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Photoperiodic-dependent Morpho-biometric changes in the Excurrent Duct System of Sexually Mature Helmeted Guinea Fowl (*Numida meleagris*)

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ABSTRACT

Photoperiod is considered to be one of the most effective environmental factors controlling the reproductive cycle and gonadal maturation in some mammalian species. However, very limited information is available on its effects on reproductive biology of the helmeted guinea fowl (*Numida meleagris*). Thus, we investigated the effects of varying photoperiods on morpho-biometry of the excurrent duct system of *Numida meleagris*. Sexually- mature male helmeted guinea fowls (n=21), were randomly assigned into three (3) photoperiodic regimes of seven birds per group (n=7); viz [Group I: Short daylight (SD) with; 8 Hour of light (HL), Group II: Moderate daylight (MD; 12 HL) and Group III: Long daylight (LD; 16 HL)]. After 8 weeks, the excurrent ducts were excised and freed of all adhering connective tissues for gross-morphological and morphometric evaluations. It was found that compared to the other treatments, the weight and diameter of the epididymis and ductus deferens were significantly increased ($P< 0.05$) in the fowls exposed to 16 HL However, no significant ($P> 0.05$) difference was observed in body weight and length of the excurrent ducts regardless of photoperiod. Overall, the observed changes in weight and diameter of the epididymis and ductus deferens of sexually- mature helmeted guinea fowl (*Numida meleagris*), are thus, a consequence of the photo-stimulatory effects of long photoperiod (16HL) exposure on reproductive activity. These findings could be useful in designing programs to improve the reproductive efficiency of *Numida meleagris*

Keywords: Biometry; Excurrent ducts; Guinea fowl; Morphology; Photoperiodism

INTRODUCTION

In guinea fowl (*Numida meleagris*), reproduction appears to be seasonal (Ayorinde and Ayeni, 1986; Abdul-Rahman *et al*., 2016; Okyere *et al*., 2020). Reproductive behaviour is inhibited by reduced weight and volume of organs during the non-breeding season (Abdul-Rahman *et al*., 2016; Mohan *et al*., 2016). No life cycle can be completed in a seasonal environment without the means to exploit the favorable season, to avoid or mitigate the unfavorable season, and to switch between the two lifestyles in a timely manner (Bradshaw and Holzapfel, 2007). Photoperiod is one of the most important predictable environmental conditions affecting seasonal reproductive behavior (Lewis *et al*., 2006; Pieri *et al*., 2014; Han *et al*., 2017). This is principally due to the fact that the change in photoperiod is entirely predictable at a given latitude both within and between the year (Bradshaw and Holzapfel, 2007). It is therefore used as a reliable cue to estimate the morpho-physiological preparations for reproduction, dormancy and/or migration (Goldman, 2001; Gwinner, 2003; Bradshaw and Holzapfel, 2007). This reproductive seasonal response is regulated by the interaction of photoperiod with the neuroendocrine components namely; hypothalamus, pituitary and gonads (HPG) that together, constitute the 'photoperiodic axis' (Sharp, 2005). In birds, photoreception occurs at three levels; the eye, pineal and deep brain photoreceptors (DBP) (Okano and Fukada, 1997; Kojima and Fukada, 1999). The photoreception at these sites is independent of each other (Siopes and Wilson, 1974).

In mammals, on the other hand, eyes are the only photoreceptors and their removal abolishes the photoperiodic response (Freedman *et al*., 1999). The specific role of long days (LD) and short days (SD)

