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Breeding ecology of Kori Bustard *Ardeotis kori strunthiunculus* in the Serengeti National Park

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The breeding ecology of the Kori Bustard *Ardeotis kori strunthiunculus* was studied in the plains of the Serengeti National Park, Tanzania in 2014 and 2015. Random transects were used to search for male courtship displays, nests, chicks and subadults. GPS satellite collars were used to locate nesting females. Linear regression analyses and *post hoc* tests were used to determine the predictors that contributed most to the variation of the dependent variables (courtship display, nest, chicks and subadults). The results indicate that courtship behaviour peaks during the short dry and short rainy season before the peaks in nests and chicks. The highest nest frequency was found in short grass habitats. Female Kori Bustard may undergo repeated nestings within a single breeding season. The adult sex ratio was female skewed during the breeding season. The Kori Bustard breeding season in the Serengeti plains is relatively long, lasting for almost nine months, and taking place during all seasons except for the long dry season. We recommend that management authorities conduct assessments of Kori Bustard recruitment as well as habitat suitability in the Serengeti ecosystem to develop future conservation strategies.

Écologie de reproduction de l'Outarde Kori *Ardeotis kori strunthiunculus* dans le Parc National de Serengeti

L'écologie de reproduction de l'Outarde Kori Ardeotis kori strunthiunculus a été étudiée dans les plaines du Parc National du Serengeti, en Tanzanie en 2014 et 2015. Des transects aléatoires ont été utilisés pour rechercher les parades nuptiales des mâles, les nids, les poussins et les subadultes. Les colliers satellites GPS ont été utilisés pour localiser les femelles nicheuses. Les analyses de régressions linéaires et post hoc ont été utilisées pour déterminer les prédicteurs qui ont le plus contribué à la variation des variables dépendantes (parade nuptiale, nid, poussins, subadultes). Les résultats indiquent que le comportement de la parade culmine pendant les courtes saisons de sècheresse et de pluie précédant les pics des nids et des poussins. La fréquence de nidification maximale a été observée dans les habitats à haute herbe. La femelle Outarde Kori peut faire des nichées répétées au cours d'une seule saison de reproduction. Le sexe ratio des adultes était déséquilibré chez les femelles pendant la saison de reproduction. La saison de reproduction de l'Outarde Kori dans les plaines du Serengeti est relativement longue, s'étalant sur presque neuf mois et se déroulant pendant toutes les saisons, à l'exception de la longue saison sèche. Nous recommandons aux autorités de gestion de mener des évaluations du recrutement de l'Outarde Kori ainsi que de ses habitats dans l'écosystème du Serengeti pour développer des stratégies de conservation futures.

Keywords: breeding, habitat, season, Serengeti plains, sex ratio

Introduction

Different birds exhibit a variety of breeding systems (Davies 1985), including a polygamy mating system in bustards. The most extreme and specialised example of breeding system is polygamy in birds and involves lekking where males display in congregation. Females visit such leks solely to assess a potential mate to copulate (Höglund and Alatalo 1995). Leks are described as 'exploded' when males within a display aggregation are separated by considerable distance and aggregation cannot be detectable until displaying males are mapped over large areas. Exploded lekking occupies a position between classical and resource-based leks and appears to be particularly

widespread among the Otididae family (Morales et al. 2001). The study of a species' breeding system and factors influencing breeding habitat selection is most important in considering conservation approaches for the species (Höglund 1996; Morales et al. 2001).

The Kori Bustard *Ardeotis kori strunthiunculus* is the largest flying bird belonging to the bustard family (Otididae). The species is indigenous to the grasslands and lightly wooded savanna of southern and eastern Africa (Lichtenberg and Hallager 2008). The population of the species is declining over its entire range due to low reproductive rates (Lichtenberg and Hallager 2008), reduced breeding (Lichtenberg and Hallager 2008), shrub encroachment, unregulated and illegal hunting, and degradation of habitat range. Currently, the species is considered as Near Threatened (BirdLife International 2016).

Kori Bustard is a polygynous species (one male mates with multiple females), which tends to be gregarious outside the breeding season (Osborne and Osborne 2001). During the breeding season, the Kori Bustard males occur either singly or gather in loose lek-like formations and perform 'balloon' displays to attract females. This behaviour is most intense in the early morning and evening (Hallager and Boylan 2004; Lichtenberg and Hallager 2008).

As in other bustard species, the female Kori Bustard makes no real nest, rather a shallow scrape on the ground, which is usually near a small clump of grass allowing the nesting female to hide. Kori Bustard clutch sizes range from one to two eggs while three eggs are rare (Osborne and Osborne 2001).

