Breeding biology of ostriches (*Struthio camelus*) in the Serengeti ecosystem, Tanzania

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Abstract

Ostrich breeding behaviour in the Serengeti ecosystem, Tanzania was investigated for differences in laying dates between low altitude western area (WA) and high altitude eastern area (EA) populations. Ostriches in WA laid eggs significantly earlier than in EA. The differences could be attributed to topography and rainfall pattern. Reliable rains in lower altitudes ensure availability of food that in turn influences the whole process of the reproductive cycle. Clutches were contributed by several females with a nest having up to 38 eggs. We also compared the frequency of observation of predators, ostriches, nests, 'singletons' (single eggs laid randomly) and broods between the two areas. There was no significant difference between WA and EA in 1) ostrich/nest ratio, indicating similar breeding densities; 2) ostrich/predator and predator/nest ratios, indicating that predation pressure was equally high; 3) nest/singleton and predator/singleton ratios, indicating that loss of nests did not vary between areas. However, there were significantly more predators, nests and ostriches compared to broods in EA than in WA, indicating a significantly lower reproductive success in EA. Using metapopulation terminology, ostriches in EA could be regarded as a 'sink' population and those in WA as a 'source' population, but investigations over longer time-periods are needed to further resolve if this is the case.

Key words: breeding, ostrich, predation, Serengeti, *Struthio camelus*

Résumé

Le comportement reproducteur des autruches dans l'écosystème du Serengeti, en Tanzanie, a été étudié pour voir les différences dans les dates de pontes entre les populations de la zone occidentale (WA) à basse altitude et de la zone orientale (EA) à plus haute altitude. Les autruches de la WA pondent significativement plus tôt que celles de l'EA. Les différences peuvent être attribuées à la topographie et au régime de la pluviosité. Les pluies fiables à plus basse altitude garantissent la disponibilité de la nourriture, ce qui influence dès lors tout le processus du cycle reproducteur. Des couvées réunissaient les œufs de plusieurs femelles – un nid a eu jusqu'à 38 œufs. Nous avons aussi comparé la fréquence d'observations de prédateurs, d'autruches, de nids, de «ingletons» (des œufs solitaires pondus au hasard) et de nichées entre les deux zones. Il n'y a pas de différence significative entre WA et EA pour 1) le ratio autruches/nids, ce qui indique des densités de reproduction similaires; 2) le ratio autruches/prédateurs et le ratio prédateurs/nids, ce qui indique que la pression de la prédation est aussi haute des deux côtés; et 3) le ratio nids/singletons et le ratio prédateurs/singletons, ce qui indique que la perte des nids ne variait pas entre les zones. Cependant, il y avait significativement plus de prédateurs, de nids et d'autruches par rapport aux nichées dans l'EA que dans la WA, ce qui indique une réussite de la reproduction significativement plus faible dans la EA. En utilisant la terminologie de la métapopulation, les autruches de la EA peuvent être considérées comme une population «puits» et celles de la WA comme une population «source», mais il faudrait faire des recherches de plus longue durée pour montrer si c'est bien le cas.

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Introduction

Ostriches *(Struthio camelus)* practise communal breeding, which involves several females laying in the same nest (Bertram, 1992; Kimwele & Graves, 2003). The territorial male prepares several scrapes on the ground out of which one becomes a nest where the female lays her eggs

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(Bertram, 1992). The first female to lay in the nest is referred to as the 'major' female while females that subsequently lay in the same nest are regarded as 'minor females'. However, only major females and territorial males provide parental care (Sauer & Sauer, 1966; Bertram, 1992). Ostriches generally breed during the dry season between July and October (Brown & Britton, 1980). The major female ostrich on average lays eleven eggs (range 8–16) (Bertram, 1992), while one to seven minor females may lay 20–40 additional eggs in the nest considerably in excess of the number that can be incubated (Sauer & Sauer, 1966; Hurxthal, 1979; Bertram, 1992). The clutch size in ostrich nests before incubation is indeterminate, but a nest may contain up to 30–40 eggs (Leuthold, 1977; Bertram, 1979). Other ratites also have communal nesting systems with multiple females laying in one nest, but only the male undertakes incubation and parental care responsibilities (Coddington & Cockburn, 1995).