light/dark cycles in timing reproductive activity is, specie dependent. In short-day breeders like sheep and goats, SD are stimulatory and LD inhibitory of reproductive behavior (Chemineau *et al*., 2007). In contrast, SD inhibit while LD stimulate reproductive activity in species responsive to LD such as horses, mice and most poultry (Chemineau *et al*., 2007). Studies on seasonal reproductive rhythms in mammals, such as in white-footed mice (*Peromyscus leucopus*), bank voles (*Myodes glareolus*), Djungarian hamsters (*Phodopus sungorus*), and Syrian hamsters (*Mesocricetus auratus*), have shown that exposure to short daylight induces testicular degeneration, mainly by reducing weight and volume (Furuta *et al*., 1994; Young and Nelson, 2001; Bonda-Ostaszewska and Wlostowski, 2015; Martinez -Hernandez *et al*., 2018). Similarly, in striped dwarf hamster (*Cricetulus barabensis*), decrease in epididymal weights were observed under SD. However, epididymal weights between moderate daylight (MD) and LD were comparable (Mou *et al*., 2020). In guinea cocks, long daylength exposure caused precocious development of testes (Ogawa *et al*.,1993). Similarly, passerines such as starlings and sparrows exposure to increasing day lengths in spring initiated gonadal maturation and breeding (Dawson *et al*., 2001; Dawson 2002).

The excurrent duct system of birds comprises the epididymal ducts and the deferent duct (Aire *et al*., 1979; Maruch *et al*., 1998; Kirby and Froman, 2021). The anatomy of these ducts is of concern to poultry breeders as well as scientific workers (Bull *et al*., 2007). The study on the reproductive system of birds is necessary to improve their production and reproduction efficiency, and to preserve their species (Vijayakumar *et al*., 2014). Though, the testis is the major reproductive organ of the male bird, the excurrent ducts play an indispensable role in the reproductive system of the male bird.

Previous studies have described the biological effects of natural or artificial light (photoperiodism) on mammalian excurrent duct system, especially the epididymis, as reported by Calvo *et al.* (1997), Jeon *et al.* (2020) and Mou *et al.* (2020) in hamsters; Olayaki *et al*. (2008) in Sprague Dawley Rats; Cruceño *et al*. (2013) in Viscacha rodent (*Lagostomus maximus maximus*); Augustave *et al.* (2020) in African Giant Rat (*Cricetomys gambianus*). However, fewer studies were reported on the effects of photoperiodism in the avian species. Still, there is paucity of information on the reproductive biology of the helmeted guinea fowl (Abdul-Rahman and Jeffcoate, 2018). Therefore, the present study was designed to investigate the morpho-biometric changes in the excurrent duct system of helmeted guinea fowl (*Numida meleagris*), subjected to artificial (controlled) photoperiod conditions.

MATERIALS AND METHODS

Study Area

The study was conducted at the Avian Research and Aqua Culture Breeding Center of the Department of Veterinary Anatomy, Ahmadu Bello University, Zaria (11°4′N, 7°42′E), located in the Northern Guinea Savannah zone of Nigeria, with a mean (± standard error) monthly photoperiod of 12.13 ± 0.13 h (Kowal and Knabe, 1972; Dzenda *et al*., 2011). The zone has nearly 12 h light: 12 h dark cycle within a 24 h period throughout the year and is characterized by three major seasons: Harmattan (November - February), hot-dry (March-May) and rainy (June- October) seasons (Ayo *et al*., 1999; Dzenda *et al*., 2011).

Animals and management

A total of twenty-one (21) sexually-mature male helmeted guinea fowls (*Numida meleagris*) weighing between 1.0-1.48kg were used in the study. Prior to their purchase, the sexes were distinguished through visualization of the vent and the use of helmet shape as well as wattle size and shape; according to the criteria described by Umosen *et al*. (2008) and Yakubu *et al.* (2022). Thereafter, the birds were transferred using standard transport basket stackable of 600 x 400 x 300 mm dimensions and transported to the Avian Research and Aqua Culture Breeding Centre in the Department of Veterinary Anatomy, Ahmadu Bello University, Zaria, where the experiment was conducted. The birds were intensively managed on deep-litter system in a fenced poultry house, in order to reduce the stress of confinement or restricted movement, and commercial feed (Vital feed® Jos, Nigeria) and water provided *ad libitum*.

