

Studies of fluid and spermatozoal transport in the extratesticular genital ducts of the Japanese quail

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INTRODUCTION

Histological studies of the structure of the avian extratesticular genital ducts have shown that the system is differentiated anatomically into an epididymal region and the ductus deferens (domestic fowl: Lake, 1957; Tingari, 1971, 1972; Aire, 1980, 1982*a*; Japanese quail: Aire, 1979*a*, 1980, 1982*a*; guinea-fowl: Aire, Ayeni & Olowo-Okoron, 1979; Aire, 1980, 1982*a*; drake: Aire, 1982*a,b*; turkey: Hess, Thurston & Biellier, 1976; Hess & Thurston, 1977; ratites: Budras & Meier, 1981). The epididymal region consists of the ductuli efferentes, connecting ducts and ductus epididymidis (Budras & Sauer, 1975; Aire, 1979*a*) arranged as shown in Figure 1. Ultrastructural studies (Tingari, 1972; Aire, 1980) showed that the ductuli efferentes are lined by a ciliated epithelium and the connecting ducts, ductus epididymidis and ductus deferens, by a nonciliated epithelium which is structurally similar throughout the length of the ducts.

The functions of the avian male genital ducts are poorly understood. Work on the domestic fowl indicates that spermatozoa develop their capacity for motility as they pass through the ducts and that this development greatly improves their ability to ascend the female reproductive tract to the site of fertilisation (Munro, 1938*a*; Howarth, 1983). Spermatozoa in the Japanese quail also improve their capacity for motility as they pass through the male ducts (Clulow & Jones, 1982). However, the duration of their passage through the ducts is only 1 to 2 days in the quail and fowl (Amir, Braun-Eilon & Schindler, 1973; de Reviers, 1975; Clulow & Jones, 1982) compared to 8 to 25 days in mammals (Rowley, Teshima & Heller, 1970; Hamilton, 1972; Robb, Amann & Killian, 1978). Further, when spermatozoa are isolated between ligatures within the ductus deferens they do not survive as long in the fowl (10–14 days; Munro, 1938*b*) or quail (5–9 days; Clulow & Jones, 1982) as in mammals (42 days; White, 1932).

The study described in this report was carried out further to investigate the role, in spermatozoal maturation and storage, of the extratesticular genital ducts in the Japanese quail and to provide a basis for subsequent physiological studies on the regulation of the luminal *milieu* along the ducts. Stereological procedures have been used to determine lengths, surface areas and volumes of different components of the ducts so that the values can be used for comparison between different parts of the duct system and for comparison with other species. The estimates have been used in this report to determine net fluid transport across the duct epithelium, spermatozoal velocity and transit times and the distribution of spermatozoa along the ducts.

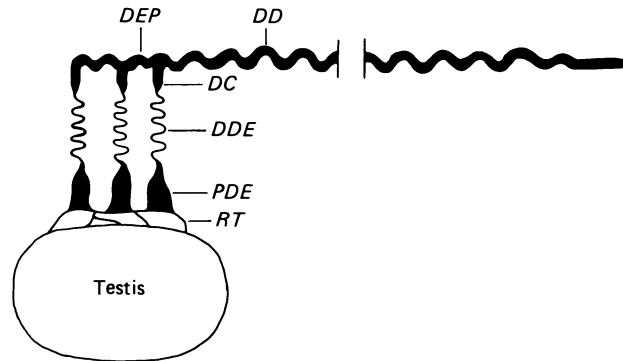


Fig. 1. Diagram showing the arrangement of the extratesticular genital ducts in the Japanese quail. Numerous ductuli efferentes leave the extratesticular portion of the rete testes (RT). Each ductulus efferens is differentiated into a cavernous proximal region (PDE) and a narrow distal region (DDE) which is joined to the ductus epididymidis (DEP) by a connecting duct (DC). The ductus epididymidis receives connecting ducts as it runs along the dorsal surface of the epididymal region of the genital ducts and the duct then continues caudally as the ductus deferens (DD).

MATERIALS AND METHODS

Mature males more than 10 weeks old and weighing approximately 150 g were maintained on a 16 L:8 D light regime for at least 6 weeks prior to examination. The arrangement of the genital ducts is shown in Figure 1.

Number of ductuli efferentes

The number and arrangement of ductuli efferentes and their associated connecting ducts were examined in 3 animals by dissecting the ductuli from their supporting stroma using jeweller's forceps after acid digestion in 1 M hydrochloric acid in 90% ethanol.