Through evolution, the timing of avian breeding seasons has generally been adjusted to maximize the number of young ones produced (Perrins, 1970). Breeding is a demanding process both in terms of energy and nutrient requirements particularly during egg formation (Nager, 2006). Breeding individuals should adjust their behaviour to maximize their expected lifetime reproductive success (Williams, 1966). Perrins (1970) suggested that, the date at which each individual actually lays is related to the food supply at the time of laying, that is, laying can not begin until food has become sufficiently abundant for each female to find enough food. Areas in the north-western part of Serengeti National Park (SNP) receive a lot more rains because of the influence of the topography and proximity to Lake Victoria than the south-eastern part of the ecosystem (Campbell & Hofer, 1995). Early rains and therefore early availability of food in the north-western part should trigger earlier breeding than in areas of the SNP that receive less rains, which is particularly relevant for the eastern area. However, laying date must be viewed as a trade-off between opposing seasonal trends affecting both parents and their offspring, i.e. a trade-off in the fitness payoffs for offspring against those of the parents (Partrigde, 1989). Abundant nourishment is needed not only for nestlings and juveniles but also to meet increased energy demands of breeding adults (Ehrlich, Dobkin & Wheye, 1988). For females, those increased demands include the energetic burden of producing eggs (Perrins, 1996; Nager, 2006), whereas males need additional energy to support vigorous displays to defend territories and for displays related to sexual activities (Andersson, 1994; Cotton, Fowler & Pomiankowski, 2004; McGlothlin, Duffy & Henry-Freeman, 2007). In case parental decisions are based on the costs and benefits of parental care, avian nest desertion should occur when the cost of attending the nest results in a reduction of parental fitness (Clutton-Brock, 1991). In avian species, most desertions occur during the clutch stage (Ricklefs, 1977). Factors that cause clutch desertion include lack of food (Anderson, 1989), low quality of parents (Wiggins, Pärt & Gustafsson, 1964) and partial clutch loss (ten Cate & Taborsky, 1992; Fernandez & Reboreda, 2000).

Although ostrich nests are well camouflaged and surprisingly hard to detect, they generally experience high predation (Bertram, 1992). Spotted hyenas (*Crocuta crocuta*), Egyptian vultures (*Neophron percnopterus*) and lions (*Panthera leo*) are the main predators of ostrich eggs (Bertram, 1992). Nests are located visually or other cues may be used such as observing parental activity like building and leaving or returning to nests with eggs or young (Collias & Collias, 1984; Martin *et al.*, 2000). Most large top predators are confined to protected areas, or to regions remote from human activity (Nowell & Jackson, 1996; Nyahongo, 2004). In areas with high densities of predators, frequency of ostrich nest predation may be high. It would therefore be expected that more single eggs are laid randomly outside the nest (singletons) in areas where nest predation is high, and therefore predation can be regarded as one of the main factors that influence reproductive success within various populations (see also Sauer & Sauer, 1966).

The most comprehensive studies on ostriches include physiology, anatomy, ostrich farming and pathology (Siegfried & Frost, 1974; Bezuidenhout, 1986; Brown, Roberts & Page, 1993; Degen *et al.*, 1994; Deeming, 1995), while little attention has been directed to ostrich breeding in the wild (but see Sauer & Sauer, 1966; Leuthold, 1977; Jarvis, Jarvis & Keffen, 1985; Bertram, 1992). To date, studies on timing of breeding have been based on correlation with temperature or other climate variables like precipitation. As a consequence, inferences have to be made cautiously. In particular, it is also possible that long-term changes in phenology are actually caused by changes in human land use patterns, pollution or different predation pressure.

