$) between the times both the females and the males spent between the consecutive provisioning visits.

Of the 50 food items brought to nests that were positively identified, 56 percent were grasshoppers while the rest was non-identified insects. A worm was observed only once. Two birds which dominantly fed on insects other than grasshoppers were in unburned and heavily grazed sites respectively.

A further twenty food items were intercepted during chick provisioning and their sizes ranged from 15 – 40 mm (mean 21 mm). Of the twenty food items, grasshoppers accounted for 60% followed by worms, crickets and flying termites, with 10% each, beetles and spiders with 5% each. All grasshoppers brought to nests had their legs, sometimes wings and head removed as well. Ninety percent of all grasshoppers brought to nest were young (nymphs).

Chicks left the nest between 11-15 days with a mean of 13.4 ± 0.96 ($n = 19$).

General observations from other nests was that as feeding intensified and chicks grew older, the female slowly withdrew from feeding the chicks so that at some stage, she completely ceased to feed them although she always remain within the territory. During the post fledgling period the male fed the chicks one at the time. Following feeding, the male walks the chick briefly with the chick following him closely as he hunts for food. How much time it takes for chicks to be on their own probably differs between pairs and it may depend on how many chicks were being fed. For example, the three birds that produced one chick each re-nested a week after fledging. Four other pairs each with three chicks were confirmed to have re-nested on the third week following from the day on which the chicks left the nest. As the time to re-
nest approached, the pair slowly led the chicks out of the territory and they were not seen for some days. And when they reappeared, they re-nested within 2-3 days of coming back. In one instance a chick which was believed to belong to same pair, was aggressively chased away by the female following its re-appearance after she had just laid the third egg in the new nest.

Based on the observations of one bird making four breeding attempts three of which were successful, it seems that under normal circumstances Rudd’s Lark can make three successful breeding attempts per breeding season. One complete breeding cycle was estimated at 47 days in the case where three chicks were fledged.

**Survival estimates**

The outcomes of daily survival rates for the nest, individual eggs and nestlings are summarized in table 6 for the two breeding season. Twenty nests qualified for Mayfield analysis for year 2002/03 and 63 for 2003/04. All nests for 2002/03 came from burned areas. Considering 2003/04 alone 51 nests from unburned areas qualified for Mayfield analysis and only 12 for burned areas. The probability that a nest would survive from start of incubation to fledging was 0.400, 0.500, 0.417 and 0.500 for year 1, year 2, year 2 burned and year 2 unburned respectively. The probability that eggs and nestling survive from start of incubation to fledging were, 0.334, 0.503, 0.226 and 0.480 for year 1, year 2, year 2 burned and year 2 unburned.

**Causes of failures**

Of a total of 33 nests that totally failed, 26 were predated, 3 were deserted, 2 were flooded and one nest failed due to chick starvation. Partial loss of eggs occurred in 6 nests and altogether 7 eggs were lost this way, while partial loss of chicks occurred in 6 nests and altogether 8
chicks were lost this way. All eggs that were partially lost disappeared between 1-2 days before hatching. A total of 11 eggs from 8 nests disappeared from nests following hatching.

Of a total of 26 nests that were considered having been predated, 14 nests were found empty but still intact and therefore were assumed to have been predated by snakes. Eight nests were found completely torn out with some egg shells inside and were assumed to have been predated by mongoose/surricates. Four nests were found completely intact but with either partial or ground eggs shells both inside and outside the nest and were taken to have been predated by mice. Fifty percent (n = 32) of the nests that were exposed were predated while only 27% (n = 37) of nests whose entrances were concealed were predated.

Of the 14 nests that were predated by snakes, eight nests were with eggs while six nests had chicks. Of the eight nests that were predated by mongoose, five nests were with eggs while 3 nests were with chicks. Artificial eggs were placed in 12 nests that were left intact following predation. Evidence of snake presence was reported in four nests, another four had signs of mice while three nests had a sign of mongoose/surricates. One nest that was assumed to have been predated by mice was never visited again following the placement of artificial eggs.

