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Histomorphological features of the male reproductive system in the Eurasian linnet (*Carduelis cannabina*): comparative insights with other avian species

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Abstract

The Eurasian linnet (*Carduelis cannabina*) is a seasonal-breeding passerine, but detailed data on its male reproductive tract are limited. This study characterized the testes, epididymides, and ductus deferentes in adult males, across reproductive states. Adult males were examined for reproductive-organ topography, morphology, and dimensions. Regional tissue samples were stained with hematoxylin and eosin (H&E). The paired testes were intra-abdominal and asymmetrical, with the left testis consistently larger and positioned slightly more cranially than the right. In reproductively active birds, testicular dimensions increased markedly, with enlarged seminiferous tubules containing abundant spermatozoa. Histologically, the testes showed highly convoluted and anastomosing seminiferous tubules, prominent Sertoli and Leydig cells, and a well-developed rete testis continuous with the efferent ductules. The epididymis was compact, flattened, and undivided into distinct head, body, and tail regions. The ductus deferens was highly convoluted, increased in diameter toward the cloaca, and terminated in a prominent seminal glomus. During reproductive activity, it showed greater tortuosity, larger diameter, and higher sperm content. Its epithelium was pseudostratified columnar and lacked intraepithelial glands. Overall, the male reproductive tract of *C. cannabina* exhibited the characteristic organization of seasonal-breeding passerines, combining seasonal testicular enlargement with specialized sperm-transport and storage structures. These findings provide baseline data for comparative avian reproductive biology and may serve as a reference for future studies on reproductive physiology and conservation of wild passerine species.

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Introduction

Birds comprise more than 7800 species distributed across 27 orders and exhibit remarkable diversity in reproductive strategies (Meyburg *et al*., 2018). Among them, the order Passeriformes (songbirds) is the largest and includes many species with pronounced seasonal breeding cycles. The Eurasian linnet (*Carduelis cannabina*, family Fringillidae) is a small passerine native to Europe, western Asia, and North Africa. It may be resident, partially migratory, or fully migratory depending on latitude and local conditions. In Iran the species is relatively abundant during winter and breeds in open woodlands, gardens, and areas with dense understory vegetation (Khaleghizadeh *et al.,* 2017). Its diet is primarily granivorous but includes insects during the breeding season. Despite its wide distribution and ecological importance, detailed morphological studies of its reproductive system remain limited compared to domestic galliforms or model passerines such as the zebra finch.

The male reproductive tract of birds differs fundamentally from that of mammals in several key respects. Testes remain permanently intra-abdominal, suspended by a short mesorchium, and lack a pampiniform plexus for counter-current heat exchange. Instead, temperature regulation relies on proximity to abdominal air sacs and, in passerines, on the specialized seminal glomus (Aire, 2007). The epididymis is compact and is not divided into the classical mammalian head, body, and tail regions. The ductus deferens is highly convoluted and, in most passerines, terminates caudally in a coiled sperm-storage organ known as the seminal glomus (or seminal sac). Accessory glands homologous to the mammalian prostate, seminal vesicles, or bulbourethral glands are absent. These structural adaptations are closely linked to the aerial lifestyle of birds and to the need for rapid, repeated sperm delivery during short breeding seasons (Aire, 1980; Aire, 2007). In domestic chickens the entire male reproductive system also remains internal, sperm remain viable at body temperature, both testes develop fully (in contrast to the single functional ovary of females), and continuous sperm production occurs throughout adult life, although quality declines with age (Jacob *et al*., 2013) .

Seasonal breeders display dramatic cyclic changes in gonadal size and activity. Testicular mass can increase several hundred-fold between the non-breeding and breeding seasons in some sparrows, driven by expansion of seminiferous tubules and proliferation of interstitial cells (Pitcher and Stutchbury, 1998; Wang *et al.,* 2022). These changes are regulated primarily by photoperiod acting through the hypothalamic–pituitary–gonadal axis, involving gonadotropin-releasing hormone (GnRH) and gonadotropin-inhibitory hormone (GnIH) (Chan and Lofts, 1974; Wang *et al.,* 2022; Yatung and Trivedi, 2025). Histological studies have shown that the annual cycle typically comprises a regeneration phase (rebuilding of tubules and interstitial tissue), an acceleration phase (recrudescence of spermatogenesis), and a culmination phase (peak sperm production), followed by regression (Aire, 2007). In contrast, domestic chickens exhibit progressive testicular growth from the first week after hatching, with seminiferous-tubule formation completed by one month of age and full spermatogenesis established by three months, accompanied by a continuous rise in the gonadosomatic index (GSI) (Mfoundou *et al*., 2022).

