

Effects of Environmental Enrichment on Ostrich Behaviours

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Abstract

This study was aimed to investigate the behavioural differences of ostrich (*Struthio camelus*) breeders reared under environmental enrichment with natural vegetation in farm conditions. The effect of enriched environment with vegetation on eating, drinking, foraging, pecking, defecation, walking, running, alert, standing, sitting, sleeping, dust bathing, preening, head shake, thermoregulation, kantel, mating, laying, threat and fight behaviours of ostriches were found similar ($P > 0.05$). The ratio of boom, courtship and displace behaviours were found higher in enriched than in gravel floor ($P=0.050$; $P=0.028$ and $P=0.001$). The foraging, dust bathing, boom, laying and displace behaviours of ostriches were affected by gender ($P=0.029$, $P=0.040$, $P=0.050$, $P=0.025$ and $P=0.001$). The eating, foraging, standing, sitting, dust bathing and laying behaviours of ostriches were affected by time of day ($P=0.010$, $P=0.023$, $P=0.049$, $P=0.026$, $P=0.018$ and $P=0.009$). There was a significant interaction of enriched environment and gender effect on eating, standing, boom and displace behaviours of ostriches ($P=0.047$, $P=0.031$, $P=0.050$ and $P=0.001$). The pecking and standing behaviours of ostriches were affected by enriched environment and time of day interaction ($P=0.027$ and $P=0.023$). As a conclusion, enriched environment with natural vegetation in paddock only affected ostriches' courtship behaviours, also affected male and female eating and standing behaviours differently.

Introduction

The ostrich is the largest and heaviest living bird (150 kg and 2.50 m in height), and it is a member of the ratite family of flightless runners. The ostrich is an African native bird that lives in semiarid plains and woodlands (Deeming, 1999). In the 1880s, commercial ostrich production began in the Africa Oudtshoorn region for feather manufacture. In the years that followed, manufacturing of its skin, eggs, and meat spread throughout the world (Şahan et al., 2000).

The definition of behaviour is a specific response to environmental variables. Ostriches in their native habitat exhibit unique behavioural patterns that allow them to adapt to their surroundings. However, in captivity, behavioural tendencies may alter due to environmental variables (Hambali et al., 2015). Ostriches, raised in farm circumstances that differ from

their natural environments, are subjected to extreme stress, which leads to yield losses (Amado et al., 2011; Muvhali, 2018).

Welfare problems are commonly found in intensive farming systems. It has been recommended to create environment that are interesting and enriching in order to lessen the severity of welfare concerns. Environmental enrichment is the process of enhancing an animal's surroundings in captivity so that it has more chances for behaviour and has better biological function (Riber et al., 2018). According to Newberry (1995), environmental enrichment should increase the animal's ability to cope with behavioural and physiological challenges. And, according to Van de Weerd & Day (2009) the successful enrichment must fulfill as follows; it should promote species-specific

behaviour, uphold or enhance health levels, enhance the production system's profitability, and be useful to use. Materials such as peck objects, perches, barriers, bales, and materials that stimulate foraging and dust bathing behaviours, outdoor access areas (free-range systems etc.), outdoor natural or artificial cover, sheds, and shades (bushes, trees etc.) are used for environmental enrichment in layer and broiler rearing (Riber et al., 2018).

On farms all around the world, ostrich farming is done and propagated using a variety of different, sometimes contradictory ways. The majority of ostriches in South Africa are kept on steppe soil or in semi-desert areas with sparse vegetation, and they are given either farm products or commercially produced feed (Kistner, 2019). Most of the world ostriches are kept in paddocks in intensive farming systems which is different from bird's natural environment (Cooper, 2000). Although there were some studies about environmental enrichment with vegetation on behaviours of broilers and layers (Jones et al., 2007; Almeida et al., 2012; Dal Bosco et al., 2014), there is limited published scientific research about environmental enrichment on behaviours of ostriches and rheas (Christensen & Nielsen, 2004; Lima et al. 2019). The aim of the study was to investigate the effects of environmental enrichment with vegetation on behaviour of male and female ostrich (*Struthio camelus*) breeders reared under intensive farming system to provide the useful information for improved management.

Materials and Methods

The study was conducted on 4 female and 2 male ostrich (*Struthio camelus*) breeder at the Bursa Uludağ University Research and Application Farm unit. Ostriches reared in trio; 1 male and 2 female in one paddock. One paddock contained 1000 m² floor area, 5 m² shelter area, 3 m high wire fence, feeders, drinkers and grass feeders. The paddock floor was covered with soil and gravel. Natural vegetation (such as; *Silybum marianum*, *Rumex ssp.*, *Malvae sylvestris*, *Xanthium strumarium*, *Bromus tectorum*, *Cynodon dactylon*) grows in paddocks over time and the vegetation routinely cut. For this study, one paddock floor vegetation left uncut and left to its natural state for one year period. Two similar sized paddocks used in the study one paddock was used as an environmental enrichment with natural vegetation group, the other paddock was used as gravel floor group (Control). All ostriches were fed with 2 kg/bird per day of a pellet ostrich breeder feed (18% CP, 2450 kcal ME) and 500 g/bird per day alfalfa. Water was supplied ad libitum. Natural sun lighting was used.