**DISCUSSION**

**Habitat selection and breeding suitability**

Rudd’s Larks appear to require stone-free areas on flat or gently-sloping hilltops and plateaus with moderately open natural grassland. Within this habitat, they require a suitable mix of grass cover and bare ground, avoiding areas with too little or too much cover. That grass cover is more important than grass height was confirmed during 2003/04 when birds breeding in territories where grass cover became very dense moved to new areas, whereas those in
territories with sufficient bare ground remained throughout the season, despite grass height reaching up to 40 cm. This work confirms Hockey et al. (1988) findings that the maximum grass height is unimportant in determining the species occurrence. The relatively low occupancy rate within its preferred habitat (38%) may relate to the requirement for a mosaic of habitats for birds to breed, although distance from source areas and small patch sizes also may be important. At one site where several pairs bred together there were three smaller but otherwise seemingly identical sites nearby that were ignored, despite being occupied briefly early in the breeding season.

Unglazed and fairly tall grass was rarely met with during this study. Transects with tall grass occurred mainly in the north and North West part of the study area where Hyparrhenia and Cymbopogon grasses dominate the hilly landscape. Rudd’s Lark has never been recorded in this type of habitat. These transects were clustered together during the first survey, although during the second survey totally different transects from other parts of the study area replaced them indicating that grass has grown tall in other parts of the study area.

Hockey et al. (1988) argued that the relatively high abundance of Rudd’s Lark at the most heavily grazed site in Matatiele suggests that intensive grazing does not necessarily affect the species adversely, provided such grazing does not lead to invasion by plants other than grasses. However, at Wakkerstroom, few nesting attempts occur in heavily grazed sites, and relatively high predation rates, indicate that these sites are not suitable for breeding. The fact that birds came back to the same sites several times (probably finding that the sites were still unsuitable for breeding) may instead be described in terms of high site fidelity rather than site suitability.

If the present preference of the intensively grazed sites by Rudd’s Lark is a carry over from the past as Hockey et al. (1988) suggested, it is possible that such places were open to some form
of invasive herbaceous plants as it is the case now. In this study some sites had forbs and one of them was heavily overrun with forbs yet birds nested there. Apparently, forbs do not matter very much as long as they are short lived annuals and occur at relatively low densities. However, a regular occurrence of some forbs at some of these sites is an indication that such farms are deteriorating. Of particular concern is the spinescent forb *Acalypha* sp. which is abundant in most heavily grazed sites. Animals avoid grazing grass tussocks containing this forb. Comparable studies on habitat selection by Rudd’s Larks at other core areas are needed in order to test the generality of the results found in this study. According to Taitton (1999) even though some grasslands can tolerate some heavy grazing the recovery of the more palatable grass species is extremely slow. This way this grasses are likely to be replaced by forbs and non palatable grasses.

**Breeding season and nest site selection**

The known egg laying dates for Rudd’s Lark spanned December to March. This work however, found out that birds can start laying as early as late October to late March provided that the habitat is suitable.

According to Götmark *et al.* (1995) and Donald (2004) larks nest sites are selected to give the incubating female good all-round visibility, so that the incubating birds can see predators approaching from a distance and slip away from the nest unnoticed. Indeed some nests had their entrances so much exposed that it appeared like a hole from the distance; most of these nests were predated. So in Rudd’s Lark nest concealment must be a trade of between hiding nest entrance so that predators would not easily see it and making it exposed so that a bird can see the intruder approach from some distance (but more chances of nest being found by predators). In a recent study Muchai (2002), found out that nest concealment is the key to nest
survival in three ecologically similar ground-nesting birds in grassland communities. However, the fact that Rudd’s Lark spend the longest period in the nest as compared to other larks is an indication that predation does not pose a serious threat to this species in suitable habitats.

Rudd’s Lark builds a relatively large domed nest and therefore requires large quantities of dry grass to construct a nest. In a recent study carried out by Muchai (2002) in the same study area it was discovered that lack of nesting material in burned areas delays birds from breeding early. Dry grass is important not only for nesting but it is also used by Rudd’s Lark during courtship display and birds have been seen with nesting material some times a week before they were ready to breed. So lack of dry grass might also delay courtship display. Many Rudd’s Lark nests at site G were located between three and sometimes four grass tussocks with a lot of dry grass underneath so that nests were very well concealed. So many birds do not nest until there are tussocks with dry grass beneath and therefore have to postpone nesting. Rudd’s Lark at site L used fresh dry grass which animals had uprooted recently during browsing and the nest dome had large amount of spiderwebs. Despite the fact that C was burned, birds there started much earlier than similar burned sites because it was moderately grazed as compared to other sites which were heavily grazed.