Although the Kori Bustard occurs in northern Tanzania, there is no published data on its breeding ecology in the Serengeti ecosystem. In this paper, we present data on Kori Bustard breeding ecology, including the occurrence of courtship displays, nest site (four different areas) and habitat (grass colour and height) selection, clutch size, breeding season and male:female sex ratio, in the grass plains of the Serengeti National Park (SNP). The aim of this study was to determine the timing and location of Kori Bustard breeding activity in the Serengeti study area. We tested the hypotheses that Kori Bustard prefer short grass and green grass habitat and that the peak of the breeding season occurs during the long rainy season (March to May). In addition, we describe temporal distribution of male courtship behaviour, nest detection and chick observations. We hypothesised that the Kori Bustard courtship displays occur before the peak of the breeding season and during the colder parts of the day, as the breeding season would be quite long and nest and chick predation are possible causes of this long breeding season.

Methods

Study area

The Serengeti National Park is one of the two main components of the Serengeti-Mara ecosystem (SME), located between latitudes 1°28'–3°17' S and longitudes 33°50'–35°20' E and extending from northern Tanzania to south-western Kenya. The SME covers a total land area of approximately 25 000 km², of which 14 763 km² lies within the SNP and 8 094 km² in the Ngorongoro Conservation Area. The average annual rainfall varies from 600 mm in the south-east plains to 1 100 mm in the north (Pennycuick 1975). The mean temperature ranges between 15 and 27 °C. The temperature is usually higher in the western parts compared with the eastern parts and may rise to more than 36 °C during the dry period. Our research focused on the southern SNP, an area dominated by short grass plains and where Kori bustards are frequently observed.

A major part of the SNP is dominated by acacia savanna woodlands and riverine forests, particularly in the western and northern parts (Senzota 1982). However, grasslands dominate in the south-east.

There are two major seasons in the ecosystem: a wet season extending from November to May and a dry season extending from June to October. These seasons are further subdivided into short dry (January to March) and long dry (July to September), as well as long rain (April to June) and short rain (October to December) seasons (Norton-Griffiths et al. 1975). Although exact start and end times for the dry and wet seasons vary annually, we used the four-season designation of Norton-Griffiths et al. for the present analyses.

Field data sampling

Data were collected over two breeding seasons between January 2014 and August 2015. During the study period we surveyed 1 878 random 1 km transects over the entire study area without transect overlap. Transects were surveyed from a vehicle, driving at a speed of approximately 20 km h⁻¹. Transect surveys were conducted from 07:00 to 18:00 during the first week of every month for four days with a maximum of 25 transects per day and a minimum of 100 transects per month.

The variables observed included (1) grass colour (green = 80-100% green, greenish = 10-80% green, and brown = 0% green); (2) grass height (short = <10 cm, medium = 11–30 cm, and tall = \geq 30 cm), which, together, defined six different habitat types; (3) season (short dry [January-March], long rainy [April-June], long dry [July-September] and short rainy [October-December]); and (4) time of day (morning = 07:00-10:00, midday = 11:00-14:00, and evening = 15:00-18:00). Grass colour was categorised as green when completely green, greenish when ranging from nearly dry to yellowish, and brown when completely dry. Grass height was measured with a tape measure (100 cm) followed by visual estimates of grass. Measurements were taken where Kori Bustard nests, chicks, subadults and courtship display were seen and estimated with the surrounding grass height when more than one Kori Bustard were observed within the same transect. The study area in the southern SNP plain was categorised into four groups of sites: south-west (SW), south-east (SE), north-west (NW) and north-east (NE) (Figure 1).

The sex of adults was determined as male when individuals were larger in body size with thick necks and/ or a darkened throat (during the breeding season) and as female when individuals were smaller in body size than males and had black on the crown (Bailey and Hallager 2003). Subadult individuals were differentiated from adults when they were observed to have different features from adult birds. Subadult males are larger resembling adult males but with a thinner neck and are larger than subadult females. Subadult females have thinner legs than adult female and a brown-black back (Osborne and Osborne 2001). The adult male and female Kori Bustard were counted during transects surveys and counts were used for determining the sex ratio in relation to the study area, seasons, sites and habitats.

Courtship display was recorded when the male Kori Bustard was displaying with a full neck and tail white plumage/feather display as described by Lichtenberg and Hallager (2008). Females hiding in the grass were treated as an indication of nesting females, and the search