Behaviour recordings were taken with binoculars and naked eye by one trained person. The observer waits for before recording the behaviours for one hour. A scan sampling method was used to monitor the behaviours of birds as described by Mitlöhner et al. (2001). For each bird, behavioural observations were

recorded at 10 min intervals for 1 h in morning, noon and evening (at 09:00; 13:00 and 17:00; respectively). All the birds were monitored for six days. The individual behaviours were recorded as eating, drinking, foraging, defecation, walking, running, alert, pecking, standing, sitting, sleeping, dust bathing, preening, head shake, thermoregulation, boom, courtship, kanteel, mating, laying, threat, displace, fight, escape described in Stewart (1994) and Amado et al. (2011).

The data was analyzed using PROC MIXED procedure of Statistical Analysis System (SAS, 2019). The model included the fixed effects of gender (male and female), environment (gravel and vegetation floor), and time of day (morning, noon and evening), replicate and all interactions. Individual bird number within each replicate was entered as a random factor. Data were presented as mean \pm standard error (SE) in all the tables. Differences were considered significant at $P \leq 0.05$ and the statistical difference at $P < 0.10$ was described as a tendency. The statistical model was as follows:

$$Y_{ij} = \mu + a_i + b_j + c_k + (ab)_{ij} + (ac)_{ik} + (abc)_{ijk} + \epsilon_{ijk}$$

where Y_{ij} = μ^{th} observation value, μ = expected mean of the population, a_i = i. enrichment effect (i=gravel and vegetation), b_j = j. gender effect (j= male and female), c_k = k. time of day effect (k= morning, noon and evening), $(ab)_{ij}$ = ij. enrichment and gender interaction effect, $(ac)_{ik}$ = ik. enrichment and time of day interaction effect, $(abc)_{ijk}$ = ijk. enrichment and gender and time of day interaction effect, ϵ_{ijk} = residual error.

Results

The effect of enriched environment with natural vegetation on ingestive behaviours of ostriches were given in Table 1. The effect of enriched environment on eating, drinking, foraging, pecking and defecation behaviour was not significant ($P > 0.05$). The gender of ostrich effected foraging behaviour, and higher foraging behaviour was observed in females ($P=0.029$). The difference in eating, drinking, pecking and defecation behaviour of male and female ostriches were similar during the study ($P > 0.05$). The eating and foraging behaviours of ostriches were affected by time of day ($P=0.01$ and $P=0.023$, respectively). The lowest eating behaviour was observed at noon, and the highest foraging behaviour was found in the morning. The drinking behaviour tends to be higher in the morning and at noon ($P=0.055$). The pecking and defecation behaviour was not changed during the day ($P > 0.05$). The effect of enriched environment with vegetation and gender interaction on eating behaviour of ostrich was found significant ($P = 0.047$), lowest eating behaviour was found in males in enrichment group. The effect of enriched environment and gender interaction on drinking, foraging, pecking and defecation behaviours of ostriches were not significant ($P > 0.05$). The effect of enriched environment and time of day interaction on ingestive behaviours of ostriches were found not significant ($P > 0.05$); except pecking behaviour ($P=0.027$). The higher pecking behaviour was observed during the evening in gravel group and during the

morning in enrichment group. The three-way interaction effect of enriched environment, gender and time of day on ingestive behaviours of ostrich was not significant ($P > 0.05$).

The effects of enriched environment with natural vegetation on locomotor and resting behaviours of ostriches were given in Table 2. The effect of enriched environment on walking, running, alert, standing, sitting, sleeping behaviours of ostrich was not significant ($P > 0.05$). The gender of ostrich tends to be affected alert and standing behaviour, and higher alert and standing behaviour was observed in males ($P=0.059$ and $P=0.079$). The difference in walking, running, sitting and sleeping behaviour of male and female ostriches were not significant ($P > 0.05$). The standing and sitting behaviours of ostriches were affected by time of day ($P=0.49$ and $P=0.026$, respectively). The lowest standing and highest sitting behaviour were observed at noon and evening. The walking, running, alert and sleeping behaviour of ostriches were not changed during the day ($P > 0.05$). The effect of enriched environment and gender interaction on standing behaviour of ostriches was found significant ($P = 0.031$), lowest standing behaviour was found in females in enrichment group. The effect of enriched environment and gender interaction on walking, running, alert, sitting and sleeping behaviours of ostriches were not significant ($P > 0.05$). The effect of enriched environment and time of day interaction on standing behaviour of ostriches was found significant ($P = 0.023$) and lowest standing behaviour was observed in gravel group during the evening. The three-way interaction effect of enriched environment, gender and time of day on locomotor and resting behaviours of ostrich was not significant ($P > 0.05$).

The effects of enriched environment with natural vegetation on comfort behaviours of ostriches were given in Table 3. The effect of enriched environment on dust bathing, preening, head shake and thermoregulation behaviours of ostrich was not significant ($P > 0.05$). The gender of ostrich effected dust bathing behaviour, and only females showed dustbathing behaviour during to study ($P=0.040$). The difference in preening, head shake and thermoregulation behaviour of male and female ostriches were not significant ($P > 0.05$). The dustbathing behaviour was observed only during the evening ($P=0.018$). The preening, head shake and thermoregulation behaviour of ostriches were not changed during the day ($P > 0.05$). The effect of enriched environment and gender interaction; and enriched environment and time of day interaction on comfort behaviours of ostriches were not significant ($P > 0.05$). The three-way interaction effect of enriched environment, gender and time of day on comfort behaviours of ostrich was not significant ($P > 0.05$); except for dust bathing behaviour ($P=0.038$).