Differences in topography within the Serengeti ecosystem, creates variations in the amount of rainfall between low and high altitudes, therefore studies on the effect of

topography on the laying dates are needed. Here, we investigated possible differences in timing of breeding (laying dates) in low and high altitude areas in SNP, Tanzania in Masai ostrich (*S. c. massaicus*) subpopulations. In addition, we compared the frequency of predators, ostriches, nests, singletons and broods between the two areas. Finally, we estimated the reproductive success of ostriches by monitoring all nests found until we could determine the fate of the nests.

Materials and methods

Study area

The study was carried out in the part of the Serengeti ecosystem i.e. Serengeti National Park (SNP) (14,763 km^2) and adjacent Ikorongo (563 km^2) and Grumeti (416 km^2) Game Reserves and Ikoma Open Area (600 km^2) (Fig. 1) from May 2005 to December 2006. The study area is part of the high interior plateau of East Africa. It slopes from its highest part (1850 m) on the eastern plains towards Speke Gulf (920 m) in the western part (Sinclair, 1995). The study area was divided into two areas based on defined altitude values, i.e., 900–1400 m (low altitude) and 1400–1800 m (high altitude) above sea level, and therefore low altitude was in the western area (WA) and high altitude in the eastern area (EA) (Fig. 1). All ostrich observations were analysed with respect to possible relationships between ostrich observations and altitudes.

In both areas, the climate is usually warm and dry with mean temperatures varying between 15°C to 25°C. The rains in the Serengeti ecosystem falls in a bimodal pattern, the short rainy season between November and January, and the long rainy season between March and May when there is heavy downpour (Norton-Griffiths, Herlocker & Pennycuick, 1975). However, the rains increase towards Lake Victoria and can fuse into one long period, particularly in the northwest, or the short rains can fail entirely especially in the southeast (Sinclair, 1995). There is an