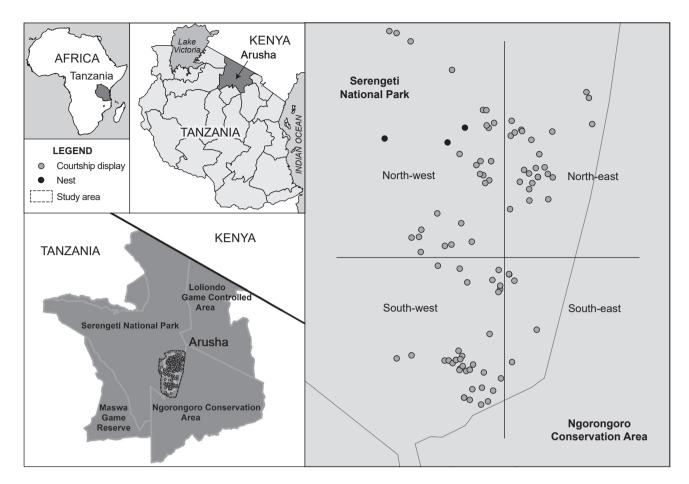


Figure 1: Map of the Serengeti National Park showing the Kori Bustard study area. Grey dots indicate male Kori Bustard courtship displays, and black dots indicate different nests of one GPS satellite collared female in 2014 and 2015

for nests was intensified. Observed nests, chicks and subadults in different habitats, sites and seasons were recorded. Egg number was recorded together with egg width and length (in mm) using a Vernier calliper.

We expressed the adult sex ratio as tertiary sex ratio (the ratio at sexual adulthood) and quaternary male:female ratio in adults past the age of sexual reproduction (Mayr 1939), as the total number of adult males divided by the sum of adult males and females observed during the fieldwork. Thus, sex ratio is expressed as a number around 0.5.

Chicks and subadults were photographed using a digital camera, and body size of subadults was estimated in relation to the size of adult birds. Kori Bustard chicks were easily identified as their mother accompanied them. The chicks studied ranged in age from one to 24 weeks. Their age was estimated based on the 2014 international studbook for the Kori Bustard (SNZP 2014) by comparing individual chicks with photographs in the book.

In addition to random transects, nests were also located using GPS satellite collars attached to nine female Kori bustards (Mmassy et al. 2017). A GPS was used to map areas used by nesting females and to locate nests. Consequently, abundance data for all variables were recorded as presence (1) or absence (0; viz. missing observations were recorded as 0) of nests, chicks or subadults.

Data analysis

To examine the relation of environmental factors (site, season, grass height, grass colour and time of day) to the frequency of courtship display, nest, chick, subadult and adult sightings, we first performed chi-square tests for each pair of variables. Next, we constructed logistic regression models to examine the association of all environmental variables taken together and our outcomes of interest. The mean sex ratio of adults males and females in different environmental factors was determined by analysis of variance (ANOVA). Fisher's exact probability test was used to determine the probability that two eggs will result in two chicks. The significance level of all statistical tests was set at $\alpha = 0.05$ ($P \le 0.05$).

Results

Courtship behaviour

In total, 1 878 transects were conducted for 19 months in which 1 157 adults Kori bustards were recorded including 94 displaying individual males. The rate of courtship display differed statistically significantly between the four sites ($\chi^2 = 29.29$, df = 3, P < 0.001). The highest rate of courtship display was observed in the NE sites (Figure 2a). The observed courtship rate in the NE was significantly higher than in the SE sites ($\chi^2 = 43.9$, df = 1, P < 0.001), as well

as that of the NW sites ($\chi^2 = 6.33$, df = 1, P = 0.012), but not in the SW sites (P > 0.05), ($\chi^2 = 2.13$, df = 1, P = 0.145). However, the rate of courtship display also differed significantly between the SE and SW sites ($\chi^2 = 25.1$, df = 1, P < 0.001), as well as between the SE and NW sites ($\chi^2 = 40.0$, df = 1, P < 0.001), but not between the SW and NW sites (P > 0.05) (Figure 2a). The courtship displays were highest in the short dry season (Figure 2b) and no courtship display was observed in the long dry season ($\chi^2 = 11.25$, df = 3, P < 0.010, Figure 2b). Furthermore, the courtship displays differed significantly between the short dry and the long wet seasons ($\chi^2 = 25.2$, df = 1, P < 0.001), as well as between the short dry and the short wet seasons ($\chi^2 = 5.84$, df = 1, P = 0.016). No significant difference in courtship behaviour was observed between different habitats (grass length [χ^2 = 4.32, df = 2, *P* = 0.116] and grass colour [χ^2 = 5.69, df = 2, *P* = 0.056]) or at different times of the day (χ^2 = 5.26, df = 2, *P* = 0.072) (Figure 2c–e).

A logistic regression analysis with behaviour (courtship or no courtship) as the dependent variable and site, season, time of day, grass height and grass colour as the independent variables indicated that only site was a significant contributor to the variation in courtship displays (Table 1).