Experimental Design

The helmeted guinea fowls (*Numida meleagris*) were randomly assigned into three photoperiodic regimes of light/dark cycle as described by Thiele (2009);

1. Group I: Short daylight (SD; 8 HL (Hour of light) lights on 7:00 h, lights off 15:00 h,
2. Group II: Moderate daylight (MD; 12 HL, lights on 7.00h, lights off 19:00h),
3. Group III: Long daylight (LD; 16 HL, lights on 7:00 h, lights off 23:00 h)

Each group consisted of seven birds per group (n=7) and the study lasted for a period of eight weeks of experimentation. Each group was demarcated by placement in a black light-tight chamber, with each partition of dimension of 200 x 110 x 100 cm; illuminated by two cool-white fluorescent lights (12W) that provided approximately 350 lux, for short-day (8L:16D), moderate-day (12L:12D) or long-day (16L:8D) photoperiod. The room temperature was kept constant at 27±2°C.

Sample collection

After exposure to varying photoperiods for the predetermined period, the guinea cocks were euthanized using intramuscular (i/m) injection of Ketamine and Xylazine combination at a dose of 35mg/kg and 5mg/kg respectively (Flecknell, 1987). Thereafter, the thoraco-abdominal cavity of each bird was dissected to exteriorize the reproductive organs. The testes together with their attached epididymis were removed. The left and right epididymis were then excised off the body of the testes, freed of all adhering connective tissues, and the ductus deferens also separated from adjoining structures for gross morphological description and morphometry.

Gross Morphological Description and Morphometry

The left and right epididymides and ductus deferens, freed of all adhering connective tissues were examined for any obvious gross morphological changes. The organs were partitioned following the anatomical description of McLelland (1991). The organs length and diameter were measured using digital vernier caliper (Mitutoyo Company, Japan) and measuring ruler. The weights of the epididymis and ductus deferens were in-turn, recorded to the nearest 0.01 gram using Mettler® electronic scale and relative weights calculated as shown below.

Relative epididymal weight: Ratio of epididymal weight to body weight:

$$\frac{\text{Paired epididymal weight (g)}}{\text{Body weight (kg)}} \times 100$$

Relative ductus deferens weight: Ratio of ductus deferens weight to body weight:

$$\frac{\text{Paired ductus deferens weight (g)}}{\text{Body weight (kg)}} \times 100$$

Ethical Statement:

The animal use for the experiment followed humane treatment according to recommended protocol for use of animal for experimental research. The research protocol was approved by the Ahmadu Bello University Institutional Animal Care and Use Committee and ethical clearance number (ABUAUC/2022/021) was subsequently issued.

Data Analysis

Data generated were expressed as mean (± standard error of the mean) (SEM). One-way analysis of variance (ANOVA) (SPSS software, version 16) was performed to test for variation in parameters. Value of $P < 0.05$ was considered statistically significant.

RESULTS

Gross Morphological Studies

Epididymis

The epididymis of the guinea fowl was not visible *in situ* due to its topographic location on the dorsomedial aspect of testis within the abdominal cavity. The epididymis was bounded cranially by the adrenal glands, medially with the descending aorta and caudal vena-cava, laterally with the respective testis and caudally continued as ductus deferens. The epididymal region appeared as an elongated tubular organ closely attached to the dorsomedial aspect of the corresponding testis and they were enclosed together within the tunica albuginea. No discrete compartments (head, body and tail regions) in epididymis was observed. The epididymis extended from the cranial (Cr) pole to the caudal (Ca) pole of the testis (Figure 1A-C), but lesser in length than the corresponding testis. The epididymis showed a drastic increase in size with increasing photoperiod with 8 HL<12 HL<16 HL groups respectively (Figure 1 A-C).