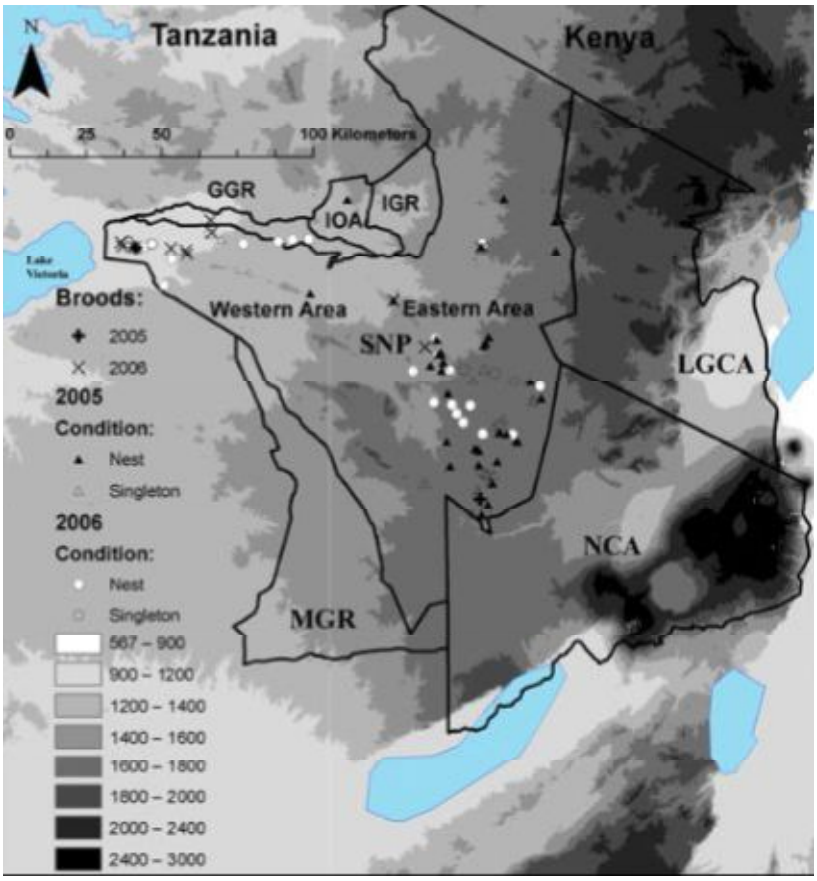


Fig 1 Map of the Serengeti ecosystem showing the study area, Serengeti National Park (SNP) and adjacent Grumeti Game Reserves (GGR), Ikorongo Game Reserve (IGR) and Ikoma Open Area (IOA) (thick black lines). Other areas in the map are Maswa Game Reserve (MGR), Ngorongoro Conservation Area (NCA) and Loliondo Game Controlled Area (LGCA). Blue areas denote lakes. Symbols denote the location of nests, singletons and broods in both 2005 and 2006

Table 1 Methods used to find nests in eastern and western areas of the Serengeti ecosystem in 2005 and 2006

	Western area		Eastern area	
Method	2005	2006	2005	2006
Head of incubating ostrich observed while driving by	33.3 (1)	0 (0)	3.3 (1)	14.3 (2)
Watching a male and female sitting and standing at a particular point repeatedly	33.3 (1)	30 (3)	46.6 (14)	28.5 (4)
Chance encounter of nest when driving by	0 (0)	40 (4)	16.7 (5)	21.4 (3)
Aerial searching with plane	0 (0)	0 (0)	0 (0)	7.1 (1)
Told by Tanzania National Park (TANAPA) rangers or other researchers	33.3 (1)	30 (3)	33.3 (10)	28.6 (4)
Total	100 (3)	100 (10)	100 (30)	100 (14)

Figures are percentages with number of observations in parentheses.

overall rainfall gradient from the dry south-eastern plains (800 mm per year) to the wet north-western area (1050 mm per year) of the SNP (Campbell & Hofer, 1995). During the study period, EA received an average rainfall of 744, SD = ±197 mm (range: 14–2658 mm) whereas WA received an average rainfall of 882, SD = ±315 mm (range: 44–3265 mm) per year (Data from Tanzania National Park Authority meteorological stations). The mean altitude in the WA is 1205 m and in the EA 1653 m above sea level (Sinclair, 1995). The study area is composed of highland savannah with mainly thorn woodland trees (with species of *Acacia, Commiphora, Ficus, Combretum* and *Podocarpus*) and extensive grass plains (Herlocker, 1976). EA is characterized by short and long grass plains, an extensive block of *Acacia* savannah woodland is found at the centre and north of EA. The WA, which extends up to the edges of Lake Victoria, is a region of wooded grassland and woodlands dominated by *Acacia* species interspersed with open grasslands (Herlocker, 1976).

Field sampling

The ostrich is the largest flightless, herbivorous bird, found in a variety of open habitat types (Brown, Urban & Newman, 1982). They mainly feed on seeds and other plant matter; occasionally they also eat animals such as locusts (Brown *et al.*, 1982). There are approximately 6000 ostriches in Serengeti National Park (data from Frankfurt Zoological Society in Serengeti). Using standardized sampling procedures, we systematically recorded all sighted ostriches, nests, broods, singletons and predators (i.e. lions and hyenas). Each encounter with a nest, singleton or brood was considered as a single observation, whereas predators and ostriches are sometimes observed in dense vegetation and hence some individuals of a herd/group may have been overlooked. Therefore we equalled each observation of predators and ostrichers, regardless of number of individuals, to one for use in the analyses.

During each breeding season (i.e. from July to October, which sometimes extended to December), we searched for nests throughout the study area. Nests were defined as scraped shallow pits with egg(s), whereas singletons were eggs that were randomly laid directly on the ground without any indication of scrapes in the vicinity. Different methods were used to find the nests (Table 1), however, all singletons were encountered by chance. Once a nest or singleton was discovered, GPS position was taken to allow subsequent visits. Visits were kept brief and as infrequent as possible in order to minimize the risk of investigators inducing nest desertion. We visited nests and singletons once a week, so as to minimize the disturbance for laying and incubating birds. Each time we visited the nests, we recorded the total number of eggs.