Stereology

One reproductive tract from each of three animals killed by decapitation with a guillotine was fixed in Bouin's fluid, embedded in Paraplast (Monoject Scientific, Kildare, Ireland) and sectioned at 5 μm . The sections were stained with haematoxylin and eosin. Six to ten sections (depending upon the animal) from each specimen were used for stereological analyses of the epididymal region and 40 sections were used for the analyses of the ductus deferens. Initially, the ductus deferens was divided for examination into four regions of equal length. However, as there was little difference in results for each of these regions the data were pooled and are presented for only two divisions, the proximal and distal ductus deferens.

The stereological procedures, which are based on Weibel, Kistler & Scherle (1966), were described in detail in an earlier report (Djakiew & Jones, 1982). The procedures were used to obtain estimates of length, surface area and volume parameters of the genital ducts and to determine the concentration of spermatozoa within the ducts. A Micropan projection microscope (Nikon, Japan) was used to magnify and project the images onto a stereological grid (magnification of $\times 100$ –300 for tissue sections and $\times 1500$ –3000 for spermatocrits).

The absolute volumes of the epididymal region and the ductus deferens were calculated from determinations of mass and density. The density of one tract from each of three animals was measured with a pycnometer (mean \pm SEM = $0.89 \pm 0.02 \text{ g cm}^{-3}$).

and the mass of each region was determined using tracts from 10 animals (one tract per animal).

All of the values described in the Results have been corrected for shrinkage due to fixation and processing. The amount of shrinkage was estimated by comparing frozen sections (cut at -20°C on a Minot cryostat, International Equipment Co., Massachusetts) and paraffin-embedded sections. Estimates of linear shrinkage (ratio of mean duct diameter of frozen : paraffin sections) were obtained for sections from the distal ductuli efferentes and the ductus deferens (10 sections per duct per animal for each of 3 animals). The shrinkage factors were much the same for both regions (distal ductuli efferentes = 1.19 ± 0.06 , ductus deferens = 1.18 ± 0.05).

Estimates of percentage luminal volume occupied by spermatozoa (spermatocrit, S) were obtained using the formula:

$$S = \frac{100 \times V_s}{V_s + V_L} (\%)$$

where V_s = volume ratio of spermatozoa;
 V_L = volume ratio of lumen unoccupied by spermatozoa.

The number of spermatozoa in each duct (N) was calculated by the formula:

$$N = \frac{S_i \times V_i}{\Sigma(S_i \times V_i)} \times \text{EGS}$$

where S_i = spermatocrit for duct i (%);
 V_i = luminal volume for duct i (mm^3);
 EGS = total number of extragonadal spermatozoa, 154×10^6 (Clulow & Jones, 1982);
 Σ = sum for all ducts.

The tubular content leaving the testis (testicular output, TO) was estimated as:

$$\text{TO} = \frac{\text{TSO} \times \text{LV}}{\text{NS}} (\mu\text{l}/\text{h})$$

where TSO = testicular spermatozoal output, $6.4 \times 10^6/\text{h}$ (Clulow & Jones, 1982);
 LV = luminal volume of the rete testis (μl);
 NS = number of spermatozoa in the rete testis.

Testicular fluid output was converted to testicular plasma output (TPO) using the formula:

$$\text{TPO} = \text{TO} - (\text{TO} \times S_{\text{RT}}) (\mu\text{l}/\text{h})$$

where S_{RT} = spermatocrit for the rete testis.

Estimates of net fluid reabsorption between two regions (R) was expressed as a percentage of the amount of plasma present at the proximal region and was calculated as:

$$R = \frac{100(S_2 - S_1)}{S_2(1 - S_1)} (\%)$$

where S_1 = spermatocrit for proximal region and S_2 = spermatocrit for distal region.

The amount of fluid reabsorbed ($\mu\text{l/h}$) between proximal and distal regions was calculated as the product of R and the plasma flow rate in the proximal region commencing with the plasma output of the testis (TPO). Values were also expressed as a function of duct surface area (A) and volume of epithelium lining the duct (V) by dividing estimates by A and V respectively where A and V are means of the proximal and distal regions under consideration.