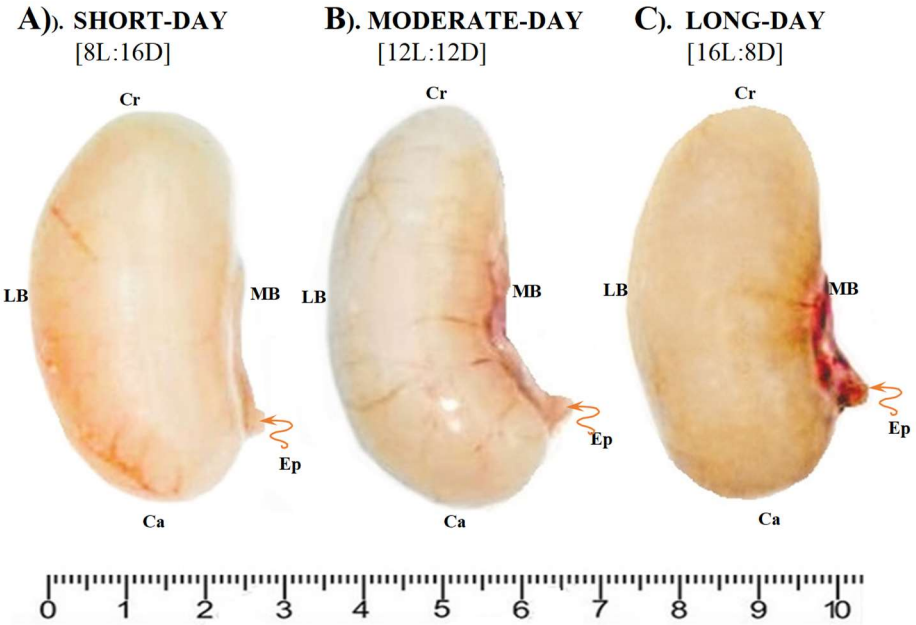

Figure 1. Photographs showing the gross morphology of the testis of sexually-mature helmeted guinea fowl (*Numida meleagris*) (**dissected**), along its length, with its attached epididymis (**Ep**) i.e. freeform scribble red arrow, **A**) Short-day [8L:16D] photoperiodic exposure. Note the epididymis is visibly shrunken (reduced) in size; in **B**) Moderate-day [12L:12D] photoperiodic exposure, the epididymis (**Ep**) appears slightly enlarged; in **C**). Long-day [16L:8D] photoperiodic exposure, the epididymis (**Ep**) is significantly swollen (enlarged) and appears congested. Cranial (**Cr**) and Caudal (**Ca**) pole of the testis, lateral (**LB**) and medial border (**MB**).

Ductus deferens

The ductus deferens in the guinea cock appeared as an extensive tube attached to the dorsal body wall by folds of peritoneum and runs posteriorly along the midline, parallel to the ureter. The ductus deferens began at the caudal termination of the epididymal region where the ductus epididymis ends. The ductus deferens appeared wavy in outline (Figure 2A-C) and was impossible to pull out into straight duct. It was initially very narrow in diameter but gradually widens from about mid-way along its length until

it reached the greatest just before it opens into the urodeum region of the cloaca. The ductus deferens showed a remarkable increase in size with more pronounced wavy outline with increasing photoperiod with 8 HL<12 HL<16 HL groups respectively (Figure 2A-C).

Gross morphometrics

Epididymis

Body weight, Absolute and relative weights of epididymis

The results on body weight, absolute and relative epididymal weights were presented in Table 1. There was no significant ($P > 0.05$) difference in the mean body weight across all the groups, regardless of photoperiod. The mean values for left epididymal weight decreased significantly ($P < 0.05$) in 8 HL compared to other treatments. Though, the mean values between 12 HL and 16 HL were not significantly different ($P > 0.05$). The right epididymal weight was significantly higher ($P < 0.05$) in 12 HL when compared to other groups. The mean values for paired epididymal weight were not significantly ($P > 0.05$) different between 12 HL and 16 HL groups. However, significant ($P < 0.05$) decrease was recorded in 8 HL compared to other groups. Relative epididymal weight was significantly decreased ($P < 0.05$) in 8 HL compared to other groups (Table 1).