We indirectly estimated the laying date on the basis of number of eggs in the nest. The assumption was that the first three eggs were laid by the major female, each egg after every second day, before the minor females started laying (Bertram, 1992). From the total number of eggs in the nest, we calculated the probable laying date by back-dating considering the first five days that the major female laid her first three eggs.

Data analyses

We used Kolmogorov–Smirnov tests to investigate if our data deviated from normality. The laying dates were found to be normally distributed, and therefore we used Student's *t*-tests for comparison of laying dates between the two areas. Because of small sample size in WA, we used Mann-Whitney *U*-tests for comparison of clutch size between the areas at the onset of incubation. Pearson Chi-square tests were used to compare the frequency of predators and that of the ostriches, nests, singletons and broods between WA and EA. Between year comparisons were not possible because of low sample sizes. However, there is no reason that number of individuals of these sedentary animals should change much between two years only, and therefore we lumped the data for further analyses. When investigating possible differences in laying dates between EA and WA, analysis was made using data collected in 2006 only, due to a small sample size with respect to laying dates from 2005. SPSS 14.0 (SPSS, 2005) was used for statistical analyses. All values are presented as mean ± standard deviation ($\bar{X} \pm SD$), and all analyses are two-tailed.

Results

Laying date and clutch size

During the study period, we obtained a total of 57 nests and 37 singletons. In 2005, there was a total of 33 nests (30 in EA and three in WA) and 21 singletons (twenty in EA and one in WA), whereas in 2006, there was a total of 24 nests (fourteen in EA and ten in WA) and sixteen singletons (ten in EA and six in WA) (Fig. 1). Mean ostrich laying date in 2006, was significantly earlier in WA (August 28 ± 21 days, n = 10) than in EA (September 17 ± 24 days, n = 12) (Student's *t*-test, $t = -2.05$, df = 20, $P = 0.05$), although this was not tested for the year 2005 because of lack of independence in the data (small sample size particularly in the WA). When considering the whole study area, the average clutch size was 25.9 ± 4.8 eggs (range = 20–38, n = 18) in the nests where laying had ended and incubation started. In WA, the clutch size was 26.8 ± 3.0 eggs (range = 23–30, n = 4), whereas in EA, it was 25.6 ± 5.2 eggs (range = 20–38, n = 14). The average clutch size in the two areas was not statistically significantly different (Mann–Whitney $U = 19.5$, $Z = -0.91$, $P = 0.37$).

Table 2 Relationship between frequency of observations of ostriches, predators, nests, singletons and broods

Relationship	EA	WA	*P*
Ostrich/Nest			
Ostrich	40.0 (1765)	55.4 (720)	**
Nest	1 (44)	1 (13)	
Ostrich/Predators			
Ostrich	12.0 (1765)	12.6 (720)	**
Predators	1 (147)	1 (57)	
Predator/Nest			
Predator	3.3 (147)	4.4 (57)	**
Nest	1 (44)	1 (13)	
Nest/Singleton			
Nest	1.5 (44)	1.9 (13	**
Singleton	1 (30)	1 (7)	
Predator/Singleton			
Predator	4.9 (147)	8.1 (57)	**
Singleton	1 (30)	1 (7)	
Predator/Brood			
Predator	36.8 (147)	5.2 (47)	*
Brood	1 (4)	1 (9)	
Nest/Brood			
Nest	11.0 (44)	1.4 (13)	*
Brood	1 (4)	1 (9	
Ostrich/Brood			
Ostrich	441.4 (1765)	80.0 (720)	*
Brood	1 (4)	1 (9)	

Numbers indicate how many observations of each item in the relationship, numbers in the parentheses indicate total number of observations of each item.
**$P > 0.05$; *$P < 0.05$ (Chi square test).