Although extensive literature exists for domestic fowl (*Gallus domesticus*), turkey (*Meleagris gallopavo*), Japanese quail (*Coturnix japonica*), and guinea-fowl (*Numida meleagris*), comparative data on wild fringillids are sparse. Early light-microscopic descriptions of the excurrent ducts of the linnet itself were provided by Aire *et al*. in 1979, yet subsequent work has focused more on ultrastructure in other wild species (e.g., cattle egret) or on the complex staging of the seminiferous epithelium cycle in the zebra finch(Aire, 2007; Bikchurina *et al*., 2025; Roopnarine *et al*., 2026). Recent reviews emphasize that while the basic cellular architecture of Sertoli and Leydig cells is conserved across birds, quantitative parameters-tubule diameter, interstitial volume fraction, sperm-storage capacity, and presence or absence of a rete testis-vary according to phylogenetic position and life-history strategy (Barker and Kendall, 1984; Ozegbe *et al*., 2012; PourhajiMotab and Rasouli, 2021).

The aims of the present study were therefore (i) to provide a detailed macroscopic and light-microscopic description of the testis, epididymis, and ductus deferens of adult male *C. cannabina*, with explicit comparison between reproductively active and inactive individuals; (ii) to quantify

linear dimensions and note topographic relationships; and (iii) to place the findings within a comparative framework that includes both classical domestic species and more recent observations on wild passerines and non-passerines. Such baseline morphological data are essential for interpreting physiological studies, assessing the impact of environmental stressors, and supporting conservation efforts directed at wild songbirds.

Materials and Methods

Eight adult male Eurasian linnets (*Linaria cannabina*; formerly *C. cannabina*) were randomly obtained from the Neyshabur region of northeastern Iran. The birds were maintained on a uniform diet for two months before examination. Reproductive status was assessed prior to euthanasia and before examination of the internal reproductive organs. Based on the known seasonal reproductive cycle of the Eurasian linnet, birds examined during the breeding period were identified as reproductively active, whereas birds examined during the non-breeding period were considered reproductively inactive. This classification was further supported by direct observation of reproductive behavior, particularly the presence or absence of reproductive vocalization (song), together with other externally observable breeding-related behaviors. Thus, four birds showing clear behavioral evidence of reproductive activity, including active song production during the breeding period, were classified as reproductively active, while four birds examined during the non-breeding period and lacking such reproductive behavior were classified as reproductively inactive. Importantly, classification was established before opening the body cavity and was not based on testicular size or subsequent histological findings (Drachmann *et al*., 1997).

Following euthanasia using an approved humane procedure, a midline incision extending from the beak to the cloaca was made. The sternum and abdominal musculature were reflected, and the topography, position, shape, and gross appearance of the testes, epididymides, and ductus deferentes were examined and photographed. Particular attention was paid to differences in testicular development between reproductively active and inactive birds. The reproductive organs were subsequently removed en bloc together with the cloacal region. Organ dimensions, including length, width, and thickness, were measured three times using a graduated ruler and digital calipers, and the mean values were recorded. Testicular dimensions were assessed at the cranial, middle, and caudal regions. The gross morphology, color, degree of development, and anatomical relationships of the epididymides and ductus deferentes were also recorded. The reproductive organs were then fixed in 10% neutral buffered formalin.

For histological examination, tissue samples were collected from the cranial, middle, and caudal regions of each reproductive organ. The samples were processed through a graded ethanol series, cleared in xylene, and embedded in paraffin. Sections 5–6 µm thick were prepared using a rotary microtome, mounted on glass slides, and stained with hematoxylin and eosin (H&E). The sections were examined under a light microscope at × 10, × 20, and × 40 magnifications, and representative photomicrographs were obtained (PourhajiMotab and Rasouli, 2021). Histological assessment included examination of the seminiferous tubules, seminiferous epithelium, interstitial tissue, rete testis, efferent ductules, epididymal ducts, and ductus deferens, with particular attention to the presence of spermatozoa and differences in the degree of reproductive development between active and inactive birds. All linear measurements were reported in millimeters (mm).