Sex ratio

The adult male:female sex ratio differed statistically significantly between different seasons (F = 13.58, df = 3 and 655,

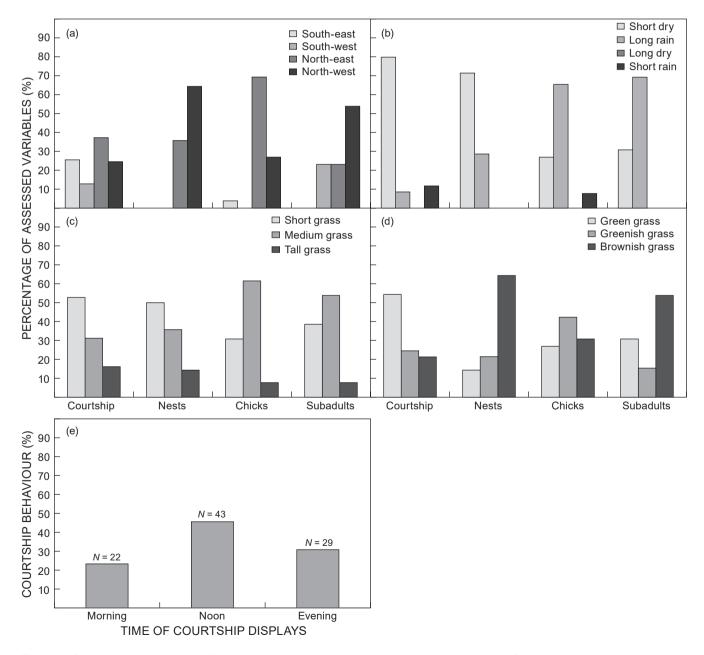


Figure 2: Observations (percentage) of courtship displays, nests, chicks, subadults and time in the Serengeti grass plains in relation to (a) site, (b) season, (c) grass height, (d) grass colour and (e) time of day of the courtship displays

Variable -	Courtship behaviour		Nests		Chicks		Subadults	
	Wald	Р	Wald	Р	Wald	Р	Wald	Р
Site	9.869	0.002	1.797	0.179	0.369	0.544	0.555	0.459
Season	0.920	0.338	0.946	0.322	3.199	0.074	0.137	0.725
Grass height	0.396	0.529	5.520	0.019	3.363	0.067	0.503	0.297
Grass colour	0.694	0.405	4.786	0.027	0.174	0.676	1.086	0.485
Time of day	1.222	0.269						
Adjusted R ²		0.056		0.209		0.053		0.031
Wald χ²		258.2		200.3		253.4		193.6
Wald p		< 0.001		< 0.001		< 0.001		<0.001

Table 1: Logistic regression analyses with dependent values (horizontally) and independent values (vertically). All independent variables were used in all tests except for time of the day, which is used only for courtship display. N = 655 for all except subadults (N = 654)

P < 0.001; Table 2). The adult male:female sex ratio was female skewed during the short wet and long wet seasons, whereas a male skewed sex ratio occurred during the long dry and short dry seasons. A Tukey *post-hoc* test revealed that the highest ratio of males to females encountered was highest in short dry season (equal ratio) than the long wet season (female skewed) (P < 0.001), and long wet season (female skewed) differed significantly from the short wet season (less female skewed) (P = 0.008).

The adult male:female sex ratio differed statistically significantly between different sites (F = 6.58, df = 3 and 654, P < 0.001; Table 2). The adult male:female sex ratio was male skewed in the SE and SW sites, whereas in the NE and NW sites it was female skewed. A Tukey *post-hoc* test revealed that the SE sites (male skewed) differed significantly from the NW sites (female skewed) (P < 0.001), and the SE sites differed significantly from the NE (female skewed) sites (P = 0.009), whereas the SW sites (equal ratio) differed significantly from the NW sites (female skewed) (P = 0.039).

The adult male:female sex ratio differed statistically significantly between different grass colours (F = 5.86, df = 2 and 655, P = 0.003; Table 2). The sex ratio was equal in the green grass habitat and female skewed in greenish and brownish grass habitats. A Tukey *post-hoc* test revealed that the male:female ratio in green grass habitat differed statistically significantly from that in brownish grass (P = 0.003). No differences in sex ratio were observed between different grass lengths.

Nests and clutch size

Overall, 14 nests with a total of 20 eggs were recorded. Among the recorded nests, five were observed in 2014 and nine in 2015. However, 36% of the nests were predated. The clutch size varied between one and two eggs. The mean (\pm SD) clutch size was 1.4 \pm 0.5 eggs (N = 14), whereas the mean egg length and width were 85.2 \pm 4.2 cm and 58.7 \pm 1.6 cm, respectively (N = 19).