Relationship between frequency of observations of predators, ostriches, nests, singletons and broods

There were 40.0 ostrich observations (n = 1765) per nest (n = 44) in EA, compared with 55.4 ostrich observations (n = 720) per nest (n = 13) in WA (Table 2). However, the difference was not statistically significant (Pearson Chi square test, $\chi^2 = 1.03$, df = 1, $P = 0.31$), indicating comparable breeding densities in the two areas.

There were 12.0 ostrich observations (n = 1765) per predator (n = 147) in EA, compared with 12.6 ostriches (n = 720) per predator (n = 57) in WA. This difference was not statistically significant (Pearson Chi square test, $\chi^2 = 0.10$, df = 1, $P = 0.75$). Furthermore, there were 3.3 predators (n = 147) per nest (n = 44) in EA, compared with 4.4 predators (n = 57) per nest (n = 13) in WA. Again, this difference was not statistically significant

(Pearson Chi square test, $\chi^2 = 0.60$, df = 1, $P = 0.44$). These results suggest that the predation pressure was equally high in the two areas.

There were 1.5 nests (n = 44) per singleton (n = 30) in EA, compared with 1.9 nests (n = 13) per singleton (n = 7) in WA, a difference that was not statistically significant (Pearson Chi square test, $\chi^2 = 0.2$, df = 1, $P = 0.65$). Furthermore, there were 4.9 predators (n = 147) per singleton (n = 30) in EA, compared with 8.1 predators (n = 57) per singleton (n = 7) in WA. Again, this difference was not statistically significant (Pearson Chi square test, $\chi^2 = 1.31$, df = 1, $P = 0.25$). These results indicate that loss of nests during egg stage did not vary between EA and WA.

There were 36.8 predators (n = 147) per brood (n = 4) in EA, compared with 5.2 predators (n = 47) per brood (n = 9) in WA, a difference that was statistically significant (Pearson Chi square test, $\chi^2 = 12.50$, df = 1, $P < 0.001$). Furthermore, there were 11.0 nests (n = 44) per brood (n = 4) in EA, compared with 1.4 nests (n = 13) per brood (n = 9) in WA. The difference between areas was statistically significant (Pearson Chi square test, $\chi^2 = 10.59$, df = 1, $P = 0.001$). Finally, there were 441.4 ostriches (n = 1765) per brood (n = 4) in EA, compared with 80.0 ostriches (n = 720) per brood (n = 9) in WA and the difference between areas was statistically significant (Pearson Chi square test, $\chi^2 = 10.14$, df = 1, $P = 0.001$). All these results indicate a significantly lower reproductive success among ostriches in EA than in WA.

Fate of the nests

None of the observed nests in any of the areas reached hatching stage, and predation accounted for more than 80% of nest destruction (total n = 47). In the WA, eleven out of thirteen nests (84.6%) were predated, while in EA, the corresponding number was 36 out of 44 nests (81.8%) (Fig. 2). Some of the nests were partially predated and thereafter abandoned, whereas other nests were just abandoned for unknown reasons. In WA, one nest (7.7%) was abandoned whereas in EA, eight nests (18.2%) were abandoned. Only one nest (7.7%) in WA had unknown fate because we left it intact after completion of the field work. Generally, all singletons were abandoned though