Results

Macroscopic observations

After reflection of the viscera, paired testes of unequal size occupied the mid-abdominal cavity on either side of the midline. Each testis was bean- or oval-shaped and positioned asymmetrically: the left testis lay slightly more cranial and was consistently larger in volume than the right. Cranial poles of both testes contacted the caudal margins of the lungs; their dorsal surfaces abutted the ventral surface of the cranial renal lobes, and in maximally active birds the contact extended to the edge of the middle renal lobe. The ventral surface of the left testis was related to the proventriculus, gizzard, left lobe of the liver and spleen, while the right testis contacted the jejunum, right hepatic lobe and gall bladder. Both testes were suspended from the dorsal body wall by a short mesorchium and were partially

enveloped laterally by the abdominal air sacs.

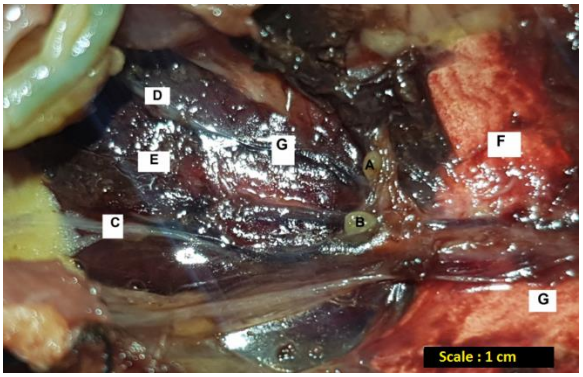


Fig. 1. Photograph of the abdominal cavity of a male Eurasian linnet (*Carduelis cannabina*) with inactive testes. A: right testis; B: left testis; C: left ductus deferens; D: right ductus deferens; E: kidneys; F, G: air sacs.

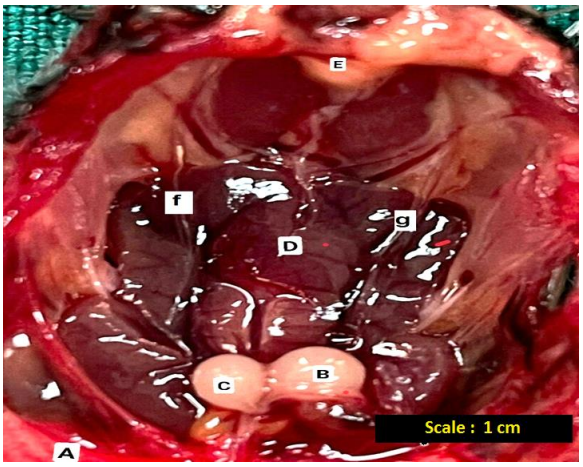


Fig. 2. Photograph of the abdominal cavity of a male Eurasian linnet (*Carduelis cannabina*) with active testes. A: air sac; B, C: testes; D: kidneys; E: cloaca; F, G: right and left ductus deferens.

Testicular dimensions increased markedly with reproductive activity. In active birds both testes were approximately twice as long and twice as wide at mid-length as in inactive adults, with the left testis remaining slightly larger than the right. Color shifted from yellowish-gray or grayish-yellow in the inactive state to creamy-white or pure white when active. When an active testis was transected, a small amount of milky fluid containing spermatozoa oozed from the cut surface.

The external surface of each testis was covered by a thin but tough connective-tissue capsule, the tunica albuginea. A testicular artery, a branch of the cranial renal artery, entered at the hilus on the medial border; no pampiniform plexus was observed. Venous drainage occurred via several short testicular veins into the caudal vena cava.

The epididymis occupied the mediodorsal surface of each testis and remained invisible from the ventral aspect even at peak activity. It appeared as a flattened oval disc approximately 0.5–1.1 mm thick, with length slightly less than half the testicular length and width approximately half the mid-testicular width. Volume increased during reproductive activity, yet the organ never developed distinct head, body or tail divisions. Color matched that of the adjacent testis. Its ventral surface was adherent to the dorsal testicular surface; its dorsal surface contacted the ventral aspect of the cranial renal lobe.

The ductus deferens was a highly convoluted, zigzag duct that ran along the ventral surface of the kidney, parallel and lateral to the ureter. Diameter was not uniform and increased gradually toward the caudal end. The left duct was slightly longer than the right because of the more cranial position of the left testis. During reproductive activity the duct became markedly more tortuous, increased in diameter by a factor of approximately 1.5, and changed color from grayish-cream to creamy-white. Caudally each duct formed a tightly coiled mass, the seminal glomus. When enlarged, the paired glomera pushed the cloacal wall outward, producing the cloacal protuberance characteristic of breeding male passerines. The duct opened on the dorsal wall of the urodeum via a small papilla (Figs. 1 and 2).

Detailed linear measurements of the testes and ductus deferens were presented in Table 1.