The effects of enriched environment with natural vegetation on reproduction behaviours of ostriches were given in Table 4. The boom and courtship behaviours were affected by enrichment, and higher

boom and courtship behaviour were observed in enrichment group ($P=0.050$ and $P=0.028$, respectively). However, the effect of enriched environment on kanel, mating and laying behaviours were similar ($P > 0.05$). Only male ostrich showed boom behaviour ($P=0.050$) and only females were showed laying behaviour ($P=0.025$). The courtship, kanel and mating behaviours did not change by the gender of ostrich ($P > 0.05$). The effect of time of day on reproduction behaviours of ostriches were found not significant ($P > 0.05$); except for laying behaviour ($P=0.009$). Laying was observed only evening during to study ($P=0.009$). The effect of enriched environment and gender interaction; and enriched environment and time of day interaction on reproduction behaviours of ostriches were not significant ($P > 0.05$). The three-way interaction effect of enriched environment, gender and time of day on reproduction behaviours of ostrich was not significant ($P > 0.05$); except for laying behaviour ($P=0.012$).

The effects of enriched environment with natural vegetation on aggressive behaviours of ostrich were given in Table 5. The effect of enriched environment, gender and time of day on threat, fight and escape behaviours of ostriches were not significant ($P > 0.05$). The effect of enriched environment and gender interaction; and enriched environment and time of day interaction on aggressive behaviours of ostriches were not significant ($P > 0.05$). However, displace behaviour was only observed in females in enriched with vegetation group ($P= 0.001$). The three-way interaction effect of enriched environment, gender and time of day on aggressive behaviours of ostrich was not significant ($P > 0.05$); except for escape and threat behaviours ($P=0.044$ and $P=0.064$).

The three-way interaction effect of enriched environment, gender and time of day on ostrich behaviours were given in Table 6. The dust bathing, laying and escape behaviours of ostriches were affected by enriched environment, gender and time of day interaction ($P=0.038$, $P=0.012$, and $P=0.044$, respectively). And the effect of triple interaction on threat behaviour tends to be significant ($P=0.064$). There was a high frequency of dust bathing and laying behaviour in both floor group for females during the evening hours. There was a high frequency of escape behaviour for females during to evening hours in enriched group. The highest threat behaviour frequency was observed for males during to morning hours in control group.

Discussion

In the study ostriches spent more time with eating, foraging, walking and standing in all investigated behaviours. Thus, these findings are corroborated by earlier researches from Ahmed & Salih (2012) and Mutiga et al. (2016).

The physical components of the enclosure design (such as shelters, plants, rocks, and pools), transient objects (such as food items, balls, and branches), and non-object stimuli (such as sounds,

climatic and lighting variables) can all be used to enrichment of captive birds. All of these categories have the potential to elicit actions brought on by the stimulation of one or more senses, and their combination can satisfy welfare-related requirements (King, 1999). There were some studies about environmental enrichment with vegetation on behaviours of poultry. Thus, in their environmental enrichment study; Stadig et al. (2017) found that Sasso T451 broilers showed generally higher activity levels and use of the area with dense vegetation (short rotation coppice) compared to grassland with artificial shelters. When Dal Bosco et al. (2014) compared the ecologically enriched range (with sorghum grass strips or mature olive trees) to the control range, they reported that enrichment encouraged free-range broilers to go outside. Also, Dawkins et al. (2003) discovered that the number of Sherwood Whites birds ranging outside was positively connected with the amount of grass, trees and bushes cover offered.

The mature tree cover in free range system effected the behaviours of the female Ross 308 broilers (Jones et al., 2007). Ostriches in the wild eat grass, berries, succulents, seeds, and tree and shrubs' leaves (Sambraus, 1994; Deeming & Bubier, 1999). Thus, access to outdoor spaces with different types of nutritious vegetation (grass/clover or chicory) boosted foraging activity in broilers, according to Almeida et al. (2012). However, in our study, the environmental enrichment with vegetation did not affect eating, drinking, foraging, pecking and defecation behaviour of ostriches. This might be due to the use of natural vegetation for environmental enrichment that did not have much nutritional value. Similar to our findings, Carvalho et al. (2017) reported there were no differences on feeding and biting behaviour of cockatiels in captivity when collard green stalks used as environmental enrichment.

The gender of ostrich effected foraging behaviour, and higher foraging behaviour was observed in females. Similar to our findings Deeming (1998) reported that females had higher foraging behaviour than males. However, there was no gender difference on eating, drinking, pecking and defecation behaviour of ostriches. These findings supported by Bertram (1992) and Mutiga et al. (2016) who found that gender did not affect feeding behaviour time budget in ostriches.

The time of day affected eating and foraging behaviours, and not affected pecking and defecation behaviours of ostriches. The higher eating behaviour was observed in the morning and evening, and the highest foraging behaviour was observed during morning. Thus, Amado et al. (2011), Ahmed & Salih (2012) and Mutiga et al. (2016) found that feed consumption was higher in the morning and in the afternoon. In reality, birds may restrict their feed consumption in order to avoid the internal heat rise caused by digestion during the warmer hours of the day. The drinking behaviour tends to be higher in the morning and at noon. But Amado et al. (2011) and

Ahmed & Salih (2012) reported that drinking behaviour was higher in the afternoon.