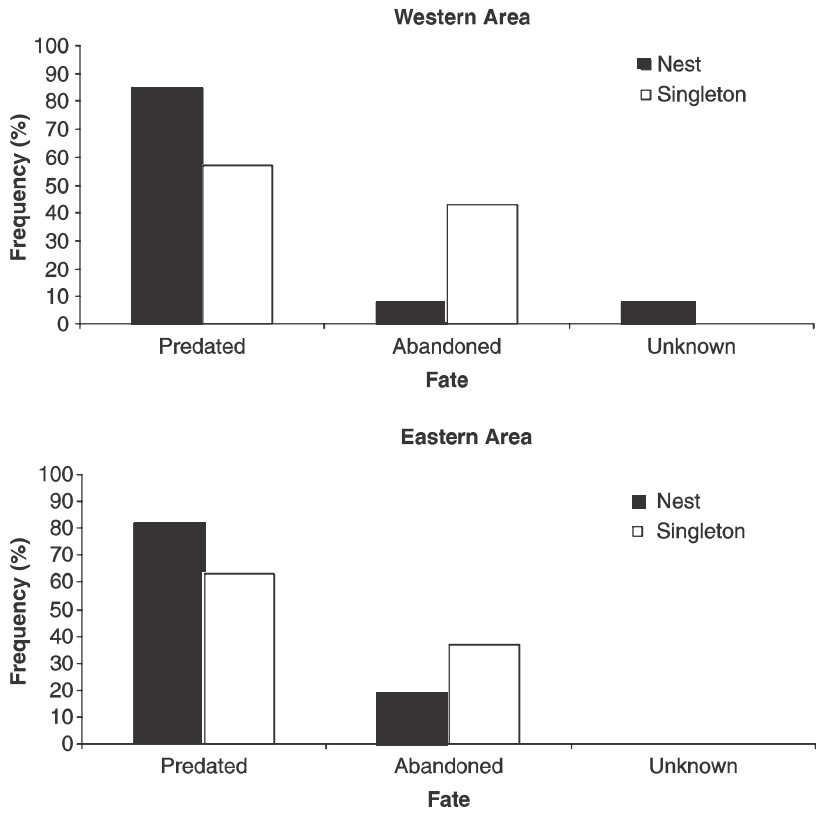


Fig 2 Fate of nests and singletons during the ostrich breeding season in the western and eastern areas of the Serengeti National Park

some of them were later predated. In WA, four singletons (57.1%) were predated whereas nineteen singletons (63.3%) were predated in EA (Fig. 2).

Discussion

Generally ostriches breed during the dry season. In East Africa, and Serengeti in particular, ostriches mainly lay between July and October (Bertram, 1978, 1992; Brown & Britton, 1980). However, we also found nests being initiated until December. Sauer & Sauer (1966) found that in the arid areas of Namibia, the overall peak in reproductive activity was just before the main rainy season of August to November. Smit (1963) recorded that the domesticated birds in the South African Little Karroo region mainly were laying from June or July until September, but some eggs appeared in nearly all months. Hurxthal (1979) recorded *massaicus* ostriches breeding mainly from September to December with a peak in early November. The laying period reported by Jarvis *et al.* (1985) for South African ostrich in Zimbabwe was mainly from July to December or early January.

Our results indicate that ostriches started laying significantly earlier in the WA than in the EA suggesting that the altitude and rainfall gradient associated with the gradient of the grassland growing season, have an influence on ostrich breeding in the ecosystem. The grassland growing season, as measured by the occurrence of live forage biomass, increases towards the northwestern area (McNaughton, 1985; McNaughton & Banyikwa, 1995). When food supplies have been lastingly rich in the area, the main ostrich reproductive period builds up gradually, and all this occur towards the end of the dry season and long before the first rainfall (Sauer & Sauer, 1966). As there is a strong selection pressure to lay eggs at the proper time (Dunn, 2004; Visser & Both, 2005; Drent, 2006), individuals need to synchronize hatching with seasonal events such that the period of maximal demand of the young coincides with the food peak (van Noordwijk, McCleery & Perrins, 1995). Ostriches are opportunistic breeders, laying soon after a localized flush of green following rains (Sauer & Sauer, 1966). This greener vegetation reappears earlier in the western area than in the eastern area because of short rains (that may fail in the eastern area) in the late dry season. Most individual females in areas richer in food than others, will tend to breed earlier than others in successive seasons each year (Perrins, 1970). The most important factor which build up the female's reproductive potential and trigger her reproductive activities at the right time is the availability of sufficient food over a length of time (Sauer & Sauer, 1966). However, birds must not only collect specific nutrients for egg formation, but also do so over a brief period when food may not be plenty (Perrins, 1970, 1996).