The duration of spermatozoal transit (T_i) and velocity (vel.) through each region of the genital ducts was calculated using the following formulae:

$$T_i = \frac{S_i V_i \times T}{\Sigma(S_i \times V_i)} \text{ (min)} \quad \text{and} \quad \text{vel}_i = \frac{L_i}{T_i} \text{ (mm/min)}$$

where $S_i V_i$ = stereological estimate of total spermatozoal volume in region i (mm^3);

T = total duration of spermatozoal transport through the spermatic ducts (1 day; Clulow & Jones, 1982);

L_i = stereological estimate of the length of the duct i (mm).

Micropuncture procedures

Samples of luminal fluid from the genital ducts were collected using micropuncture procedures (Djakiew & Jones, 1983) in order to obtain direct estimates of spermatozoal concentration. Quail were anaesthetised with 5-sec-butyl-5-ethyl-thiobarbituric acid (Inactin: Byk Gulden Pharmaceuticals, Konstanz, West Germany) administered intramuscularly at a dose of 200 mg/kg and were killed at the completion of micropuncture by an overdose of anaesthetic. Samples of luminal fluid were collected from the seminiferous tubules, the proximal end of the ductuli efferentes, ductus epididymidis and the proximal and distal ends of the ductus deferens. The samples were diluted in formal saline and spermatozoa counted in a modified Neubauer haemocytometer.

Statistical estimates

Standard errors are given with mean values in the text and Tables except in Tables 3 and 4 where the values are derived by the product or division of two means (Djakiew & Jones, 1982). The standard errors were calculated from estimates of the variance between animals.

RESULTS

The volume of the epididymal region (mean \pm SEM from 10 animals) was $49.6 \pm 3.4 \text{ mm}^3$ and that of the ductus deferens was $95.6 \pm 5.0 \text{ mm}^3$. The number of ductuli efferentes and associated connecting ducts was estimated to be 43 ± 2 (mean \pm SEM from 3 animals).

Stereological estimates of duct length, surface area and volume are summarised in Table 1. The plasma output of the testis was estimated to be $222 \mu\text{l/h}$. Other values derived from the estimates in Table 1 are shown in Tables 2–4. Table 2 shows stereological estimates of spermatocrit and number of spermatozoa in each region together with determinations of spermatozoal concentration from the micropuncture samples. Table 3 shows estimates of net fluid flux across the duct epithelium and indicates that there is a net reabsorption of fluid by all of the ducts. Table 4

Table 1. *Morphometry of the male genital ducts of the Japanese quail. Values are means \pm SEM from 3 quail*

Parameter	Rete testis	Proximal ductuli efferentes	Distal ductuli efferentes	Connecting ducts	Ductus epididymidis	Ductus deferens
Total duct length (mm)	—	—	868 \pm 328	153 \pm 57	83 \pm 23	488 \pm 102
Total duct volume (mm ³)	2.1 \pm 0.5	18.2 \pm 2.8	3.7 \pm 0.8	2.5 \pm 1.2	5.1 \pm 1.7	62.0 \pm 6.9
Volume of epithelium (mm ³)	0.6 \pm 0.2	7.8 \pm 1.2	2.2 \pm 0.4	1.1 \pm 0.4	1.6 \pm 0.3	14.7 \pm 1.6
Volume of lumen (mm ³)	1.6 \pm 0.4	10.4 \pm 1.6	1.5 \pm 0.3	1.3 \pm 0.7	3.6 \pm 1.4	47.3 \pm 6.3
Surface area of lumen (mm ²)	62 \pm 11	285 \pm 52	94 \pm 21	40 \pm 15	45 \pm 10	518 \pm 78
Surface area of basal border (mm ²)	61 \pm 12	283 \pm 59	146 \pm 34	49 \pm 18	52 \pm 12	596 \pm 97
Luminal S.A./luminal vol. ratio	43.4 \pm 10.0	27.5 \pm 2.7	65.3 \pm 6.9	39.0 \pm 8.8	14.7 \pm 3.9	10.9 \pm 0.3
Epithelial vol./lumen vol. ratio	0.37 \pm 0.05	0.76 \pm 0.01	1.54 \pm 0.15	1.03 \pm 0.20	0.51 \pm 0.12	0.32 \pm 0.05

Table 2. *Estimates of spermatozoal concentrations from micropuncture samples, and estimates of spermatocrits and number of spermatozoa per region from stereological determinations. Means \pm SE means from 5 quail for the micropuncture determinations and 3 quail for the stereological estimates*