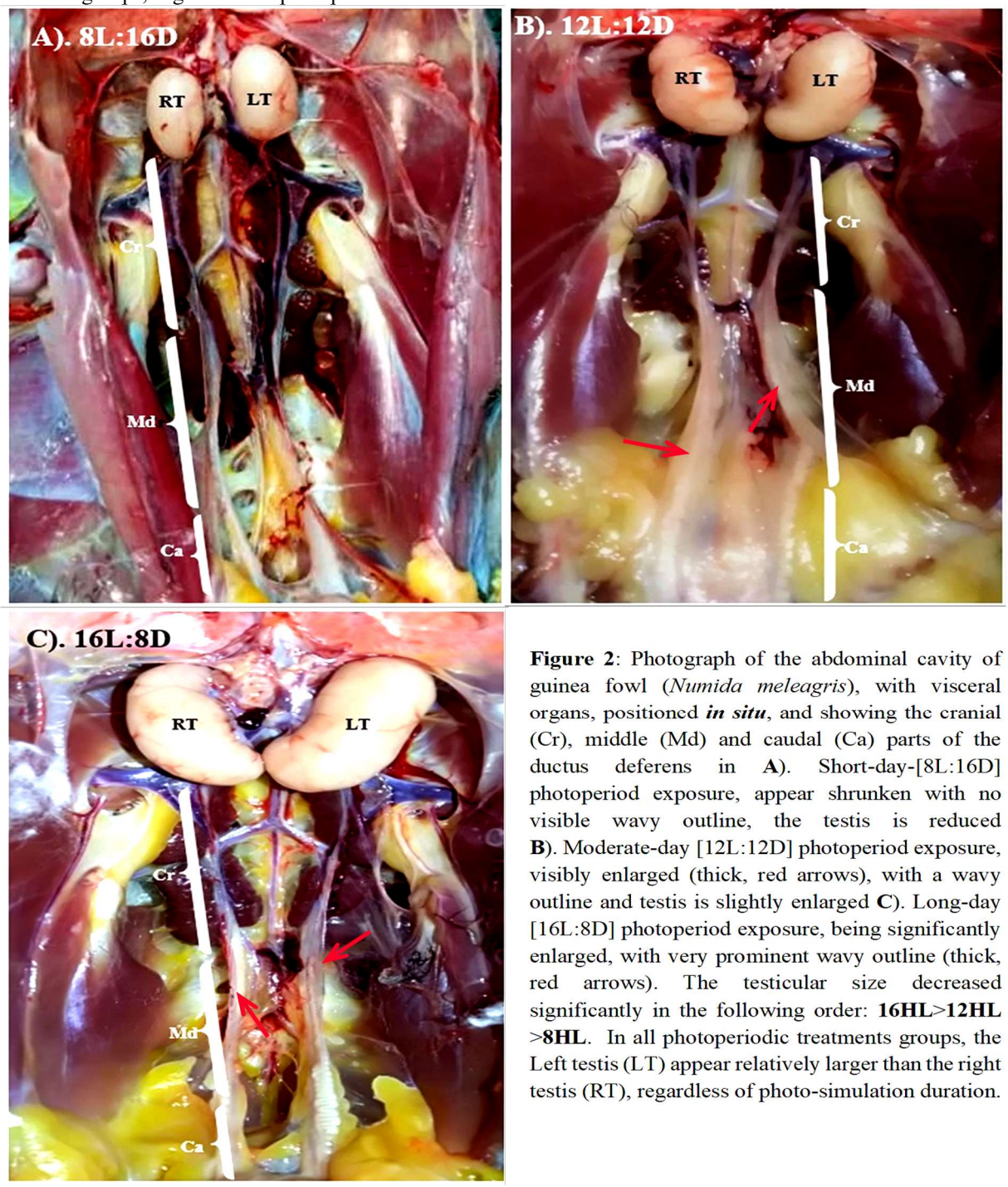

Figure 2: Photograph of the abdominal cavity of guinea fowl (*Numida meleagris*), with visceral organs, positioned ***in situ***, and showing the cranial (Cr), middle (Md) and caudal (Ca) parts of the ductus deferens in **A**). Short-day-[8L:16D] photoperiod exposure, appear shrunken with no visible wavy outline, the testis is reduced **B**). Moderate-day [12L:12D] photoperiod exposure, visibly enlarged (thick, red arrows), with a wavy outline and testis is slightly enlarged **C**). Long-day [16L:8D] photoperiod exposure, being significantly enlarged, with very prominent wavy outline (thick, red arrows). The testicular size decreased significantly in the following order: **16HL>12HL >8HL**. In all photoperiodic treatments groups, the Left testis (LT) appear relatively larger than the right testis (RT), regardless of photo-simulation duration.

Table 1: Variation in the body weights, absolute and relative epididymal weights in helmeted guinea fowl (*Numida meleagris*) exposed to varying photoperiods (n=7)

Parameters	Experimental groups		
	8HL	**12HL**	**16HL**
BW (kg)	1.76 ± 0.15[a]	1.44 ± 0.11[a]	1.43 ± 0.62[a]
LEW (g)	0.04 ± 0.00[a]	0.06 ± 0.01[b]	0.08 ± 0.00[b]
REW (g)	0.03 ± 0.00[a]	0.12 ± 0.01[b]	0.06 ± 0.00[a]
PEW (g)	0.07 ± 0.01[a]	0.18 ± 0.01[b]	0.14 ± 0.01[b]
RlEW (%)	0.00 ± 0.00[a]	0.01 ± 0.00[b]	0.01 ± 0.00[b]

[a,b] Values with the same superscript alphabets in the same row do not differ significantly at (P < 0.05). BW: body weight, LEW: left epididymal weight, REW: right epididymal weight, PEW: paired epididymal weight and RlEW: relative epididymal weight

Length and diameter of the epididymis

Regardless of photoperiod, there was no significant difference ($P > 0.05$) in the left and right epididymal lengths across all the photoperiodic treatment groups. However, the mean epididymal diameters in guinea fowl exposed 8 HL decreased significantly ($P < 0.05$) when compared to 16 HL (Table 2).