In the present study, the average clutch size ranged from 20–38 (n = 18), which is more or less similar to the clutch size reported by Bertram (1978) for *massaicus* ostrich in Tsavo National Park that varied between twenty and 36 eggs. Hurxthal (1979) rerecorded average clutch sizes for *massaicus* in two years as 35.5 (n = 13) and 47.0 (n = 14). However, there were cases where a number of singletons were laid outside the nests. Occurrence of these singletons might have been attributed to major female reluctance to allow minor females to lay additional eggs after the incubation start or nest predation. We did not witness a major female denying a minor female from laying on her nest, although Bertram (1992) observed major females being reluctant to leave their nests after the start of incubation, whereas Sauer & Sauer (1966) emphasized that singletons could be a result of exhaustive runs from sources of danger or by hens lacking a mate. However, the ratio of predators to singletons and predators to nests did not differ significantly between the two areas suggesting that loss of nests due to predators that might have led to the occurrence of singletons did not vary between the areas.

Although ostriches show defence behaviour to protect their nests (Bertram, 1992; F. Magige *et al.*, pers. observ.), nest predation was extremely high in the SNP; $\sim$ 80% of the nests were predated. With respect to the high nest predation, it seems to make sense that eggs of different females were laid in the same nests. Probably ostriches do lay in as many nests as possible to reduce the probability of complete nest destruction. Female ostriches never lay in a previously predated nest, and therefore it is reasonable to conclude that a female on the urge to lay an egg but finds her nest predated or partially predated will lay a singleton egg outside the nest or potentially into the nest of another major female. These singletons were commonly found randomly scattered not even close to the already established nests. This situation is different from the one where eggs are ejected and scattered outside the nests some few meters away at the onset of incubation when excessive eggs are laid communally than can be incubated (see also Sauer & Sauer, 1966; Bertram, 1992; Kimwele & Graves, 2003). In addition, all singletons together with some nests

were abandoned, probably because of the partial predation of nests in particular, or spread of eggs by golden jackals (*Canis aureus*) or black backed jackals (*C. mesomelas*), which mainly played around with eggs but could not crush them (F. Magige *et al.*, pers. observ.). However, we have no evidence that nest desertions were caused by our frequent visitations. In common with ostriches, rheas (*Rhea americana*)) also have high rates of nest desertion during the laying stage (Fernandez & Reboreda, 2000). Studies on rheas have shown a high rate of nest desertion commonly associated with egg predation particularly in the early laying stages (Fernandez & Reboreda, 2000, 2002; Sales, 2006). The difference between rheas and ostriches is that most cases of nest desertion in rheas were associated with the loss of a few eggs and therefore the male had the possibility of continuing incubation (Fernandez & Reboreda, 2000) whereas in ostriches nest desertion was the result of nest destruction (desertion was compulsory).

There was no significant difference between the ratio of ostriches to nests between WA and EA, indicating similar breeding densities. However, fewer nests were obtained in the WA, which might be attributed to the difficulty of discovering nests in the densely vegetated western corridor, suggesting that visibility of eggs was a major factor in their discovery. Therefore, nest density in WA could potentially be significantly higher than the one observed. The ratio of ostriches, predators, nests and singletons to broods was significantly different between the two areas with high frequency of broods in the western area indicating that the reproductive success was quite high in the western area. The results obtained in this study seem to indicate an existence of metapopulation dynamics in the Serengeti ecosystem, where the western area can be regarded as a 'source' and eastern area as a 'sink' population. Source–sink dynamics are used to describe how variation in habitat quality, competitors or predators may affect the population growth or decline of organisms in space (Dias, 1996; Hanski, 1999). Further studies for longer time-periods are therefore required to reveal in more detail the existence of ostrich metapopulations in the Serengeti ecosystem.

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