Table 1. Mean linear measurements (mm) of the testes and ductus deferens in adult male Eurasian linnets (*Carduelis cannabina*). (n = 8; 4 active and 4 inactive birds).

	Organ / Parameter	Active (n = 4)	Inactive (n = 4)
Right testis	Length	2.55± 0.36	1.40± 0.10
	Width (anterior)	1.54± 0.25	0.25 ± 0.15
	Width (middle)	2.08 ± 0.80	0.58 ± 0.03
	Width (posterior)	1.50 ± 0.28	0.25± 0.05
Left testis	Length	2.63 ± 0.25	1.40 ± 0.20
	Width (anterior)	1.53 ± 0.25	0.33 ± 0.16
	Width (middle)	2.08 ± 0.30	0.60 ± 0.17
	Width (posterior)	1.60 ± 0.48	0.33 ± 0.28
Right ductus deferens	Convoluted length	23.0 ± 2.86	21.3 ± 3.64
	Width	0.31 ± 0.06	0.20 ± 0.20
Left ductus deferens	Convoluted length	23.5 ± 3.2	22.0 ± 1.7
	Width	0.35 ± 0.06	0.22 ± 0.03

Microscopic observations

Testis: the tunica albuginea consisted of delicate fibroelastic connective tissue that sent short trabeculae into the parenchyma; these trabeculae did not produce distinct lobulation. A true mediastinum testis was absent. The parenchyma comprised highly convoluted, anastomosing seminiferous tubules separated by sparse interstitial tissue rich in Leydig cells. In active birds the tubules possessed large lumina filled with spermatozoa; in inactive birds the tubules were narrower, the epithelium thinner, and the interstitium relatively more prominent.

The germinal epithelium progressed continuously from spermatogonia resting on the basal lamina through primary and secondary spermatocytes and early and late spermatids to mature spermatozoa free in the lumen. Spermatogonia were spherical with peripheral nuclei; primary spermatocytes were the largest cells and displayed prominent chromatin networks; secondary spermatocytes were intermediate in size; early spermatids were small and round with euchromatic nuclei, while late spermatids elongated and oriented with their heads embedded in Sertoli-cell cytoplasm and tails projecting into the lumen. Spermatogenesis followed the classical three-phase sequence of multiplication, growth, and maturation.



Fig. 3. Photomicrograph of the testicular tissue of the Eurasian linnet showing seminiferous tubules and interstitial tissue enclosed by the tunica albuginea. (H&E stain, × 40). T: tunica albuginea; S: seminiferous tubule; I: interstitial tissue.

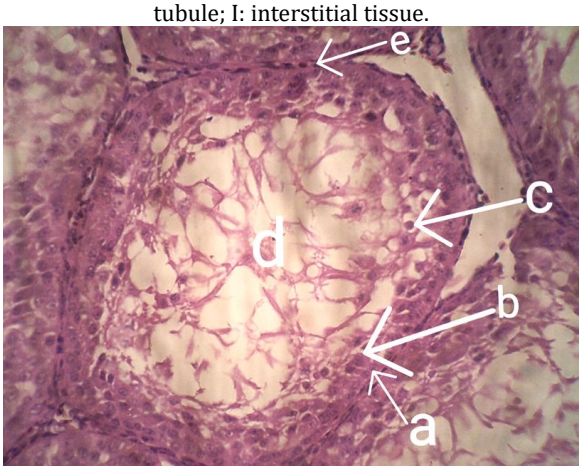


Fig. 4. Photomicrograph of the seminiferous epithelium (germinal epithelium) of an adult Eurasian linnet testis. The epithelium progresses from spermatogonia resting on the basal lamina to spermatozoa free in the lumen. (H&E stain, × 400). a: spermatogonium; b: primary spermatocyte; c: spermatid; d: spermatozoon; E: myoid cell.

Short straight tubules, lined solely by Sertoli-like cells (cuboidal or squamous), connected the seminiferous tubules to a rete testis composed of irregular, thin-walled channels located within the connective tissue on the mediadorsal aspect of the testis adjacent to the epididymis. The rete extended longitudinally from the cranial to the caudal pole of the epididymal region. Sertoli cells possessed large, pale nuclei and extended throughout the full thickness of the epithelium, providing mechanical support and nutritional exchange. Interstitial Leydig cells were spherical to polyhedral; their cytoplasm contained lipid droplets that were more abundant in inactive testes. Melanocytes were also present in the interstitium and contributed to the darker coloration of inactive gonads (Figs. 3 and 4).