According to MacLean (1970), Donald (2004) some species of larks in desert and steppe environments have their nest entrance facing away from the sun. This study confirms Allan (2001) that nest entrance aspects are not important for Rudd’s Lark since it inhabits a cooler area as compared to their counterparts in the Kalahari.
Clutch and egg size

This work confirms Allan (2001) suggestions that three is the typical clutch size for Rudd’s Lark. Perrins & Birkhead (1983), outlined a number of factors that influence clutch size between and within species. Although there was no significant differences found between both clutch sizes and volumes from burned and unburned sites (despite small sample sizes from burned areas) almost all four egg clutches came from one site which was unburned and lightly grazed and nearly all of them were laid between December and January. The results from this work support Perrins & Birkhead (1983), findings that clutch size decreases as the breeding season progresses.

According to Perrins & Birkhead (1983), breeding is a dangerous process as it places additional energetic demands on a breeding pair and also there is an increased chance of being predated during breeding. As a result species living in different environments and habitats must have different ways of dealing with this problem. One way of dealing with this problem is to adjust limits to the breeding seasons of the birds and the clutch size they produce (Perrins & Birkhead 1983). On a recent study on energy and water budget amongst larks breeding in arid zone, (Tielman, et al. 2004) found out that parent-brood units of arid zone species used less water per gram mass than species from mesic regions. This finding supports the hypothesis that decreasing food and water favour lower energy and water requirements of parents and young, reduces growth rates, and clutch size with increasing aridity (Tielman, et al. 2004.)

In a more recent study, Lloyd (2004) found out that the breeding activity of nine out of the 11 bird species increased following rainfall, while the clutch size of over 50% of the 11 species increased with an increase in rainfall. Although no relationship was investigated on the
influence of rainfall on initiation of breeding and on clutch size in this study, it is apparent that rainfall did not have any influence on clutch size since most of the eggs were laid almost in one habitat within a short period of time whereas most of the breeding season was relatively wet. Although it is possible that rainfall could have some influence on initiation of breeding there was not enough evidence to support this in this study. In both years breeding was initiated well before rains and clutches from second year (which was relatively a wet year) did not differ significantly to those from the first year.

Based on the above it appears that habitat was important in influencing variations in clutch sizes. Within a species, Perrins & Birkehead (1983) related different-sized clutches in different habitats to absolute levels of food abundance. Although Muchai (2002) found that management practices may affect food availability and therefore clutch size, he argued that overall nest predation may be a more important force in driving evolution of avian clutch size than food supply. During this study although birds nested in large densities at site L during 2002/03, clutch of four was never recorded. This might have been in response to both high predation rates and higher densities that were experienced at the site (burned and lightly grazed) at that time. On the contrary, birds at site G (unburned and lightly grazed) produced four egg clutches despite nesting in higher densities because of nest concealment which was offered by habitat heterogeneity which existed at the site. So apparently, birds at G laid four egg clutches early in the season which would coincide with peak of food availability and clutch size decreased to three which was in line with decreasing food availability as the season waned. For example, Perrins & Birkhead (1983) associated the observed decline of clutch size as the season progresses to both food scarcity and increase in predation. Based on the above discussion it is possible that food availability, nesting densities and predation interact to influence clutch size in different habitat.
**Incubation and nestling duration**

In Larks, incubation generally lasts between ten and fourteen days and is usually undertaken by the female alone, though the male shares the incubation in some desert dwelling species (Donald 2004). In the case of Rudd’s Lark the female alone incubated the eggs unaided by the male. Although the males are supposed to be larger than the females in southern African larks and amongst the primarily insectivorous larks (De Juana, et al. 2004), there was no obvious sexual dimorphism in Rudd’s Lark. Apart from the fact that few birds were ringed which helped to tell apart the incubating bird from the one which never incubated eggs, one of the two birds often sang and displayed and this bird never incubated eggs. According to (Donald, 2004 and De Juana 2004), only male birds sang and displayed, therefore the bird which sang and displayed was considered to be male. Occasionally the incubating bird flew out to join the second bird which was calling it from the ground where it was apparently fed before flying back to the nest. The male bird was observed only once taking food to the female who did not response to his call from the ground. This same male was at the same time taking care of the only one chick which the pair had recently fledged. The fledged chick was fed several times during the period of the observation.