Site	Sperm. Conc. (10 ³ sperm. μ l ⁻¹)	Spermatocrit (%)	No. spermatozoa
Seminiferous tubule	38 \pm 10	—	—
Rete testis	—	0.2 \pm 0.04	4.6 \times 10 ⁴
Ductuli efferentes:			
Proximal	76 \pm 49	0.2 \pm 0.05	3.2 \times 10 ⁵
Distal	—	1.9 \pm 1.44	5.4 \times 10 ⁵
Connecting ducts	—	9.4 \pm 1.86	2.3 \times 10 ⁶
Ductus epididymidis	2151 \pm 865	12.4 \pm 2.79	8.6 \times 10 ⁶
Proximal ductus deferens	2256 \pm 282	14.7 \pm 1.19	66.5 \times 10 ⁶
Distal ductus deferens	2276 \pm 377	18.4 \pm 1.70	75.6 \times 10 ⁶

summarises estimates of duration of spermatozoal transit and velocity. These estimates are described below for each region of the duct system.

Rete testis

The rete testis consists of narrow channels and lacunae lined by a simple squamous or low cuboidal epithelium (mean \pm SEM height = 8.0 \pm 0.7 μ m). It is the smallest part (2.3% of total volume) of the extratesticular genital ducts and spermatozoa spend less time (25 seconds) in this region than elsewhere in the system. The ratio of surface area of luminal border: luminal volume is large. Nevertheless, as estimates of spermatocrit for the rete testis and proximal ductuli efferentes are much the same it is concluded that there is little net fluid transport across the duct epithelium.

Table 3. *Estimates of plasma flux (reabsorption) across the epithelium lining the genital ducts of the male Japanese quail. Mean estimates from stereological determinations on 3 quail. Values are expressed as percentages and $\mu\text{l/h}$ per region, per surface area of luminal border and per volume of duct epithelium*

Region	% Proximal* region	% TPO†	Cumulative % TPO‡	$\mu\text{l/h}$	$\mu\text{l/cm}^2/\text{h}$	$\mu\text{l/mm}^3/\text{h}$
RT-proximal DE	6.3	6.3	6.3	13.9	8.0	3.31
Proximal DE-distal DE	91.5	85.8	92.0	190.3	100.4	37.91
Distal DE-DC	81.9	6.5	98.6	14.5	21.6	8.68
DC-DEP	26.8	0.4	98.9	0.9	2.1	0.67
DEP-proximal DD	17.8	0.2	99.1	0.4	0.1	0.05
Proximal DD-distal DD	23.5	0.2	99.3	0.4	0.2	0.05

* % of plasma entering proximal region reabsorbed between proximal and distal region.

† Plasma reabsorption between sites as a percentage of testicular plasma output (TPO).

‡ Cumulative reabsorption of plasma at sites along the genital ducts expressed as % of TPO.

RT, rete testis; DE, ductuli efferentes; DC, connecting ducts; DEP, ductus epididymidis; DD, ductus deferens.

Table 4. *Estimate from stereological data of mean duration of spermatozoal transit and velocity through each region of the genital ducts of the Japanese quail. Means from 3 quail.*

Duct	Duration	Velocity mm/min
Rete testis	25 seconds	
Ductuli efferentes		
Proximal	3 minutes	
Distal	5 minutes	4.00
Connecting ducts	22 minutes	0.16
Ductus epididymidis	80 minutes	1.04
Ductus deferens	22.2 hours	0.37

Ductuli efferentes

The proximal part of the ductuli consists of irregularly shaped interconnected caverns and so estimates of duct length would be meaningless. The distal ductules are tubular (mean \pm SEM diameter of $51.0 \pm 3.2 \mu\text{m}$). The ductuli are lined by a columnar epithelium (mean \pm SEM height of $25.6 \pm 3.4 \mu\text{m}$ proximal, $15.6 \pm 1.6 \mu\text{m}$ distal). Although they only make up 19% of the total volume of the genital ducts, altogether the ductuli constitute the greatest length of duct system being almost twice as long as the ductus deferens. Nevertheless, individual distal ductuli are only about 20.2 mm long so that spermatozoa only spend about 5 minutes passing through them and a total of 8 minutes passing through the total length of all the ductuli efferentes. The ratio of surface area of the luminal border:luminal volume is larger for the ductuli than for other parts of the extratesticular duct system. The ductuli also reabsorb more fluid than other parts of the system. Indeed, between the proximal and distal ends of the ductuli, 190.3 $\mu\text{l/h}$ of fluid is reabsorbed (equivalent to 85.8% of the fluid leaving the testis) compared to a total of 0.4–0.9 $\mu\text{l/h}$ for more caudal regions. When expressed as a function of surface area of epithelium facing the duct lumen and

epithelial volume, net fluid transport from the ductuli is, respectively, $100.4 \mu\text{l}/\text{cm}^2$ lumen S.A/h and $37.9 \mu\text{l}/\text{mm}^3$ epithelial volume/h.

