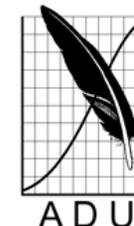


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TERRITORY ESTABLISHMENT AND THE MATING SYSTEM OF THE NOMADIC MONOTONOUS LARK *MIRAFRA PASSERINA*

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The Monotonous Lark *Mirafra passerina* is one of the least known members of the genus. This may be ascribed to its nomadic habits which makes it difficult to know when or where breeding will occur and the fact that outside the breeding season they are silent and very inconspicuous. This has led some authors to suggest that it is an intra-African migrant, yet it has never been recorded outside of its known range in southern Africa (Thompson 1983; Penry 1994). Its movements are linked to rainfall and breeding usually occurs where substantial rain has fallen in the recent past (Tarboton 2001). Monotonous Larks then erupt in large numbers in suitable habitat which is announced by a very distinctive and monotonous call that is sung throughout the day and night, sometimes by several thousand males. We were fortunate to be present when Monotonous Larks erupted on three separate occasions spanning two breeding seasons in the Polokwane Nature Reserve (23°56'16"S, 29°28'26"E, 1350 masl), in the Limpopo Province, South Africa. This enabled us to study aspects of their behaviour from their arrival until their departure. Here we present information on observations made regarding territory establishment and the mating system of Monotonous Larks.

At Site 1 (23°58'02"S, 29°28'09"E), the birds arrived on 1 December 2003 and remained there until March 2004. The arrival of the birds at Sites 2 (23°58'48"S, 29°30'16"E) and 3 (23°56'56"S, 29°28'42"E) were on 16 December 2006 and 26 December 2006 respectively and

most birds had left the reserve by the end of March 2007 although one bird was flushed from tall *Hyparrhenia hirta* grassland near Site 2 in May 2006.

Prior to the arrival of birds in the Polokwane Nature Reserve in December 2006, small groups of 2–4 males were heard calling at various localities around the city of Polokwane from the middle of November 2006 onwards. No breeding was recorded at any of these sites and the calling males usually dispersed within 1–3 days. On 16 December 2006 approximately eight males were heard calling at Site 2 in the Polokwane Nature Reserve but their numbers increased rapidly over the next 3 days. The arrival of Monotonous Larks at Site 3 on 26 December 2006 followed the same pattern.

Upon arrival at Sites 2 and 3, adult Monotonous Larks (21♂♂; 12♀♀) were captured in mist-nets and individually banded with a combination of coloured plastic leg bands to aid in individual identification. Colour-marked males were observed closely in order to obtain a crude estimate of their territory sizes. The sizes of 10 territories were determined within five days of arrival and another 10 territories were mapped 25–30 days after arrival. This was done by recording the five most distant calling posts of a male on a portable GPS (Garmin 3), importing the coordinates into the ArcView GIS software package and estimating the area within these points. As the territories were relatively small and the habitat open, it was possible to estimate territory sizes of unmarked males as well by observing them closely for a few hours.

Perhaps the most notable characteristic of Monotonous Larks is the incessant singing of males throughout the day and most of the night. Males sang from a perch, in flight and even on the ground – sometimes while foraging (Fig. 1). One male was recorded calling 1090 times over a 1 hour period from 08:40–09:40, three days after their arrival. During this time, he was silent for only four minutes during which he foraged, chased rival males or courted females. The frequency of calling decreased during the warmest part of the day to



Figure 1 - A male Monotonous Lark singing from the ground.

476 calls per hour (13:00–14:00), but increased again to 907 calls towards the late afternoon (17:00–18:00). Males called most intensely for the first 8–16 days following their arrival after which there was a marked decrease in the frequency of singing. This decrease coincided with many females starting with nest construction and incubation.

Calling was interspersed with regular short, singing display flights over the male's territory. During the display flight, the male ascended to a height of 5–10 metres and circled his territory by alternating between rapidly beating his wings and gliding, resulting in a very characteristic bouncing display flight. While singing, a male puffs out his throat and the contrast between the white throat and the buff

breast gives the impression of a pulsating cravat.

Males establish territories through almost continuous singing, regular short display flights and the chasing of rival males throughout the day and night. These demanding activity levels lead to weaker or perhaps inexperienced males vacating their territories which, in turn, are occupied by fitter neighbouring males. Thus, there is a discrepancy in the size of territories soon after arrival ($\bar{x} = 0.43 \text{ ha} \pm 0.10$, range: 0.28–0.63, $n = 10$) compared to those when breeding commenced ($\bar{x} = 1.03 \text{ ha} \pm 0.58$, range 0.45–2.63, $n = 10$). The only other reference to the size of Monotonous Lark territories is by Tarboton (2001) who reported territories ranging in size from 0.5 ha to approximately 2 ha. The pattern of territory establishment as reported here could explain the variation in the sizes of territories reported by Tarboton (2001). Males that vacate their territories presumably leave the breeding grounds as none of them were seen again. It appears that there is a small window of opportunity for breeding and once that has passed, breeding becomes risky and it is more worthwhile to seek other suitable breeding grounds than to remain behind and attempt breeding under sub-optimal conditions.