**Variations in incubation**

Both within and between species, variation in incubation period is likely to be determined at least partly by a trade off between nest survival, which will decrease with longer incubation periods, and rates of energy expenditure by the incubating birds, which may be limited by food availability (Donald *in press*). The maximum of 15 days of incubation was recorded at least once in this study and this was at site G where birds had a very high rate of survival. During this study incubating birds often spend short time outside the nest and this may indicate that
food was easily available in suitable habitats. Evidence of one bird bringing food to an incubating bird might be a further indication males were making up for the much needed energy spent by incubating females by providing them with food. According to Perrins & Birkhead (1983), reproduction is an energy costly process as most non-passerine birds do not have energy reserves like the passerines. Ideally it was necessary to compare rate of incubation between burned and unburned sites, but this was not possible due to small sample size from burned areas. For example, one of the birds that were compared here was from unburned and heavily grazed site, this bird spent the longest time outside the nest looking for food both during incubation and chick provisioning and it also flew over the longest distances during both incubation and chick provisioning. In a more recent study Donald (in press), suggested that ambient temperature may play important part in determining the incubation period in Skylark *Alauda arvensis*, and so might influence time-dependent mortality. The influence of temperature and rainfall on clutch size and duration of incubation was not studied in this research and this needs further attention, especially the influence of climate change on incubation.

**Causes of breeding failure**

The fact that there were no significant differences between the rates at which food items were delivered to the nests might be further evidence that food availability was not a problem in this unburned habitats. Although the influence of habitats on food had already been discussed above, ideally this comparison should have at least been between burned and unburned sites. Again this comparison was hampered by small sample from burned sites.

The commonest cause of nest failure is predation, which one estimate suggests accounts for an average of 80% of nest failure across a wide range of species and habits (Martins 1993). Allan
(2001) noted a low breeding success where eight of the 11 nests failed; and he speculated that such a failure might have been caused by nest inspection. Although only few nest dimension measurements were undertaken in this study in order to try and minimize human-induced disturbance, Rudd’s Lark did not seem to be affected by frequent visits that were carried out at various stages of incubation. As a further example, two Rudd’s Larks, one during 2002/03 and another one 2003/04 that were nesting close to the road at site L, did not desert the nest despite frequent disturbances from various groups of tourists who were shown same pair most of the time. Therefore such an observed failure might have resulted from predation rather than disturbance, particularly if the site was burned as it was the case at L during the 2002/03. The increase in reproductive success during the first four months can be related to the four egg clutch but also to less predation. Reproductive success declined from February despite an increase in the number of nests that were being found as birds were begin to nest on burned sites as well. This can be linked to decrease in clutch size and an increase in predation.

According to Donald (2004) and De Jauna (2004), being open nesters, larks suffer very high rates of nest predation. In this study Rudd’s Lark experience far less predation rates when compared to other ground nesting birds that co-existed and bred at the same time and sometimes within the same territory as Rudd’s Lark. This might be partly due to the domed nature of the nest and the fact that some nests were so very well concealed. For an example, a flock of Black Crows Corvus capensis were found on three consecutive visits feeding close to one Rudd’s Lark nest which was raising four chicks and yet the nest was never predated. So a domed structure might have been some response to high predation rates that might have happened in the distant past for Rudd’s Lark. According to Donald (2004), since larks generally occur at low densities, it is likely that much nest predation is incidental, rather than targeted by predators specializing in taking lark nests. In this study too there was no indication
that Rudd’s Lark nests were being predated by one particular predator. Artificial eggs that were predated by either mice or mongoose had a clear tooth marks on them, the only difference being the size of the tooth marks. Plasticine eggs that were visited by snakes were found deformed and pushed into the nest, while eggs filled with wax were removed from nests and sometimes had some cracks on them.

According to Muchai (2002), theoretically, nest predation increases with activity at nests, and predation rates should peak during the nestling stage when birds are feeding young. Muchai (2002) tested this hypothesis using the three ecologically similar species and found out that predation rates did not increase with increase in nest visits. In this study Rudd’s Lark had very low predation rates during nestling stage than during incubation and the few chicks that were taken were taken at the age of 1 to 5 days, only one nest with chicks was predated between 6 and 8 days. Newly hatched chicks between day one and four days begged for food when the nests were being visited by the observer, this behaviour ceased as soon as their eyes were fully opened (after four days). Once their eyes were fully opened chicks laid on top of each other with their heads tightly pressed against each other and made no slightest move during the presence of the researcher at the nest. Furthermore most birds fed very close to the nest and rarely called when taking food to the nest. This might describe why chicks had such a low predation rates.