Based on data obtained from a bird with a GPS satellite collar, we observed a female undertaking repeated nesting attempts during the study period. This female nested three times in different locations in the NW sites during a single breeding season in March and May 2014 and again in January 2015. The nesting distance between two nests in 2014 was 2.6 km. The distance between the second nest in 2014 and the nest in 2015 was 9.3 km. Observed number of nests was statistically different between sites

Table 2: Distribution of Kori Bustard sex ratio (number of males/ number of males + number of females; values > 0.5 indicate skewed female ratio whereas values < 0.5 indicate more males), in relation to site, season, habitat, grass colour and time during breeding season (N = 1 157 observations of adult Kori Bustards)

Variable categ	ories	Sex ratio ± SD	No. of Kori Bustard observations	No of transects
Site	SE	0.62 ± 0.46	66	317
	SW	0.51 ± 0.46	95	263
	NE	0.43 ± 0.45	294	510
	NW	0.36 ± 0.45	203	807
Season	Short dry	0.51 ± 0.46	441	781
	Long rain	0.22 ± 0.36	134	610
	Long dry	0.58 ± 0.49	6	208
	Short rain	0.43 ± 0.46	78	298
Grass height	Short	0.46 ± 0.46	323	1 131
- 0	Medium	0.41 ± 0.45	260	746
	Tall	0.49 ± 0.46	9	20
Grass colour	Green	0.51 ± 0.45	299	588
	Greenish	0.41 ± 0.45	151	413
	Brownish	0.37 ± 0.47	208	896

 $(\chi^2 = 11.70, df = 3, P = 0.008;$ Figure 2a), with the highest number of nests (64.3% of the total observations) found in the NW sites. Most nests were observed during the short dry season (71.4% of the total observations); however, a few nests were also recorded during the long wet season (28.6% of the total observations; Figure 2b). No significant difference in observed nests between seasons ($\chi^2 = 2.363$, df = 3, P = 0.501) and grass height (χ^2 = 0.159, df = 2, P = 0.923) was observed, probably due to the low sample size (Figure 2c). Furthermore, most nests were found in the brownish grass habitat ($\chi^2 = 10.70$, df = 2, P = 0.005, N = 9; Figure 2d). The difference in number of observed nests between green and greenish grass was statistically significant ($\chi^2 = 7.733$, df = 1, P = 0.005). A logistic regression analysis with the presence of nests as the dependent variable and site, season, grass height and grass colour as the independent variables indicated that nests were associated with brownish and short grass (Table 1, Figure 2c and d).

Chicks and subadults

Females with chicks were observed 25 times. Among these observations each female had a single chick and

only one female was observed with two chicks, making a total of 26 chicks, with an average brood size of 1.0 chicks per brood. Again, 23 subadult Kori bustards were recorded, 69.2% during the long wet season and 30.8% during the short dry season ($\chi^2 = 19.82$, df = 3, P < 0.001, Figure 2b). A Fisher's exact probability test (P = 0.004) indicated that there were significantly more two-egg nests (8/14) than two-chick broods (1/26), indicating that many two-egg nests do not result in two chicks. There was a slightly significant difference in the observed chicks found between sites ($\chi^2 = 8.73$, df = 3, P = 0.033), with (69.2%, N = 18) of chicks found in NE (Figure 2a). The majority of the 26 chicks of different ages ranging from one day to two months were recorded during the long wet season (65.4%, N = 17) followed by the short dry season (26.9%, N = 7) and short wet season ($\chi^2 = 34.13$, df = 3, P < 0.001; Figure 2b). The observed chicks in the short dry season and long wet season were significantly higher ($\chi^2 = 32.054$, df = 1, P < 0.001), as well as between the long wet and short wet seasons ($\chi^2 = 6.265$, df = 1, P = 0.012). No significant difference in observed chicks were found between different habitats (grass height [$\chi^2 = 5.50$, df = 2, P = 0.064], although 61.5% [N = 16] were found in medium height; grass colour $[\gamma^2 = 6.47, df = 2, P = 0.039]$, although 42.3% [N = 11] of chicks were found in green grass habitat; Figure 2c and d).

A logistic regression analysis with presence of chicks or no chicks indicated that grass height and season were almost significant contributors to the variation in the distribution of chicks, with chicks observed more frequently when grass was high (Table 1).

Finally, a logistic regression analysis with presence/ absence of subadults as the dependent variable and site, season, habitat and grass colour as the independent variables indicated that only season was a predictor for the variation in observed subadult encounter rates (Table 1).

Discussion

The aim of this study was to determine the timing and location of the Kori Bustard breeding activity in the Serengeti study area. We tested the hypotheses that Kori Bustards prefer short grass and green grass habitat and that the peak of the breeding season occurs during the long wet season (March to May). In addition, we described temporal distribution of male courtship behaviour, nest detection and chick observations. We hypothesised that the Kori Bustard courtship displays occur earlier before the peak of the breeding season and during the colder parts of the day and that the breeding season would be quite long, and examined nest and chick predation as a possible cause of this long breeding season.