Food as environmental enrichment should be encouraged due to its favorable impacts on animal welfare; substantial variations in walking, foraging, eating feces, and pacing behaviours of male Greater rheas in zoo with enrichment with fruits were identified (Lima et al. 2019). Christensen and Nielsen (2004) used sand-covered areas with barren or enriched with cabbage, coniferous cones, and sticks and they reported that environmental enrichment improves the welfare of chicks by increasing exploration and decreasing pecking without compromising food consumption in commercially reared ostrich chicks. However, in the study lowest eating behaviour was found in males in enrichment group. But there was no interaction between enrichment and gender on drinking, foraging, pecking and defecation behaviours of ostriches. Also, there was no interaction between enrichment and time of day on ingestive behaviours of ostriches; except for pecking behaviour. The higher pecking behaviour was observed in the evening in gravel group and in morning in enrichment group.

Lubac & Mirabito (2001) and Mirabito et al. (2001) found that shaded regions under established trees prompted the broilers to lie down, whereas standing was the prevalent behaviour in non-shaded areas. Also, according to Csermely et al. (2007), ostriches kept in captivity exhibit stood-still behaviour more often because of frustration or a constrained environment. Another study, Carvalho et al. (2017) reported that collard green stalks when used as environmental enrichment, decreased sleep behaviour in cockatiels at captivity. However, in the study, the environmental enrichment with vegetation did not affect walking, running, alert, standing, sitting, sleeping behaviour of ostriches. This may be because the natural vegetation used for environmental enrichment did not contain plants or trees that were too tall or large to hinder the movements of birds. Similar to our results, Carvalho et al. (2017) also reported that collard green stalks were used as environmental enrichment of cockatiels in captivity, but its use did not significantly affect locomotion and resting behaviour of birds.

The gender of ostrich tends to be affected alert and standing behaviour, and higher alert and standing behaviour was observed in males. This could be because females were always busy while performing behaviours like foraging. Thus, males exhibited a proportionally higher percentage of time in the alert state than females, according to Mutiga et al. (2016). In the study there was no gender difference on walking, running, sitting and sleeping behaviour of ostriches. But males spent more time with resting than females, according to Mutiga et al. (2016).

The time of day affected standing and sitting behaviours, and was not affected walking, running, alert and sleeping behaviours of ostriches. The lowest standing and highest sitting behaviour were observed at noon and evening. There were some studies reported that ostriches stand still more in the morning (Amado et

al., 2011; Ahmed & Salih, 2012). Also, in accordance with our findings Mutiga et al. (2016) discovered that daytime had no effect on alertness behaviour of ostriches.

The lowest standing behaviour was found in females in enrichment group. However, there was no interaction between enrichment and gender on walking, running, alert, sitting and sleeping behaviours of ostriches. Also, there was no interaction between enrichment and time of day on walking, running, alert, sitting and sleeping behaviours of ostriches; except for standing behaviour. The lowest standing behaviour was observed in gravel group during the evening.

For thermoregulation, ostriches tend to breathe frequently (panting) to cope with the heat during hot hours (Maloney, 2008). In the study, the environmental enrichment with vegetation did not affect dust bathing, preening, head shake and thermoregulation behaviour of ostriches. In accordance with our results, Carvalho et al. (2017) reported that collard green stalks were used as environmental enrichment of cockatiels in captivity, but its use did not significantly affect body surface temperature and maintenance behaviour of birds.

Dust bathing and preening is a crucial behaviour for ostriches to maintain optimum feather health. The gender of ostrich effected dust bathing behaviour, and only females showed dustbathing behaviour during to study. However, there was no gender difference on preening, head shake and thermoregulation behaviour of ostriches. But males spend more time preening than females, according to Mutiga et al. (2016).

The time of day effected dustbathing behaviours, and was not affected preening, head shake and thermoregulation behaviours of ostriches. However, ostriches preening more frequently in the morning than in the afternoon (Deeming & Bubier, 1999). The dustbathing behaviour was observed only in the evening. Our results were similar with Amado et al. (2011) and Ahmed & Salih (2012) who found that dust bathing was observed generally late hours of the day. High temperatures during the day may have contributed to a decrease in birds' activity. There was no interaction between enrichment and gender; and also enrichment and time of day on comfort behaviours of ostriches.

In our study, the environmental enrichment with vegetation effected boom and courtship behaviour of ostriches and higher boom and courtship behaviour were observed in the enrichment group. Thus, Cooper et al. (2010) show that ostriches are opportunistic breeders whose reproduction is reliant on the quality and quantity of feed. However, the environmental enrichment with vegetation did not affect kantel, mating and laying behaviours of ostriches.

The gender of ostrich affected boom and laying behaviour. Thus, according to Aravinth & Selvan (2015) and Mukhtar et al. (2017) rhythmic booming sound signals the onset of mating in the male and helps attract female attention for courtship. Additionally, males do

the "kantel" breeding dance to attract females for reproduction in ostriches. However, there was no gender difference on courtship, kantel and mating behaviours of ostriches.

Mating activity in ostriches was seen throughout the morning hours, according to Sambraus (1994). But, in our study, time of day was only affected laying behaviour among all of the reproduction behaviours. Laying was observed only in the evening during study. Supporting our findings Brassó et al. (2020) reported that ostrich eggs were typically laid in the afternoon or early evening. There was no interaction between enrichment and gender; and also enrichment and time of day on reproduction behaviours of ostriches.