Ductus deferens

Absolute and relative weights of ductus deferens

The mean values for left and right ductus deferens and the paired ductus deferens weights reduced significantly ($P<0.05$) in guinea fowl exposed to 8 HL. Similarly, the relative ductus deferens weights were significantly decreased ($P < 0.05$) in guinea fowl exposed to 8 HL compared to other groups (Table 3).

Length and diameter of ductus deferens

The mean values for left and right ductus deferens length across all the groups were not significantly ($P>0.05$) different, regardless of photoperiod. Also, the cranial and middle mean diameters for left and right ductus deferens were not significantly different ($P>0.05$) in all the exposed groups. However, the caudal mean diameter of the left and right ductus deferens were significantly reduced ($P< 0.05$) in the 8 HL cocks, compared to 16 HL (Table 4).

Table 2: Variation in the lengths and diameters of the epididymis of helmeted guinea fowl (*Numida meleagris*) exposed to varying photoperiods (n=7)

Parameters	Experimental groups		
	8HL	**12HL**	**16HL**
LEL (mm)	12.05 ± 0.95[a]	12.55 ± 1.03[a]	13.63 ± 0.52[a]
REL (mm)	10.48 ± 0.95[a]	11.35 ± 1.18[a]	11.31 ± 1.18[a]
LED (mm)	2.00 ± 0.59[a]	2.18 ± 0.07 [a,b]	2.38 ± 0.04[b]
RED (mm)	1.81 ± 0.08[a]	2.08 ± 0.08[a,b]	2.20 ± 0.04[b]

[a,b] Values with the same superscript alphabets in the same row do not differ significantly at (P < 0.05). LEL: left epididymal length, REL: right epididymal length, LED: left epididymal diameter and RED: right epididymal diameter

Table 3: Variation in the absolute and relative weights of the ductus deferens of helmeted guinea fowl (*Numida meleagris*) exposed to varying photoperiods (n=7)