Efferent ductules leaving the rete were lined by simple-to-pseudostratified columnar epithelium that was partly ciliated. Some cells bore cilia while others were non-ciliated and secretory; the epithelium rested on a thin basal lamina and was surrounded by a delicate connective-tissue sheath containing sparse smooth-muscle cells.

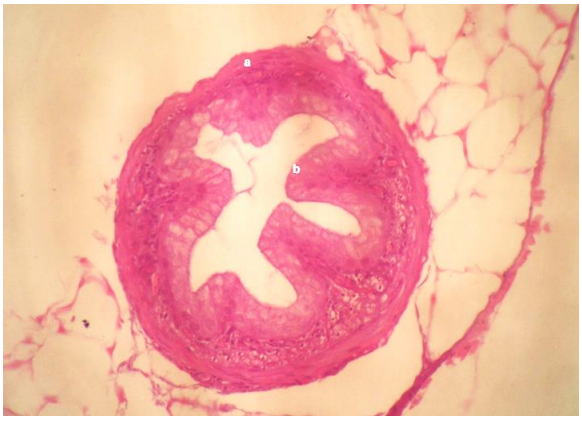


Fig. 5. Photomicrograph of a transverse section of the ductus deferens. (H&E stain, × 40). a: muscular layer of the ductus deferens; b: pseudostratified columnar epithelium.

Epididymis: efferent ductules branched throughout the entire length of the organ rather than being restricted to a cranial "head" region. They emptied via short connecting ductules into the epididymal duct proper. Epithelium of the efferent ductules was simple-to-pseudostratified columnar and ciliated; epithelium of the connecting ductules and epididymal duct was pseudostratified columnar, predominantly non-ciliated or bearing only sparse cilia, and showed signs of secretory activity. In active birds the lumina were enlarged and contained moderate numbers of spermatozoa and residual spermatids; interstitial cells hypertrophied. In inactive birds the ducts were narrower and largely empty of spermatozoa.

Ductus deferens: Cross-sections revealed a wall composed of denser connective tissue and progressive layers of smooth muscle that thickened toward the cloaca. The epithelium was pseudostratified columnar, taller than that of the epididymis, predominantly non-ciliated, and lacked intraepithelial glands. In active birds the lumen was densely packed with spermatozoa; in inactive birds both diameter and sperm content were markedly reduced. Near the cloacal opening the muscular and connective-tissue coats reached their greatest thickness (Fig. 5).

Discussion

The gross and histological organization of the male reproductive tract of *C. cannabina* conforms closely to the general avian pattern, as also observed for other organ systems in *A. griseogularis* (Rasouli *et al*., 2020). Asymmetry with a larger left testis is widespread among birds and is attributed to embryonic transfer of germ cells from the right to the left gonad during early development (Aire, 2007; Singh, 2018). This left-sided dominance is already evident in the juvenile and becomes more pronounced once full reproductive activity is attained. In domestic chickens a similar left–right asymmetry in length and overall size is observable from the first week after hatching and persists through sexual maturity (Mfoundou *et al.,* 2022). Seasonal enlargement of approximately twofold in the linnet is modest compared to the 300- to 500-fold increases reported in some sparrows (Pitcher and Stutchbury, 1998; Wang *et al*., 2022), yet is consistent with the size constraints imposed by flight; excessively large gonads would compromise aerodynamic performance. Color change from lipid-rich yellowish or melanocyte-darkened inactive testes to white active testes reflects the expansion of seminiferous tubules and the consequent dispersion of interstitial cells, a pattern documented across a wide range of seasonal breeders (Chan and Lofts, 1974; Aire, 2007). In contrast, domestic chickens show progressive whitening and increased surface vascularization as they approach and pass sexual

maturity at three months of age (Mfoundou *et al.*, 2022).

Absence of a mediastinum testis and of a pampiniform plexus is universal in birds and reflects the permanent intra-abdominal location of the gonads (Aire, 2007; Jacob *et al*., 2013). Temperature regulation is achieved instead by proximity to the abdominal air sacs and, in passerines, by the cooler microenvironment of the seminal glomus, whose temperature is approximately 4°C lower than deep cloacal temperature. The presence of a well-defined rete testis and short straight tubules aligns *C. cannabina* with domestic fowl, Japanese quail, and guinea-fowl rather than with certain corvids or terns in which the rete is reduced or absent (Barker and Kendall, 1984; Aire, 2007). Recent ultrastructural work on the cattle egret has demonstrated dilated intercellular spaces in the rete epithelium and active spermiophagy at the junction between proximal and distal efferent ductules (Roopnarine *et al.,* 2026); comparable light-microscopic features were noted in the linnet, although electron-microscopic confirmation remains desirable.