The use of strong methods like environmental enrichment, imprinting, foster parenting, and regular handling can help reduce stress and address many of the constraints put on behaviour due to stress in domestic chicks (Jones & Waddington, 1993). However, in the study, the environmental enrichment with vegetation effected displace behaviour, but enrichment did not affect threat, fight and escape behaviour of ostriches.

The gender of ostrich affected displace behaviour, but did not affect threat, fight and escape behaviour of ostriches. The time of day did not affect aggressive behaviours of ostriches. However, according to Fericean et al. (2022), aggressive behaviours were higher in the morning than in the afternoon and at night. There was no interaction between enrichment and gender; and also, enrichment and time of day on aggressive behaviours of ostriches; except for displace behaviour. The displace behaviour was only observed in females in the enriched with vegetation group.

Conclusion

Due to the stress caused by adverse environmental conditions, ostriches grown on crowded farms begin to exhibit abnormal behaviours (Şahan et al., 2000). Thus, Kock (1996a, 1996b), giving captive ostriches access to a more natural habitat appears to reduce their stress and agitation. Also, by enabling animals to express more of their species-specific behavioural repertoire and to accommodate a wider range of behavioural options, enriched environments can improve the welfare of animals (Van de Weerd & Day, 2009).

As a conclusion, ostriches are kept in paddocks in open areas in intensive farming systems. Vegetation growing in the paddocks is routinely cleaned and production is carried out in an environment different from bird's natural environment. Environmental enrichment with natural vegetation in paddock only affected ostriches' courtship behaviours, also effected male and female eating and standing behaviours differently. Through behavioural research, it is possible to identify animals' stressful conditions and enhance their wellbeing. Regarding environmental enhancement

and welfare in ostrich welfare issues, there is much to learn.

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Table 1. Effects of enriched environment on ingestive behaviours of ostriches (number of bouts/hour)

Enrichment		Eating	Drinking	Foraging	Pecking	Defecation
Floor	Gravel	0.13 ± 0.02	0.021 ± 0.01	0.10 ± 0.02	0.07 ± 0.02	0.03 ± 0.01
	Vegetation	0.11 ± 0.02	0.014 ± 0.01	0.09 ± 0.02	0.05 ± 0.02	0.01 ± 0.01
<i>P</i>		<i>0.593</i>	<i>0.453</i>	<i>0.728</i>	<i>0.344</i>	<i>0.220</i>
Gender	Male	0.12 ± 0.02	0.011 ± 0.01	0.07 ± 0.02 ^b	0.06 ± 0.01	0.01 ± 0.01
	Female	0.12 ± 0.02	0.024 ± 0.01	0.13 ± 0.02 ^a	0.07 ± 0.01	0.02 ± 0.01
<i>P</i>		<i>0.995</i>	<i>0.167</i>	<i>0.029</i>	<i>0.661</i>	<i>0.424</i>
Time of Day	MO	0.14 ± 0.02 ^a	0.035 ± 0.01 ^a	0.15 ± 0.02 ^a	0.08 ± 0.02	0.03 ± 0.01
	NO	0.06 ± 0.02 ^b	0.012 ± 0.01 ^{ab}	0.08 ± 0.02 ^b	0.05 ± 0.02	0.01 ± 0.01
	EV	0.16 ± 0.02 ^a	0.007 ± 0.01 ^b	0.07 ± 0.02 ^b	0.06 ± 0.02	0.02 ± 0.01
<i>P</i>		<i>0.010</i>	<i>0.055</i>	<i>0.023</i>	<i>0.628</i>	<i>0.471</i>
Floor X Gender						
G X Male		0.16 ± 0.03 ^a	0.017 ± 0.01	0.07 ± 0.02	0.07 ± 0.02	0.03 ± 0.01
G X Female		0.10 ± 0.03 ^{ab}	0.026 ± 0.01	0.13 ± 0.02	0.07 ± 0.02	0.02 ± 0.01
V X Male		0.08 ± 0.03 ^b	0.006 ± 0.01	0.07 ± 0.02	0.04 ± 0.02	-
V X Female		0.14 ± 0.03 ^a	0.023 ± 0.01	0.12 ± 0.02	0.06 ± 0.02	0.02 ± 0.01
<i>P</i>		<i>0.047</i>	<i>0.681</i>	<i>0.728</i>	<i>0.649</i>	<i>0.220</i>
Floor X Time of day						
G X MO		0.14 ± 0.03	0.05 ± 0.01	0.13 ± 0.03	0.05 ± 0.02 ^{ab}	0.03 ± 0.01
G X NO		0.07 ± 0.03	0.02 ± 0.01	0.11 ± 0.03	0.07 ± 0.02 ^{ab}	0.01 ± 0.01
G X EV		0.16 ± 0.03	-	0.07 ± 0.03	0.10 ± 0.02 ^a	0.04 ± 0.01
V X MO		0.14 ± 0.03	0.02 ± 0.01	0.14 ± 0.03	0.10 ± 0.02 ^a	0.03 ± 0.01
V X NO		0.04 ± 0.03	0.01 ± 0.01	0.06 ± 0.03	0.04 ± 0.02 ^{ab}	0.01 ± 0.01
V X EV		0.16 ± 0.03	0.02 ± 0.01	0.07 ± 0.03	0.02 ± 0.02 ^b	0.01 ± 0.01
<i>P</i>		<i>0.893</i>	<i>0.255</i>	<i>0.357</i>	<i>0.027</i>	<i>0.529</i>
Floor X Gender X Time of Day						
<i>P</i>		<i>0.696</i>	<i>0.903</i>	<i>0.999</i>	<i>0.606</i>	<i>0.821</i>

^{a,b}: The different superscripts on numbers represent a significant difference between them ($P < 0.05$).