Parameters	Experimental groups		
	8HL	**12HL**	**16HL**
LDW (g)	0.08 ± 0.01[a]	0.10 ± 0.01[a,b]	0.12 ± 0.01[b]
RDW (g)	0.07 ± 0.00[a]	0.09 ± 0.01[a b]	0.10 ± 0.01[b]
PDW (g)	0.15 ± 0.01[a]	0.19 ± 0.03[a,b]	0.23 ± 0.02 [b]
RlDW (%)	0.01 ± 0.00[a]	0.01 ± 0.00[b]	0.02 ± 0.00[b]

[a,b] Values with the same superscript alphabets in the same row do not differ significantly at (P < 0.05). LDW: left ductus deferens weight, RDW: right ductus deferens weight, PDW: paired ductus deferens weight and RlDW: relative ductus deferens weight

DISCUSSION

The macroscopic appearance of the epididymis in this study as spindle shaped and flattened organ attached very intimately to the dorsomedial surface, extending from the cranial pole to the caudal pole of the testis are in accordance with the report of Aire *et al*. (1979) in Japanese quail, Budras and Meier (1981) in Ostrich, Bull *et al*. (2007), González-Morán and Soria-Castro (2010) in domestic fowl and Abdul-Rahman and Jeffcoate (2018) in the guinea fowl. The epididymal region was enclosed by capsule together within the tunica albuginea as reported by El-Saba and Abdrabou (2013) in pigeon. Again, the observed *non-discrete* epididymal divisions into head, body and tail regions concurs with the report of Razi *et al*. (2010) in Iranian white rooster. Also, the *in situ* topographic location of the epididymis of the guinea cock used in this study in the dorsomedial aspect of testis agrees with the observation of Tamilselvan *et al*. (2021).

The gross appearance of the ductus deferens in this study as arising from the caudal termination of the epididymal region where the ductus epididymis end is consistent with the findings of Bull *et al*. (2007) in domestic fowl. The diameter of the ductus deferens was initially narrow but begins to increase gradually about mid-way along its length until it

attains its greatest diameter just before it opens into the cloaca. In addition, the duct assumes a wavy outline as it progresses caudally parallel to the respective ureter. Similar features were observed by Aire *et al*. (1979), Noori and Mirhish (2018) in guinea cocks and Khatun and Das (2019) in adult Khaki Campbell duck.

Table 4: Variation in the lengths and diameters of the ductus deferens of helmeted guinea fowl (*Numida meleagris*) exposed to varying photoperiods (n=7)

Parameters	Experimental groups		
	8HL	**12HL**	**16HL**
LDL (mm)	109.00 ± 3.19[a]	109.60 ± 2.44[a]	114.40 ± 1.33[a]
RDL (mm)	106.80 ± 3.12[a]	106.00 ± 3.01[a]	111.00 ± 2.08[a]
LCrD (mm)	0.68 ± 0.05[a]	0.68 ± 0.06[a]	0.79 ± 0.03[a]
LMD (mm)	1.38 ± 0.10[a]	1.29 ± 0.17[a]	1.58 ± 0.63[a]
LCaD (mm)	2.12 ± 0.04[a]	2.23 ± 0.12[a,b]	2.58 ± 0.05[b]
RCrD (mm)	0.61 ± 0.04[a]	0.61 ± 0.06[a]	0.63 ± 0.05[a]
RMD (mm)	1.23 ± 0.09[a]	1.31 ± 0.16[a]	1.31 ± 0.11[a]
RCaD (mm)	2.01 ± 0.02[a]	2.19 ± 0.15[a,b]	2.46 ± 0.03[b]

[a,b] Values with the same superscript alphabets in the same row do not differ significantly at ($P < 0.05$). LDL: left ductus deferens length, RDL: right ductus deferens length, LCrD: left cranial ductus deferens diameter, LMD: left middle ductus deferens diameter, LCaD: left cauda ductus deferens diameter, RCrD: right cranial ductus deferens diameter, RMD: right middle ductus deferens diameter and RCaD: right caudal ductus deferens diameter.