Connecting ducts, ductus epididymidis and ductus deferens

When viewed in histological sections the structure of the epithelia lining the ducts is similar. The height of the epithelium is much the same in the connecting ducts ($20.7 \pm 1.5 \mu\text{m}$) and ductus epididymidis ($21.6 \pm 2.0 \mu\text{m}$) but reduces to $15.0 \pm 1.3 \mu\text{m}$ at the caudal end of the ductus deferens. The diameter of the ducts in these regions is, respectively, $200 \pm 25.7 \mu\text{m}$, $348 \pm 29.0 \mu\text{m}$ and $500 \pm 46.0 \mu\text{m}$.

The connecting ducts occupy only 2.7% of the total volume of the extratesticular duct system. When the lengths of individual ducts are added together the total length is about twice as long (193 mm) as the ductus epididymidis, but only 32% of the length of the ductus deferens and 18% of the total length of all the ductuli efferentes. Each connecting duct is only 3.6 mm long. However, because the spermatozoa have been concentrated in the ductuli efferentes transit time through the connecting ducts (22 minutes) is longer than through the ductuli efferentes (8 minutes). The ratio of surface area of luminal border:luminal volume is high for the connecting ducts but it is not associated with a large net fluid transport across the duct epithelium ($0.9\text{--}14.5 \mu\text{l h}^{-1}$).

The ductus epididymidis occupies 5.5% of the volume of the extratesticular ducts and it is much shorter (83 mm) than the ductus deferens (488 mm). The latter occupies 66% of the duct system; it contains most of the extragonadal spermatozoa (92.3%) and they spend much longer (22.2 hours) in this duct than in other parts of the extratesticular duct system. Spermatocrits show that there is little net fluid transport in the ductus epididymidis or ductus deferens.

DISCUSSION

To our knowledge this is the first detailed, quantitative study of spermatozoal and fluid transport in all regions of the avian male genital ducts. Due to several features of the avian duct system, it is considered that stereological methods are the most appropriate methods for this sort of study. One feature of the avian genital ducts which precludes the use of conventional histological methods involving linear measurements of duct dimensions is that profiles of a duct are usually irregularly shaped and arranged so that there is little chance of seeing round profiles in histological sections, particularly in the proximal part of the epididymal region where the ducts are not tubular. Conventional histological procedures involving autoradiography of ^3H -thymidine-labelled spermatozoa are also of limited value for studying spermatozoal transport in the avian ducts. This is because transport through some regions, such as the rete testis is too rapid (30 seconds) to be determined with a pulse of labelled spermatozoa. Other features of the duct system limit the application of micropuncture procedures to study the luminal fluids. In this respect it is not possible confidently to identify some regions (e.g. connecting ducts) from external morphology and because the testis and its ducts are closely attached to the dorsal wall of the abdomen, it is not possible satisfactorily to support the epididymal region independently without its being affected by the animal's ventilation movements.

The stereological data described in this report are in broad agreement with those of Aire (1979*b*) who determined volume ratios for the genital ducts of the Japanese quail as well as two other birds. The only noteworthy discrepancy between this and Aire's (1979*b*) report is that Aire found that the ductus epididymidis occupies a much smaller proportion of the epididymal region (2.4%) than was found in this study (10.4%).

This discrepancy may be due to differences in defining the epididymal region, as the boundary of the epididymal region and the ductus deferens is not distinct. Further, the frequency of connecting ductules is high in this boundary region so that slight variation in sampling may lead to large variations in the proportion of ductules and the amount of the ductus (epididymidis) which is considered to be part of the epididymal region.