**Threats and recommendations**

For a critically endangered species like Rudd’s Lark, all factors which are responsible for bringing down the member of Rudd’s Lark should be considered as equally important. It is important however to determine the major threats and to try and halt them or minimize them. The results of this study however, show that the main threat to survival of Rudd’s Lark has
little to do with its breeding biology. This is based on high productivity observed in suitable habitat during this study. The major threat therefore is human induced habitat loss which results from grassland conversion to other forms (to fields and residential areas) and grassland degradation through inappropriate fires and high stocking rates. During this study period two sites where Rudd’s Lark was recorded have been given to small-scale farmers through the Land Redistribution Programme. This include the site which yielded 38 nests during 2003/04. It will almost certainly exclude larks through a combination of settlement and associated changes in land-use, including subdivision into small, intensively-farmed plots growing crops, particularly maize, and grazing a wider diversity of animals (including goats, horses and donkeys) which were not there before. The residents on these communal lands claim the government promised them tractors to plough the land, but this has not materialised. So far another suitable site for Rudd’s Larks has been transformed into field growing supplementary feed for animals this study time. The most sensible conservation measure would be to halt conversion of grasslands into other forms and secondly to manage the remaining grassland remnants in a way that will encourage the breeding of Rudd’s Larks.

Hockey et al. 1988 suggested that Rudd’s Lark would be favoured under management regime of annual burning and winter heavy grazing. Barnes 2000 however, argues that this is impossible as grass palatability is reduced in winter and so the grass is then burned, and stock moved to lower altitude or supplementarily fed. Ironically, the observations from this study is that most farms are heavily overgrazed by late autumn to the extent that when they are burned in early spring some sites becomes partially burned as there was not enough fuel load to carry the fire. Birds that bred early on such sites select these patches for nesting. The results from this work however, found out that although these annually burned and heavily grazed areas are often frequented by displaying males they are not suitable since most males are not paired and
even if they do breed they do so at very low densities and at very low survival rates. According to Van Horne (1983), Vickery et al. (1992) and Donald et al. (2002), in assessing the importance of any habitat to breeding birds, it is necessary to determine not only the number of birds present but also the contribution it makes to the overall recruitment of new birds to the population, since territory density may not reflect habitat quality as defined by productivity.

Since the sites were burned during the last week of October 2003/4 birds were observed moving between sites until late February when they attempted to breed. The fact that birds came back to their favoured breeding sites a number of times and still did not nest or only few of them nested clearly indicated that such sites were still not suitable.

A lot of effort was put into trying to find more nests from these sites (L & C) later in a season when birds had eventually come back to breed. Despite this effort, very few nests were found, and most of those that were found were without chicks indicating that most nests could have been predated during the incubation stage. For example, one Rudd’s Lark at site D was preyed three consecutive times before it became successful while another one at P was predated twice and only became successful on the third attempt. This indicates that rates of predation might be higher on burned/unburned heavily grazed sites. A further evidence for this comes from high predation rates that were observed at L during 2002/03, out of 13 nests only four fledged and all of them were bred earlier in the breeding season. Since few nests that were found with chicks at this burned site survived, it inflated the overall breeding success (daily survival estimates) as the daily survival rates of the chicks was hundred percent.

Based on the observations from this study and those from Muchai 2002, it is recommended that burning be carried out every second year and that grazing should be moderate to light. Burning
should be carried out only during early to mid spring and late burning should be avoided. Sites that happen to be heavily grazed during late autumn should not be burned during the following breeding season. This will ensure the heterogeneity enhanced by selective grazing by cattle which Rudd’s Lark need for nest concealment and for feeding during breeding period. Burning should be rotated such that some sites will be burned when other remains unburned in the same year. This will benefit many ground nesting birds as Muchai 2002 has suggested, but rotational burning will also benefit Botha’s Lark. Botha’s Lark is in the second highest category of threat after Rudd’s Lark and it co-occurs with Rudd’s Lark in Wakkerstroom.

Although the results from this work shows that these annually burned and heavily grazed sites are not suitable for breeding of Rudd’s Lark, the results from recent data analysis on habitat requirements and breeding biology of Botha’s Lark shows that it would benefit from keeping grass during the main breeding season (October to December). The presence and absence of Botha’s Lark were noted on the same transects on which Rudd’s Lark were searched for. Data analysis on Botha’s Lark indicated that it has a very narrow window period to breed (October - December). Birds nested on fairly short grass (4 - 6 cm) either recently burned or unburned and heavily grazed. The results on Botha’s Lark habitat selection and breeding biology will have been presented else where.