An important finding in this study is that courtship behaviour is influenced by season and site. Breeding occurs almost throughout the year as chicks were observed in all seasons except the long dry season. Females undergo several breeding attempts in a single season if the previous nest is predated. Sex ratio is male skewed during the long dry and short dry seasons.

The results indicate that the courtship behaviour of the Kori Bustard in the Serengeti plain peaks during the short dry and short wet seasons, and before the peak of nests

and chicks. As birds normally have their young in the nest when food is abundant, they must lay eggs sometime earlier (Perrins 1970). Previously published data on the density of Kori Bustard in the Serengeti plains indicated that during the short dry season individual Kori Bustards become more abundant in the study area than in other seasons (Mmassy et al. 2017). The appearance of a high number of individual Kori Bustards during that season may reflect the onset of the breeding season. Our hypothesis that the breeding season starts earlier before the long wet season also corresponds with a study on Australian Bustard Eupodotis australis (Ziembicki 2010). We also postulated that courtship display would occur in the short grass habitat, as this would allow females to see displaying males easily, which we observed (Figure 2c). Other studies on the Little Bustard Tetrax tetrax conducted in central Spain have found that males and females occupied areas with abundant food resources during the breeding season as reproductive territories (Traba et al. 2008; Tarjuelo et al. 2013). However, this does not apply to all bustard species. A recent study in Spain on the Great Bustard Otis tarda found the short grass habitat to be important during courtship as it increased the visibility of displaying males to females (Alonso et al. 2012), although the study did not control for the grass length.

The courtship displays occurred with highest frequency during the noon hours. This finding differs slightly from our prediction that courtship display occurs during the morning and late afternoon. The result corresponds to observations of Kori Bustard in captivity (i.e. in zoos), where they have been found to display during noon (Girsch 2012) as well as during the morning, afternoon and evening hours (Hallager and Boylan 2004). It is, however, not known if it was statistically tested and how often it was observed. These differences in the time of courtship displays between Kori Bustards in captivity and natural habitats also may be due to variations in environmental conditions such as temperature, although more research is needed to explore whether this is the case.

The sex ratio of the Kori Bustard in the SNP tended to be female skewed, and in most cases significantly so. During the long wet (late breeding) season, the sex ratio was extremely female skewed. This may be due to the role of the male Kori Bustard during breeding and nesting periods, as its presence is most important at early stages of the breeding season. Research on Little Bustard has shown that courting is the main duty of males during the breeding season (Jiguet and Bretagnolle 2001) and that male Little Bustards do not seem to participate in the parental investment beyond the provision of gametes during mating (Jiguet et al. 2000; Moreira et al. 2004). Our research suggests that because male Kori Bustards do not participate in incubation or take care of the offspring, they may migrate to other areas. Post-mating migration has been reported in Great Bustard males in summer regions. Environmental factors such as searching for feeding ground and conducive ambient temperature have been explained as the cause of post-mating migration in Little Bustard (Morales et al. 2000; Alonso et al. 2009). However, more research is needed to test whether partial migration of male Kori Bustard after mating occurs in the Serengeti plains, together with the destination and distance, as there are indications that bustard density drops dramatically in the study area after the breeding season terminates (Mmassy et al. 2017).

A high percentage of nests was observed in short grass habitat and most chicks were sighted in sites with medium height grasses. Results from Great Bustard studies on nest-site selection have suggested that females look for habitats with good visibility while incubating (Magaña et al. 2010). Similarly, research on the breeding habitat of the Houbara Bustard Chlamydotis macqueenii in the Central Steppe of Iran indicates that the Houbara Bustard nests in short grass habitats to spot approaching predators (Aghainajafi Zadeh et al. 2010). What is more, research on the Asian Houbara Bustard Chlamydotis (undulata) macqueenii in Mori, Xinjiang, China and in central Saudi Arabia have found that these species breed in habitats with significantly lower grass height (Combreau and Smith 1997; Yang et al. 2003). The camouflage and spotting of enemies due to predation might lead Kori Bustards to nest in short grass and hide chicks in the medium grass height.

The highest frequency of subadults appeared during the long rainfall season and after the peak of nests and chicks. The latter was observed to take place during the short dry, short wet and long wet seasons. Observations of chicks during the short dry, the short wet and long wet seasons implies that the Kori Bustard breeding season may last for almost nine months (from October to June), covering all seasons except the long dry season.