The differences in the bio-morphometric parameters (body weight, organs absolute and relative weights, length and diameter) of the epididymis and ductus deferens were evaluated upon exposure to varying photoperiods. Again, the non-significant difference observed in the body weights of guinea fowl exposed to varying photoperiods are in agreement with the findings of Kenfack *et al*. (2020) and Zubairu *et al*. (2021) in African giant rat (AGR). Though, guinea cock under 8 HL appeared to display a non-significant increase in body weight relative to other photo-stimulated (exposed) groups. These findings are at variance with the report of substantial weight gain observed with increased photoperiod as earlier documented by Assia and Boulakoud (2014) in pigeons,Tolvaro *et al*. (2015) in laboratory rats and Kyere *et al.* (2021) in guinea fowls. Interestingly, longer photoperiod is related to both higher energy intake and energy expenditure level, resulting in larger weight gain (Kyere *et al*., 2021). However, in guinea fowl, flightiness, fits of panic and extreme noise increased with increasing light intensity resulting in more energy expended than conserved. This might account for the non-significant change in body weight observed. Detrimental effect on weight gain from exposure to continuous light was also reported by Kyere *et al*. (2021) in guinea fowl.

The significant increase in left and paired epididymal weights observed in guinea fowl exposed to long photoperiod are consistent with the report of Mou *et al*. (2020) in striped dwarf hamsters (*Cricetulus barabensis*). On the contrary, Tamilselvan *et al*. (2021) reported higher epididymal weight without photoperiodic treatment in guinea fowls. Variations in age and breed might be responsible for the disparity in these sets of observations. Relative epididymal weight differed significantly among all the treatment groups. Photo-induction may have been responsible for the significant increase observed in guinea fowl exposed to 12 HL and 16 HL. The length of the epididymis did not differ significantly in all the groups, regardless of photoperiod. This indicated that photoperiod had no effects on the length of the epididymis. Without photoperiodic treatment, Aire *et al*. (1979) reported a length of about 15 mm in guinea cocks. A similar finding was also documented by Tamilselvan *et al*. (2021) in the same species. The diameter of right and left epididymis appeared significantly greater in guinea fowl exposed to 16 HL. The aforementioned change observed, are, thus, a consequence of photo-induction under this light condition.

The observed significant increase in the left and right ductus deferens as well as relative ductus deferens weight following exposure to longer photoperiod most especially the 16 HL are bio-morphometric pointers to a consequence of photo-induction under these lighting conditions. In addition, the non-significant difference in the ductus deferens length in all the groups indicated that photoperiod did not have effect on ductus deferens length. Without photoperiodic treatments, Noori and Mirhish (2018) documented lower than the values reported in the present study. Photoperiodic treatment, variations in age and breed could have been responsible for the observed differences. The observed increased in caudal diameter of the ductus deferens in guinea fowl exposed to 16 HL could be linked to the consequence of the photo-stimulatory effects of this lighting condition on the reproductive morphological response observed in this study.

Conclusion

This study has shown that the epididymal and ductus deferential bio-morphometric (weights and diameter) parameters were remarkably altered in the helmeted guinea fowl (*Numida meleagris*) exposed to varying photoperiods. Again, these alterations were largely due to the photo-stimulatory effects of long photoperiod (16L:8D) exposure on the reproductive activity.

The findings from this study would be useful, especially to guinea fowl breeders/producers in designing appropriate intervention programs necessary to improve the reproductive efficiency, in this specie, regardless of the season.

Conflict of interest

The authors declare that they have no conflict of interest

Authors' Contributions

BA, UMB and SMH participated in experimental design and data interpretation. BA and GIJ conducted the experiments and were involved in all sample collections; BA and UMB performed data analyses and wrote the entire manuscript; UMB critically revised the entire manuscript and approved of final version; OJO, MTA, ASM and ZM significantly contributed to data preparation and final proof-reading. All authors read and approved the final manuscript.

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