Conservation of both Rudd’s Lark and Botha’s Lark therefore requires proactive management. For example, even though moderate to light grazing is recommended, different farms are on different stages of deterioration. Therefore how much stock is placed into a farm should, amongst others, be determined by the present growth of grass (which in turn is determined by moisture availability) and by state of the farm. On the one hand if Botha’s Lark is to be encouraged, farms need to be heavily stocked with sheep in wet years during the main breeding
seasons in order to keep the grass fairly short. In a recent study Muchai (2002) proposed that
the current intensive grazing pressure and periodic burning should be relaxed by reducing
stocking rates and burning less frequently to benefit grassland bird species.

Currently a very small population of Rudd’s Lark falls under nature reserves, the proposed
Grassland Biosphere Reserve (e.g. Barnes 2000), would hold a large population of Rudd’s
Lark. However, the lessons from a lark reserve in Spain and the findings from this study
implies that if such a reserve is to be established in South Africa, conditions favouring both
Rudd’s Lark and Botha’s Lark and many other ground nesting birds, can be brought about
through manipulation of habitat variables by controlled use of fire and grazing.

The fact that virtually all Rudd’s Larks occur on privately owned lands means that the species’
conservation is dependent on the goodwill of landowners to maintain pastoral farming and
appropriate management of grasslands. Tarboton (1997) suggested that providing landowners
with incentives to manage parts of the grasslands on their farms for particular species or
communities of birds can be an effective conservation strategy.
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Habitat requirements and conservation status of Rudd's Lark *Heteromirafra ruddi* in South Africa. *Biological Conservation*. 45: 255-266.


*Auk* **109**: 706-710.
Fig. 1 The study area around Wakkerstroom, Mpumulanga, north-east South Africa, showing the distribution of study sites discussed in the text. Symbols represent recent fire history and grazing intensity in 2003/04.
First survey NMDS ordination plots

(a) 

(b) Grass height
c) Grass cover

d) Bareground

**Fig. 2** Shows an NMDS ordination plots of presence and absence of Rudd's Lark a) with respect to grass height b), grass cover c) and bareground d) during the first survey. Bigger circles indicate the high value.
Second survey NMDS ordination plots

a)  

b) Grass height
Fig. 3 Shows an NMDS ordination plots of presence and absence of Rudd’s Lark a) with respect to grass height(cm) b), grass cover c) and bareground d) during the second survey.
40 suitable transects

First survey

Fig. 4 a)
Fig. 4 Shows an NMDS ordination plots of 40 suitable transects with respect to presence and absence of Rudd’s Lark. (a) first survey, (b) second survey. Grass height increases to the right and bare ground increases to the left. E4C2 1 is a transect name, and b attached to it means that birds were recorded there during both surveys while letters F and S in front of the transect number indicate that birds were recorded there during the first and second surveys respectively but not both.
Fig. 5. Numbers of Ruddős Lark nests initiated throughout the breeding season at burned (shaded bars) and unburned sites (open bars) during 2003/04.

Fig. 6. Seasonal changes in the breeding success of Ruddős Lark during 2003/04.
Table 1. Total number of transects done at each habitat based on topographical features relative to the presence and absence of Rudd’s Lark.

<table>
<thead>
<tr>
<th>Land</th>
<th>No. of transects</th>
<th>% availability</th>
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<th>present</th>
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<tr>
<td>Flat/gentle plateaux &amp; hilltops</td>
<td>40</td>
<td>0.39</td>
<td>25</td>
<td>15</td>
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<tr>
<td>Flat/gentle valley bottoms &amp; lowlands</td>
<td>17</td>
<td>0.17</td>
<td>17</td>
<td>0</td>
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<tr>
<td>Steep to shallow slopes</td>
<td>46</td>
<td>0.45</td>
<td>46</td>
<td>0</td>
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<tr>
<td>sum</td>
<td>103</td>
<td>1.00</td>
<td>88</td>
<td>15</td>
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Table 2. Average habitat characteristics of combined transects and territory data for the two surveys.