The relatively dense clustering of territories shortly after their arrival in the area ($\bar{x} = 0.43 \text{ ha} \pm 0.10$) enable males to see females and rival males and respond appropriately when they enter a given male's territory. As weaker males vacate their territories, the territories get larger and there are fewer rival males to contend with. However, it also becomes increasingly difficult to remain vigilant over large territories. Thus, a territory of an optimum size would be large enough to support the breeding pair throughout the breeding cycle, but small enough to enable a male to respond to rival males in his territory and to prevent the female from mating with rival males by accompanying her closely.

The mating system of the Monotonous Lark is complex and is initially characterised by promiscuity and in the latter stages of the breeding cycle by monogamy. Upon arrival and during the initial stages of



territory establishment, females moved freely between territories in search of high quality habitat for foraging and breeding. During this time, males attempted to intercept and copulate with any female passing through its territory. On one memorable occasion DE witnessed a female crossing the territories of four males in succession. As she flew over a territory, the resident male tried to chase her down, only to give up as she approached the edge of his territory. The neighbouring male then continued the chase and so it went on until she eventually landed. The males were so intent on displaying and calling, that they sometimes continued calling and “flutter-flying” while chasing the female. Some males were also observed leaving their territories to seek extra-pair copulations with a nearby female. This was generally uncommon as they risked physical attack by the resident male, their territory being invaded by a rival male, and/or a rival male mating with any females present in its territory.

The object of a male Monotonous Lark’s reproductive strategy was to force a female that entered its territory to be grounded and to get her to stay there by perching nearby or hovering above her (Fig. 2). The female, in turn, repeatedly attempted to “escape”, only for the male to try and chase her down again by dive-bombing her and forcing her to land again. This “cat-and-mouse” type of behaviour was repeated several times before a female either succeeded in escaping or remained in male’s territory.

Once a female was settled on the ground, a male attempted copulation or returned to a nearby perch to resume calling and display flights, fend off rival males or continued to intercept any other females that entered his territory. However, by doing this, he risked a grounded female escaping or mating with another male. If a male succeeded in grounding a female, she was guarded closely for the next few days to weeks to make sure that no other male mated with her.



Figure 2 – A male Monotonous Lark hovering above a female.

Within the mating system, two types of females can be identified, namely α and β females. The former generally started laying later after the arrival of Monotonous Larks at a breeding site ($\bar{x} = 17.05$ days \pm 4.97, range: 7–24, $n = 42$), were closely accompanied by the male during foraging and nest construction, received the benefits of the male acting as a sentry during nesting and providing assistance during the nestling period. The latter normally started laying sooner after arrival ($\bar{x} = 10.47$ days \pm 5.71, range: 6– 19, $n = 15$), did not have any of the benefits of α females mentioned above, and was solely responsible for all aspects of breeding. Males tolerated β females nesting in their territories but did not provide any assistance during breeding.



According to de Juana *et al.* (2004), larks are monogamous although extra-pair paternity and bigamy has been reported for the Skylark *Alauda arvensis* (Delius 1965; Donald 2004). The mating system of the Monotonous Lark appears to be unique amongst the Alaudidae as pair-formation in this species is preceded by a period of promiscuity followed by a shift to monogamy. A high density of territories, as observed in this study shortly after arrival, is generally associated with increased extra-pair copulations (Birkhead and Møller 1992) and extra-pair fertilizations in birds (Westneat and Sherman 1997). Since female birds are generally receptive for approximately five days prior to laying the first egg until the day prior to laying the last egg in a clutch, it is in a male's interest to guard a female for at least this period to ensure paternity of the offspring. The indifference that a male displays towards a female that starts laying within a few days after arrival, i.e. a β female, reflects his uncertainty of paternity-assurance. A male is more likely to invest in mate guarding, acting as a sentry and parental duties if he is sure of paternity of the offspring. As the territory establishment stage progresses, the density of territories decrease which reduces the opportunities for extra-pair copulations. This is because there are fewer males (the weaker males vacate their territories), fewer receptive females (some β females have already started laying) and larger territories. This, in turn, allows comparatively more time for pair-bond formation and the mating system changes to a monogamous system.

This interesting mating system has checks in place to ensure that both sexes select the fittest individuals. A male that calls and displays for long periods will not only attract females, but also advertises to females that he occupies a high quality habitat and as such has time available for these activities. Females are more likely to visit these territories and mate with males that call and display intensely. Such males are almost certainly in good physical condition enabling them to be more alert and to intercept females entering their territory. The "cat-and-mouse" chasing behaviour observed may be a manner in which a female tests a male's fitness and vigilance, which

are important considerations during the incubation, nestling and post-fledging periods. Although a β female nesting in the territory of a high quality male is tolerated by the resident male, she receives no assistance from the resident male. A β female benefits indirectly from the resident male's superior vigilance, which may alert the female to potential predators. Furthermore, high quality males are more likely to occupy territories in 'better' habitat which will be beneficial when raising young as a single parent.

The mating system as reported here would fit an opportunistically breeding nomadic species well. The initial promiscuous stage ensures that at least some males will sire at least some young when favourable conditions present itself. The shift to a monogamous mating system and its associated biparental care is likely to ensure a higher probability of breeding success when conditions are optimal.

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