We were unable to acquire enough samples to test if female Kori bustards undergo several breeding attempts within a single breeding season if the nest is predated. Although we observed one female Kori Bustard that nested twice within a single season, this is not enough to justify the case statistically. Observations of few nests, chicks and subadults may indicate a predation loss of nests and chicks or it is due to few observations owing to low detectability of chicks and nests because they may be hidden in the tall grass to protect themselves from being detected by predators. The nest predation in the present study accounted for 36% loss of the observed nests. We found evidence of predation through GPS-monitored nests. Crushed eggs and presence of teeth marks, such as those of mongooses or jackals, remained on egg shells. Again, research on other bustard species seems to support this finding. For example, a study in central Spain showed that up to 39% of Great Bustard clutches are lost due to egg predation (Magaña 2007). Similarly, in research on Asian Houbara Bustard 85% of nests were lost because of predation (Koshkin et al. 2016). Nest predation is the primary source of nest loss across a wide diversity of species (Ricklefs 1969: Martin 1993). In Great Bustard nest losses and chick mortality are largely attributed to predation and starvation (Magaña 2007; Abdulkarimi et al. 2010). This may apply to the Kori Bustard, being a grasslands ground-nesting bird.

The mean clutch size of Kori Bustard found in this study might be small compared with the mean clutch size of other bustard species (Osborne and Osborne 1998; Rocha et al. 2013; Koshkin et al. 2016). Great Bustards in Spain and Hungary are shown to have an even smaller clutch size (Morales et al. 2002; Watzke 2007). As for the number of chicks per brood, we observed an average brood size of 1.0 chicks per brood, which indicates that at least one chick can be raised by a single female and raising of two chicks may be rare.

We conclude that the peak frequency of courtship displays occurs during the early stages of the breeding season. The Kori Bustard nests in tall and medium grass habitats and it can undergo several breeding attempts within a single breeding season due to nest predation. Few observations of nests, chicks and subadults may support the prediction that nest predation may be high. Other reasons, which may contribute to nesting failure and need to be studied, include predation of nesting females, climate change and fire regime management. The male-skewed sex ratio after the mating period may indicate a post-breeding migration of males. Finally, we conclude that the breeding season of Kori Bustards in the Serengeti plain is relatively long because chicks were observed for several months, with the exception of the long dry season. A study of Kori Bustard breeding ecology is of great importance as it is a Near Threatened species, listed in Appendix II of CITES. It is therefore crucial to understand its breeding ecology for further action towards conservation of the species. We recommend that management authorities conduct a recruitment assessment of Kori Bustards in the Serengeti ecosystem to develop future strategies for the conservation of the species. This should include studies on habitat preferences by the species inside and outside the protected areas, the buffer zones and seasonal migration grounds.

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References

- Abdulkarimi R, Daneshyar M, Barati A. 2010. Current status of the Great Bustard Otis tarda in Boukan, West Azerbaijan, Iran. Podoces 5: 63–68.
- Aghainajafi Zadeh S, Hemami MR, Heydari F. 2010. Investigation wintering and breeding habitat selection by Asiatic Houbara Bustard (*Chlamydotis macqueenii*) in central steppe of Iran. *International Journal of Environmental and Ecological* Engineering 4: 521–524.
- Alonso JC, Magaña M, Álvarez-Martínez JM. 2012. Male display areas in exploded leks: the importance of food resources for male mating success. *Behavioral Ecology* 23: 1296–1307.
- Alonso JC, Palacín C, Alonso JA, Martín CA. 2009. Post-breeding migration in male Great Bustards: low tolerance of the heaviest Palaearctic bird to summer heat. *Behavioral Ecology and Sociobiology* 63: 1705–1715.
- Bailey T, Hallager S. 2003. Management of bustards in captivity. *Avicultural Magazine* 109(1): 1–8.