<table>
<thead>
<tr>
<th></th>
<th>Oct-Jan</th>
<th></th>
<th></th>
<th></th>
<th>Jan-March</th>
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<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STDv</td>
<td>Median</td>
<td>Range</td>
<td>Mean</td>
<td>STDv</td>
<td>Median</td>
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<tr>
<td>Sites with Rudd's (n = 81, 76)</td>
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<tr>
<td>Grass cover</td>
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<td>0.95</td>
<td>6.4</td>
<td>4.8-8.5</td>
<td>7.02</td>
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<td>7.1</td>
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<td>Bareground</td>
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<td>0.67</td>
<td>1.8</td>
<td>0.2-3.6</td>
<td>1.35</td>
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<td>Dead matter</td>
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<td>0-0.5</td>
<td>0.00</td>
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<td>Grass height</td>
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<td>3.5</td>
<td>1.95-7.33</td>
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<td>Sites without Rudd's (n = 90, 94)</td>
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<td>1.43-24.38</td>
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Table 3. Average habitat characteristics within the 40 suitable transects in terms of topography.

<table>
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<tr>
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<th>Oct-Jan</th>
<th></th>
<th></th>
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<th>Jan-Mar</th>
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<td>STDv</td>
<td>Min</td>
<td>Max</td>
<td>mean</td>
<td>Stdv</td>
<td>min</td>
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<td>Grass cover</td>
<td>6.11</td>
<td>0.76</td>
<td>4.58</td>
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<td>7.15</td>
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<tr>
<td>Bareground</td>
<td>1.82</td>
<td>0.31</td>
<td>1.25</td>
<td>2.28</td>
<td>1.42</td>
<td>0.60</td>
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<td>0.46</td>
<td>0.00</td>
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<td>0.28</td>
<td>0.29</td>
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<td>0.19</td>
<td>1.50</td>
<td>0.29</td>
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<td>0.02</td>
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<td>1.23</td>
<td>2.53</td>
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<td>6.26</td>
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<td>3.55</td>
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<td>0.00</td>
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<td>0.75</td>
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<td>3.17</td>
<td>1.43</td>
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<td>8.05</td>
<td>4.28</td>
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Table 4. The number of nests initiated at each site during 2002/03 and 2003/04, all sites had been burned a during 2002/03 except for site A.

<table>
<thead>
<tr>
<th>Site</th>
<th>Habitat</th>
<th>1st Year</th>
<th>2nd Year</th>
<th>Longitude</th>
<th>Latitude</th>
<th>Altitude</th>
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<tbody>
<tr>
<td>A</td>
<td>unburned, moderately grazed</td>
<td>0</td>
<td>0</td>
<td>27 06' 21.6&quot;</td>
<td>30 08' 2.7&quot;</td>
<td>1722</td>
</tr>
<tr>
<td>B</td>
<td>unburned, lightly grazed</td>
<td>2</td>
<td>3</td>
<td>27 09' 38.2&quot;</td>
<td>30 04' 40.1&quot;</td>
<td>1869</td>
</tr>
<tr>
<td>C</td>
<td>burned, moderately, grazed</td>
<td>2</td>
<td>9</td>
<td>27 10' 43.3&quot;</td>
<td>30 04' 49.4&quot;</td>
<td>1846</td>
</tr>
<tr>
<td>D</td>
<td>unburned, heavily grazed, degraded</td>
<td>3</td>
<td>5</td>
<td>27 11' 36.5&quot;</td>
<td>30 05' 39.8&quot;</td>
<td>1863</td>
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<tr>
<td>E</td>
<td>unburned, moderately grazed</td>
<td>0</td>
<td>1</td>
<td>27 13' 55.9&quot;</td>
<td>30 08' 3.2&quot;</td>
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<tr>
<td>F</td>
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<td>0</td>
<td>0</td>
<td>27 13' 49.2&quot;</td>
<td>30 03' 57.5&quot;</td>
<td>1838</td>
</tr>
<tr>
<td>G</td>
<td>unburned, lightly grazed</td>
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<td>38</td>
<td>27 13' 58.1&quot;</td>
<td>30 02' 27.5&quot;</td>
<td>1848</td>
</tr>
<tr>
<td>H</td>
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<td>0</td>
<td>0</td>
<td>27 14' 42.9&quot;</td>
<td>30 01' 29&quot;</td>
<td>1829</td>
</tr>
<tr>
<td>I</td>
<td>unburned, lightly grazed</td>
<td>1</td>
<td>0</td>
<td>27 14' 30.6&quot;</td>
<td>30 02' 37.9&quot;</td>
<td>1843</td>
</tr>
<tr>
<td>J</td>
<td>burned, moderately, grazed</td>
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<td>0</td>
<td>27 16' 32.9&quot;</td>
<td>30 01' 22.9&quot;</td>
<td>1784</td>
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<tr>
<td>K</td>
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<td>0</td>
<td>27 16' 40.3&quot;</td>
<td>30 02' 10.4&quot;</td>
<td>1771</td>
</tr>
<tr>
<td>L</td>
<td>burned, heavily grazed</td>
<td>13</td>
<td>4</td>
<td>27 17' 37.3&quot;</td>
<td>30 02' 54.2&quot;</td>
<td>1840</td>
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<tr>
<td>M</td>
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<td>0</td>
<td>27 16' 21.8&quot;</td>
<td>30 03' 56.5&quot;</td>
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<tr>
<td>N</td>
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<td>0</td>
<td>2716' 7.3&quot;</td>
<td>30 06' 29.3&quot;</td>
<td>1844</td>
</tr>
<tr>
<td>O</td>
<td>unburned, heavily grazed</td>
<td>0</td>
<td>1</td>
<td>27 17' 40.3&quot;</td>
<td>30 02' 57.3&quot;</td>
<td>1838</td>
</tr>
<tr>
<td>P</td>
<td>unburned, moderately grazed, degraded</td>
<td>0</td>
<td>3</td>
<td>27 17' 14.4&quot;</td>
<td>30 03' 14.9&quot;</td>
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<tr>
<td>Q</td>
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<td>0</td>
<td>0</td>
<td>27 18' 22.3&quot;</td>
<td>30 08' 6.3&quot;</td>
<td>1809</td>
</tr>
<tr>
<td>R</td>
<td>unburned, heavily grazed</td>
<td>1</td>
<td>0</td>
<td>27 21' 17.9&quot;</td>
<td>30 12' 11.5&quot;</td>
<td>2056</td>
</tr>
<tr>
<td>S</td>
<td>unburned, heavily grazed</td>
<td>0</td>
<td>0</td>
<td>27 23' 15.9&quot;</td>
<td>30 11' 5.7&quot;</td>
<td>1990</td>
</tr>
<tr>
<td>T</td>
<td>unburned, moderately grazed</td>
<td>0</td>
<td>2</td>
<td>27 23' 7.7&quot;</td>
<td>30 13' 29.1&quot;</td>
<td>2018</td>
</tr>
<tr>
<td>U</td>
<td>burned, heavily grazed</td>
<td>1</td>
<td>3</td>
<td>27 26' 26.5&quot;</td>
<td>30 17' 16.4&quot;</td>
<td>1843</td>
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</table>