The epididymis of *C. cannabina* is typical of passerines: compact, undivided, and located on the mediadorsal testicular surface (Bellamy and Kendall, 1985; Aire, 2007). Branching of efferent ductules throughout its length precludes formation of distinct head, body, and tail segments, a condition shared with most non-passerines but contrasting with the caudal concentration of efferent ductules reported in some corvids. Spermatozoa are sparse within the epididymal duct even during peak activity and are stored primarily in the seminal glomus. This storage strategy is a hallmark of passerines and may have evolved to permit rapid multiple ejaculations while keeping testicular mass compatible with flight. Epithelial spermiophagy within the glomus and terminal ductus has been documented in several passerine species and likely serves to remove residual or defective spermatozoa (Chiba *et al*., 2011). In domestic chickens the ductus deferens itself constitutes the principal site of sperm storage, and external pressure applied to this region is routinely used for semen collection in artificial-insemination programs (Jacob *et al.,* 2013).

The ductus deferens is highly convoluted and increases in diameter caudally under the influence of smooth muscle, as described in domestic fowl and turkey. The absence of intraepithelial glands distinguishes the linnet from the domestic chicken and aligns it more closely with other wild passerines and the turkey (Tingari, 1971; Hess *et al*., 1976; Bull *et al*., 2007). The seminal glomus functions both as a storage reservoir and as a site of final sperm maturation. Recent detailed staging of the seminiferous epithelium cycle in the zebra finch has revealed a more complex organization than previously recognized in non-passerines, with each stage containing spermatids at two or three maturation steps (Bikchurina *et al.*, 2025); the three-phase spermatogenic sequence observed light-microscopically in the linnet is consistent with this framework.

Seasonal cyclic changes regeneration of tubules and interstitial cells, acceleration of gametogenesis, and culmination with maximal sperm production-mirror those reported in Eurasian tree sparrows, European starlings, and other multi-brooded passerines under photoperiodic control (Chan and Lofts, 1974; Bellamy and Kendall, 1985; Yatung and Trivedi, 2025). In domestic chickens, by contrast, testicular development is essentially continuous: seminiferous-tubule formation is completed by one month of age, all spermatogenic cell types are present by three months (sexual maturity), and the GSI reaches its highest values at this stage before plateauing. Apoptotic resorption of selected seminiferous tubules, observed in one-week-old chicks, appears to participate in the physiological regulation of germ-cell numbers during early post-hatch growth (Mfoundou *et al*., 2022). Comparative data therefore indicate that while the basic cellular architecture of Sertoli and Leydig cells is conserved across birds and even shares many features with mammals (Al-Tememy, 2010; Razi *et al*., 2010; Ozegbe *et al*., 2012), quantitative parameters (tubule diameter, interstitial volume fraction, sperm-storage capacity, and the relative development of the rete testis) are finely tuned to phylogenetic position and life-history strategy (Aire, 2007; Ozegbe *et al*., 2012). Domestic chickens, selected for continuous high fertility, lack the pronounced seasonal regression characteristic of wild passerines such as the linnet (Jacob *et al*., 2013; Mfoundou *et al*., 2022).

Limitations of the present study include the modest sample size (eight birds) and restriction to light microscopy. Future investigations employing transmission electron microscopy,

immunohistochemistry of cytoskeletal and extracellular-matrix proteins, quantitative morphometry across the full annual cycle, and correlation with circulating hormone levels would further refine understanding of species-specific adaptations in this and related fringillids.

In conclusion, the male reproductive system of the Eurasian linnet exhibits the classic passerine architecture: asymmetric intra-abdominal testes that enlarge seasonally, a compact undivided epididymis, a highly convoluted ductus deferens terminating in a seminal glomus, and a functional rete testis. The absence of intraepithelial glands in the deferent duct and the prominence of the seminal glomus as the principal sperm reservoir distinguish it from domestic galliforms while aligning it with other wild songbirds. Together, these findings demonstrate marked reproductive-state-associated remodeling of the male reproductive tract in the Eurasian linnet and provide baseline anatomical and histological data for comparative studies of passerine reproductive biology. The data provide a useful reference for comparative avian histology and for future studies of reproductive physiology and conservation of fringillid finches.

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Conflict of Interest

The authors declare no conflict of interest.

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