Data are presented as LSM ± SEM.

G: Gravel, V: Vegetation, MO: Morning, NO: Noon, EV: Evening, - : No Behaviour.

Table 2. Effects of enriched environment on locomotor and resting behaviours of ostriches (number of bouts/hour)

Enrichment		Walking	Running	Alert	Standing	Sitting	Sleeping
Floor	Gravel	0.13 ± 0.02	0.003± 0.003	0.027 ± 0.01	0.10 ± 0.01	0.083 ± 0.01	0.018±0.01
	Vegetation	0.11 ± 0.02	0.006± 0.003	0.022 ± 0.01	0.09 ± 0.01	0.041 ± 0.01	0.006±0.01
<i>P</i>		<i>0.460</i>	<i>0.468</i>	<i>0.709</i>	<i>0.493</i>	<i>0.109</i>	<i>0.290</i>
Gender	Male	0.12 ± 0.02	0.006± 0.003	0.039 ± 0.01	0.11 ± 0.01	0.083 ± 0.01	0.014±0.01
	Female	0.11 ± 0.02	0.003± 0.003	0.010 ± 0.01	0.08 ± 0.01	0.041 ± 0.01	0.010±0.01
<i>P</i>		<i>0.854</i>	<i>0.611</i>	<i>0.059</i>	<i>0.079</i>	<i>0.101</i>	<i>0.707</i>
Time of Day	MO	0.10 ± 0.02	0.003± 0.004	0.037 ± 0.01	0.12 ± 0.02 ^a	0.015 ± 0.02 ^b	0.007±0.01
	NO	0.12 ± 0.02	0.011± 0.004	0.026 ± 0.01	0.10 ± 0.02 ^{ab}	0.103 ± 0.02 ^a	0.025±0.01
	EV	0.14 ± 0.02	-	0.011 ± 0.01	0.07 ± 0.02 ^b	0.069 ± 0.02 ^{ab}	0.004±0.01
<i>P</i>		<i>0.388</i>	<i>0.134</i>	<i>0.372</i>	<i>0.049</i>	<i>0.026</i>	<i>0.250</i>
Floor X Gender							
G X Male		0.13 ± 0.03	0.006± 0.004	0.044 ± 0.02	0.10 ± 0.02 ^{ab}	0.117 ± 0.03	0.022±0.01
G X Female		0.12 ± 0.03	-	0.010 ± 0.02	0.11 ± 0.02 ^a	0.049 ± 0.03	0.013±0.01
V X Male		0.11 ± 0.03	0.006± 0.004	0.033 ± 0.02	0.13 ± 0.02 ^a	0.050 ± 0.03	0.006±0.01
V X Female		0.11 ± 0.03	0.007± 0.004	0.010 ± 0.02	0.06 ± 0.02 ^b	0.033 ± 0.03	0.007±0.01
<i>P</i>		<i>0.789</i>	<i>0.468</i>	<i>0.709</i>	<i>0.031</i>	<i>0.324</i>	<i>0.641</i>
Floor X Time of day							
G X MO		0.11 ± 0.03	-	0.030 ± 0.02	0.16 ± 0.02 ^a	0.030 ± 0.03	-
G X NO		0.10 ± 0.03	0.008± 0.005	0.030 ± 0.02	0.11 ± 0.02 ^{ab}	0.143 ± 0.03	0.045±0.01
G X EV		0.17 ± 0.03	-	0.022 ± 0.02	0.04 ± 0.02 ^c	0.076 ± 0.03	0.008±0.01
V X MO		0.08 ± 0.03	0.004± 0.005	0.04 3± 0.02	0.09 ± 0.02 ^{bc}	-	0.013±0.01
V X NO		0.13 ± 0.03	0.013± 0.005	0.02 2± 0.02	0.09 ± 0.02 ^{bc}	0.063 ± 0.03	0.005±0.01
V X EV		0.11 ± 0.03	-	-	0.10 ± 0.02 ^{bc}	0.061 ± 0.03	-
<i>P</i>		<i>0.399</i>	<i>0.874</i>	<i>0.628</i>	<i>0.023</i>	<i>0.547</i>	<i>0.149</i>
FloorX Gender X Time of Day							
<i>P</i>		<i>0.385</i>	<i>0.630</i>	<i>0.924</i>	<i>0.474</i>	<i>0.595</i>	<i>0.985</i>

^{a,b,c}: The different superscripts on numbers represent a significant difference between them (*P*<0.05).

Data are presented as LSM ± SEM.