Total 23 69
Table 5. Distribution of egg clutches by month for the two consecutive breeding seasons 2002/3 and 2003/4

<table>
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<tr>
<th>Year</th>
<th>Clutch size</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>Total</th>
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<tbody>
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<td>Year 2002/3</td>
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<td>1</td>
<td>8</td>
<td>4</td>
<td>1</td>
<td>18</td>
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<tr>
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<tr>
<td>Year 2003/4</td>
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<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
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<td>5</td>
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<td>3</td>
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Table 6. Summary of Mayfield daily survival estimates (SE), during incubation and chick rearing for two breeding seasons 2002/03 and 2003/04, the number in brackets represents exposure in days.

<table>
<thead>
<tr>
<th></th>
<th>Year 1</th>
<th>Year 2</th>
<th>burned</th>
<th>unburned</th>
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<tr>
<td><strong>Incubation period (14 days)</strong></td>
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<tr>
<td>Nest survival</td>
<td>0.929 ± 0.018 (198.5)</td>
<td>0.97 ± 0.008 (434)</td>
<td>0.94 ± 0.034 (49.5)</td>
<td>0.97 ± 0.008 (383.5)</td>
</tr>
<tr>
<td>Egg survival</td>
<td>0.939 ± 0.1 (411.5)</td>
<td>0.97 ± 0.004 (1266)</td>
<td>0.90 ± 0.021 (178.5)</td>
<td>0.98 ± 0.005 (1116)</td>
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<tr>
<td><strong>Nestling period (14)</strong></td>
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<tr>
<td>Nest survival</td>
<td>1(60)</td>
<td>0.98 ± 0.007 (371.5)</td>
<td>1(70)</td>
<td>0.98 ± 0.009 (299.5)</td>
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<tr>
<td>Chick survival</td>
<td>1(175)</td>
<td>0.97 ± 0.97 (764)</td>
<td>1(163)</td>
<td>0.97 ± 0.006 (764)</td>
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</table>