- BirdLife-International 2016. *Ardeotis kori*. The IUCN Red List of Threatened Species. e.T22691928A93329549. Available at http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.IUCN.
- Combreau O, Smith TR. 1997. Summer habitat selection by Houbara bustards introduced in central Saudi Arabia. *Journal of Arid Environments* 36: 149–160.
- Davies NB. 1985. Cooperation and conflict among dunnocks, *Prunella modularis*, in a variable mating system. *Animal Behaviour* 33: 628–648.
- Girsch D (ed.). 2012. *The Kori Bustard SSP Newsletter*. December 2012, vol. 10. Washington, DC: Kori Bustards Species Survival Plan, Association of Zoos.
- Hallager S, Boylan J (eds). 2004. Kori Bustard Species Survival Plan (*Ardeotis kori*) husbandry manual. Washington, DC: National Zoological Park.
- Höglund J. 1996. Can mating systems affect local extinction risks? Two examples of lek-breeding waders. *Oikos* 77: 184–188.
- Höglund J, Alatalo RV. 1995. *Leks*. Princeton: Princeton University Press.
- Jiguet F, Arroyo B, Bretagnolle V. 2000. Lek mating systems: a case study in the Little bustard *Tetrax tetrax*. *Behavioural Processes* 51: 63–82.
- Jiguet F, Bretagnolle V. 2001. Courtship behaviour in a lekking species: individual variations and settlement tactics in male Little bustard. *Behavioural Processes* 55: 107–118.
- Koshkin M, Burnside RJ, Packman CE, Collar NJ, Dolman PM. 2016. Effects of habitat and livestock on nest productivity of the Asian houbara *Chlamydotis macqueenii*. *European Journal of Wildlife Research* 62: 447–459.
- Lichtenberg EM, Hallager S. 2008. A description of commonly observed behaviors for the kori bustard (*Ardeotis kori*). *Journal of Ethology* 26: 17–34.
- Magaña M. 2007. Reproductive behavior of the great bustard. PhD thesis, Complutense University of Madrid, Spain.
- Magaña MMA, Alonsojuan C, Martin CA, Bautistaluis M, Martin B, Bautista LM, Martin B. 2010. Nest-site selection by Great bustards *Otis tarda* suggests a trade-off between concealment and visibility. *Ibis* 152: 77–89.
- Martin TE. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* 141: 897–913.
- Mayr E. 1939. The sex ratio in wild birds. *American Naturalist* 73: 156–179.
- Mmassy EC, Fyumagwa RD, Jackson CR, Bevanger K, Røskaft E. 2017. Kori bustard (*Ardeotis kori struthiunculus*) occurrence in the Serengeti grass plains, northern Tanzania. *African Journal of Ecology* 55: 298–304.
- Morales MB, Alonso JC, Alonso J. 2002. Annual productivity and individual female reproductive success in a Great Bustard *Otis tarda* population. *Ibis* 144: 293–300.
- Morales MB, Alonso JC, Alonso JA, Martín E. 2000. Migration patterns

in male Great bustards Otis tarda. The Auk 117: 493-498.

- Morales MB, Jiguet F, Arroyo B. 2001. Exploded leks: what bustards can teach us. *Ardeola* 48: 85–98.
- Moreira F, Morgado R, Arthur S. 2004. Great bustard *Otis tarda* habitat selection in relation to agricultural use in southern Portugal. *Wildlife Biology* 10: 251–260.
- Norton-Griffiths M, Herlocker D, Pennycuick L. 1975. The patterns of rainfall in the Serengeti ecosystem, Tanzania. *African Journal* of *Ecology* 13: 347–374.
- Osborne T, Osborne L (eds). 1998. Ecology of the Kori bustard in Namibia. Windhoek: Ministry of Environment and Tourism Permit Office.
- Osborne T, Osborne L 2001. Ecology of the Kori bustard in Namibia. Windhoek: Ministry of Environment and Tourism Permit Office.
- Pennycuick L. 1975. Movements of the migratory wildebeest population in the Serengeti area between 1960 and 1973. *African Journal of Ecology* 13: 65–87.
- Perrins CM. 1970. The timing of birds 'breeding seasons. *Ibis* 112: 242–255.
- Ricklefs RE. 1969. An analysis of nesting mortality in birds. Washington, DC: Smithsonian Institution Press.
- Rocha P, Morales MB, Moreira F. 2013. Nest site habitat selection and nesting performance of the Great Bustard Otis tarda in southern Portugal: implications for conservation. Bird Conservation International 23: 323–336.
- Senzota RBM. 1982. The habitat and food habits of the grass rats (*Arvicanthis niloticus*) in the Serengeti National Park, Tanzania. *African Journal of Ecology* 20: 241–252.
- SNZP (Smithsonian National Zoological Park). 2014. International studbook for the Kori Bustard (*Ardeotis kori*). Washington, DC, SNZP.
- Tarjuelo R, Paula Delgado M, Bota G, Morales MB, Traba J, Ponjoan A, Hervás I, Mañosa S. 2013. Not only habitat but also sex: factors affecting spatial distribution of Little Bustard *Tetrax tetrax* families. *Acta Ornithologica* 48: 119–128.
- Traba J, Morales MB, de la Morena ELG, Delgado MP, Krištín A. 2008. Selection of breeding territory by Little Bustard *Tetrax tetrax* males in central Spain: the role of arthropod availability. *Ecological Research* 23: 615–622.
- Watzke H. 2007. Reproduction and causes of mortality in the breeding area of the Great Bustard in the Saratov region of Russia. *Bustard Studies* 6: 53–64.
- Yang WK, Qiao JF, Combreau O, Gao XY, Zhong WQ. 2003. Breeding habitat selection by the Houbara Bustard *Chlamydotis* [*undulata*] *macqueenii* in Mori, Xinjiang, China. *Zoological Studies* 42: 470–475.
- Ziembicki M. 2010. Ecology and movements of the Australian bustard *Ardeotis australis* in a dynamic landscape. PhD thesis, University of Adelaide, Australia.

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