G: Gravel, V: Vegetation, MO: Morning, NO: Noon, EV: Evening, - : No Behaviour

Table 3. Effects of enriched environment on comfort behaviours of ostriches (number of bouts/hour)

Enrichment		Dust Bathing	Preening	Head Shake	Thermoregulation
Floor	Gravel	0.005 ± 0.00	0.07 ± 0.01	0.007 ± 0.01	0.06 ± 0.02
	Vegetation	0.005 ± 0.00	0.04 ± 0.01	0.016 ± 0.01	0.05 ± 0.02
		<i>1.000</i>	<i>0.259</i>	<i>0.220</i>	<i>0.564</i>
Gender	Male	-	0.05 ± 0.01	0.017 ± 0.01	0.05 ± 0.02
	Female	0.010 ± 0.00	0.06 ± 0.01	0.007 ± 0.01	0.06 ± 0.02
		<i>0.040</i>	<i>0.884</i>	<i>0.161</i>	<i>0.929</i>
Time of Day	MO	-	0.05 ± 0.02	0.013 ± 0.01	0.02 ± 0.03
	NO	-	0.07 ± 0.02	0.012 ± 0.01	0.08 ± 0.03
	EV	0.015 ± 0.00	0.04 ± 0.02	0.011 ± 0.01	0.06 ± 0.03
<i>P</i>		<i>0.018</i>	<i>0.397</i>	<i>0.980</i>	<i>0.317</i>
Floor X Gender					
	G X Male	-	0.08 ± 0.02	0.011 ± 0.01	0.06 ± 0.03
	G X Female	0.010 ± 0.01	0.05 ± 0.02	0.003 ± 0.01	0.07 ± 0.03
	V X Male	-	0.03 ± 0.02	0.022 ± 0.01	0.04 ± 0.03
	V X Female	0.010 ± 0.01	0.06 ± 0.02	0.010 ± 0.01	0.05 ± 0.03
<i>P</i>		<i>1.000</i>	<i>0.145</i>	<i>0.748</i>	<i>0.963</i>
Floor X Time of Day					
	G X MO	-	0.07 ± 0.02	0.008 ± 0.01	0.04 ± 0.04
	G X NO	-	0.09 ± 0.02	-	0.05 ± 0.04
	G X EV	0.015 ± 0.01	0.03 ± 0.02	0.013 ± 0.01	0.10 ± 0.04
	V X MO	-	0.02 ± 0.02	0.017 ± 0.01	0.01 ± 0.04
	V X NO	-	0.06 ± 0.02	0.023 ± 0.01	0.11 ± 0.04
	V X EV	0.015 ± 0.01	0.05 ± 0.02	0.008 ± 0.01	0.02 ± 0.04
<i>P</i>		<i>1.000</i>	<i>0.269</i>	<i>0.285</i>	<i>0.224</i>
FloorX Gender X Time of Day					
<i>P</i>		<i>0.038</i>	<i>0.796</i>	<i>0.407</i>	<i>0.963</i>

Data are presented as LSM ± SEM.

G: Gravel, V: Vegetation, MO: Morning, NO: Noon, EV: Evening, - : No Behaviour

Table 4. Effects of enriched environment on reproduction behaviours of ostriches (number of bouts/hour)

Enrichment		Boom	Courtship	Kantel	Mating	Laying
Floor	Gravel	-	0.010 ± 0.01 ^b	0.022 ± 0.01	0.009 ± 0.00	0.003 ± 0.00
	Vegetation	0.008 ± 0.00	0.036 ± 0.01 ^a	0.013 ± 0.01	0.009 ± 0.00	0.003 ± 0.00
<i>P</i>		0.050	0.028	0.462	1.000	1.000
Gender	Male	0.008 ± 0.00	0.025 ± 0.01	0.025 ± 0.01	0.011 ± 0.00	-
	Female	-	0.021 ± 0.01	0.010 ± 0.01	0.007 ± 0.00	0.007 ± 0.00
<i>P</i>		0.050	0.743	0.185	0.452	0.025
Time of Day	MO	0.008 ± 0.00	0.009 ± 0.01	0.011 ± 0.01	0.007 ± 0.01	-
	NO	0.004 ± 0.00	0.022 ± 0.01	0.035 ± 0.01	0.007 ± 0.01	-
	EV	-	0.038 ± 0.01	0.007 ± 0.01	0.013 ± 0.01	0.010 ± 0.00
<i>P</i>		0.263	0.133	0.103	0.588	0.009
Floor X Gender						
G X Male		-	0.017 ± 0.01	0.033 ± 0.01	0.011 ± 0.01	-
G X Female		-	0.003 ± 0.01	0.010 ± 0.01	0.007 ± 0.01	0.007 ± 0.00
V X Male		0.017 ± 0.00	0.033 ± 0.01	0.017 ± 0.01	0.011 ± 0.01	-
V X Female		-	0.039 ± 0.01	0.010 ± 0.01	0.007 ± 0.01	0.007 ± 0.00
<i>P</i>		0.050	0.403	0.462	1.000	1.000
Floor X Time of day						
G X MO		-	0.013 ± 0.01	0.022 ± 0.01	-	-
G X NO		-	-	0.030 ± 0.01	0.013 ± 0.01	-
G X EV		-	0.017 ± 0.01	0.013 ± 0.01	0.013 ± 0.01	0.10 ± 0.00
V X MO		0.017 ± 0.01	0.005 ± 0.01	-	0.013 ± 0.01	-
V X NO		0.008 ± 0.01	0.045 ± 0.01	0.040 ± 0.01	-	-
V X EV		-	0.059 ± 0.01	-	0.013 ± 0.01	0.010 ± 0.00
<i>P</i>		0.263	0.116	0.503	0.215	1.000
FloorX Gender X Time of Day						
<i>P</i>		0.233	0.865	0.907	0.992	0.012

^{a,b}: The different superscripts on numbers represent a significant difference between them ($P < 0.05$).

Data are presented as LSM ± SEM.

G: Gravel, V: Vegetation, MO: Morning, NO: Noon, EV: Evening, - : No Behaviour

Table 5. Effects of enriched environment on aggressive behaviours of ostriches (number of bouts/hour)

Enrichment		Threat	Fight	Escape	Displace
Floor	Gravel	0.016 ± 0.01	0.011 ± 0.01	-	-
	Vegetation	0.006 ± 0.01	-	0.008 ± 0.00	0.016 ± 0.00
<i>P</i>		<i>0.277</i>	<i>0.153</i>	<i>0.097</i>	<i>0.001</i>
Gender	Male	0.017 ± 0.01	0.011 ± 0.01	0.003 ± 0.00	-
	Female	0.005 ± 0.01	-	0.005 ± 0.00	0.016 ± 0.00
<i>P</i>		<i>0.179</i>	<i>0.153</i>	<i>0.638</i>	<i>0.001</i>
Time of Day	MO	0.017 ± 0.01	0.008 ± 0.01	-	0.005 ± 0.00
	NO	0.007 ± 0.01	-	0.004 ± 0.00	0.007 ± 0.00
	EV	0.009 ± 0.01	0.008 ± 0.01	0.007 ± 0.00	0.012 ± 0.00
<i>P</i>		<i>0.611</i>	<i>0.590</i>	<i>0.415</i>	<i>0.422</i>
Floor X Gender					
G X Male		0.028 ± 0.01	0.022 ± 0.01	0.006 ± 0.01	-
G X Female		0.003 ± 0.01	-	0.010 ± 0.01	-
V X Male		0.006 ± 0.01	-	-	-
V X Female		0.007 ± 0.01	-	-	0.033 ± 0.01
<i>P</i>		<i>0.147</i>	<i>0.153</i>	<i>0.638</i>	<i>0.001</i>
Floor X Time of day					
G X MO		0.033 ± 0.01	0.017 ± 0.01	-	-
G X NO		0.005 ± 0.01	-	-	-
G X EV		0.008 ± 0.01	0.017 ± 0.01	-	-
V X MO		-	-	-	0.010 ± 0.01
V X NO		0.008 ± 0.01	-	0.008 ± 0.01	0.015 ± 0.01
V X EV		0.010 ± 0.01	-	0.015 ± 0.01	0.025 ± 0.01
<i>P</i>		<i>0.161</i>	<i>0.590</i>	<i>0.415</i>	<i>0.422</i>
Floor X Gender X Time of Day					
<i>P</i>		<i>0.064</i>	<i>0.736</i>	<i>0.044</i>	<i>0.493</i>

Data are presented as LSM ± SEM.

G: Gravel, V: Vegetation, MO: Morning, NO: Noon, EV: Evening, - : No Behaviour

Table 6. The three-way interaction effect enriched environment, gender and time of day on ostrich behaviours (number of bouts/hour)

Floor X Gender X Time of Day	Dust Bathing	Laying	Threat	Escape
G X M X MO	0.000 ± 0.01 ^b	0.000 ± 0.00 ^b	0.067 ± 0.01 ^a	0.000 ± 0.01 ^c
G X M X NO	0.000 ± 0.01 ^b	0.000 ± 0.00 ^b	0.000 ± 0.01 ^c	0.000 ± 0.01 ^c
G X M X EV	0.000 ± 0.01 ^b	0.000 ± 0.00 ^b	0.017 ± 0.01 ^b	0.000 ± 0.01 ^c
G X F X MO	0.000 ± 0.01 ^b	0.000 ± 0.00 ^b	0.000 ± 0.01 ^c	0.000 ± 0.01 ^c
G X F X NO	0.000 ± 0.01 ^b	0.000 ± 0.00 ^b	0.010 ± 0.01 ^b	0.000 ± 0.01 ^c
G X F X EV	0.029 ± 0.01 ^a	0.020 ± 0.00 ^a	0.000 ± 0.01 ^c	0.000 ± 0.01 ^c
V X M X MO	0.000 ± 0.01 ^b	0.000 ± 0.00 ^b	0.000 ± 0.01 ^c	0.000 ± 0.01 ^c
V X M X NO	0.000 ± 0.01 ^b	0.000 ± 0.00 ^b	0.017 ± 0.01 ^b	0.017 ± 0.01 ^b
V X M X EV	0.000 ± 0.01 ^b	0.000 ± 0.00 ^b	0.000 ± 0.01 ^c	0.000 ± 0.01 ^c
V X F X MO	0.000 ± 0.01 ^b	0.000 ± 0.00 ^b	0.000 ± 0.01 ^c	0.000 ± 0.01 ^c
V X F X NO	0.000 ± 0.01 ^b	0.000 ± 0.00 ^b	0.000 ± 0.01 ^c	0.000 ± 0.01 ^c
V X F X EV	0.029 ± 0.01 ^a	0.020 ± 0.00 ^a	0.020 ± 0.01 ^b	0.029 ± 0.01 ^a
<i>P</i>	0.038	0.012	0.064	0.044

^{a,b}: The different superscripts on numbers represent a significant difference between them ($P < 0.05$).

Data are presented as LSM ± SEM.

G: Gravel, V: Vegetation, M: Male, F: Female; MO: Morning, NO: Noon, EV: Evening, - : No Behaviour.