There seems to be good general agreement between findings from the stereological studies and findings determined by more conventional methods. For example, considering the duration of spermatozoal transit through the ducts, values determined by stereological techniques were 110 minutes and 22.2 hours, respectively, for spermatozoa to travel through the epididymal region and ductus deferens whilst the corresponding values determined by spermatozoal counts of homogenates (Clulow & Jones, 1982) were 108 minutes and 22.2 hours. Further, determinations of spermatozoal concentrations based on stereological spermatocrits and haemocytometer counts of micropuncture samples show similar trends and produce similar values for total fluid reabsorption (99.3% stereology, 98.2% micropuncture). However, calculated values for fluid reabsorption differ, depending on the method of determination. For example, the stereological estimates indicate that the ductus epididymidis and ductus deferens reabsorb 37.1% of the plasma leaving the testis whereas the micropuncture studies indicate that only 5.5% of the plasma is reabsorbed. Such differences are explained in part by the variation between individual animals since the two procedures were performed on different animals. For example, differences between animals in the size of the ductus epididymidis are clearly visible during dissection even without any quantitative procedure being employed.

An outstanding feature of the extratesticular genital ducts in the quail is the considerable amount of fluid that they reabsorb. For example, our estimates indicate that the rate of plasma reabsorption is much greater in the ductuli efferentes of the quail ($100 \mu\text{l}/\text{cm}^2/\text{h}$) than the ductuli efferentes ($12.7 \mu\text{l}/\text{cm}^2/\text{h}$; Jones & Jurd, 1987) or proximal convoluted tubules ($2.2 \mu\text{l}/\text{cm}^2/\text{h}$; House, 1974) of the rat. This high rate of absorption in the quail ductuli is associated with the very high rate of fluid production by the testes ($133 \mu\text{l}/\text{g}/\text{h}$) which is much greater than that reported for mammals ($5\text{--}40 \mu\text{l}/\text{g}/\text{h}$; Waites & Gladwell, 1982). The structure of the ductuli efferentes is clearly adapted for fluid reabsorption. The main adaptations are the arrangement of the system into a large number of narrow ducts arranged in parallel to provide a large ratio of luminal surface area:luminal volume. Ultrastructural features of the epithelium lining the ductuli are also characteristic of a transporting epithelium (Tingari, 1972; Hess & Thurston, 1977; Aire, 1980). In particular the non-ciliated, Type 1 cells described by Aire (1980) are characterised by a large number of basally located mitochondria and a well developed apical brush border with deep canaliculi forming pinocytotic vesicles at the base. Aire (1980) concluded that fluid reabsorption occurs principally in the proximal ductuli efferentes with the resultant formation of a dense mass of spermatozoa in the distal ductuli efferentes. Our findings confirm that the concentration is about ten times higher in the distal than proximal ductuli. However, this does not necessarily indicate that the rates of fluid reabsorption differ between the two regions since the estimate is based on the mean spermatozoal concentration in each region. Furthermore, a comparison of spermatocrits in the distal ductuli efferentes and connecting ducts shows that there is a tenfold increase in the concentration of spermatozoa between these regions.

Although the duration of spermatozoal transport through the genital ducts of the quail is briefer than the duration of transport in mammals (see Introduction) it is

considered that this is a reflection of the distance that spermatozoa must travel in the quail (575 mm, Table 1) compared to mammals (3380 mm in the rat; Djakiew & Jones, 1982) and does not reflect a difference in the velocity of spermatozoal transit. This proposal is based on calculations (using data from Djakiew & Jones, 1982, and Robb *et al.* 1978) which show that spermatozoal velocity through the rat epididymis (caput, corpus = 0.39 mm/min, cauda = 0.20 mm/min) is similar to that in the quail ductus deferens (0.37 mm/min, Table 4).

A limitation of earlier studies on the extratesticular genital ducts of birds is that only one region of the duct system was examined (see review by Lake, 1966), so that from individual studies it is not possible to make conclusions about the relative contribution of different ducts to the overall functions of the system. However, the physiological parameters described in this report indicate that there is a division of labour in the genital ducts of the quail into two functional regions, the ductuli efferentes and the more caudal region of the duct system. The ductuli efferentes are clearly adapted for fluid reabsorption (see above) and are not immediately associated with spermatozoal maturation (Clulow & Jones, 1982). Further, the microanatomical adaptations for fluid reabsorption, involving the arrangement of a large number of short ducts in parallel, also favour short transit times for spermatozoa.

Work on the embryological development (Budras & Sauer, 1975; Croisille, 1981) and the structure of the duct mucosa in adults (Tingari, 1971, 1972; Aire, 1979; Aire *et al.* 1979a; Aire, 1982; this study) indicates that the connecting ducts, ductus epididymidis and ductus deferens form one functional unit. Estimates of fluid reabsorption and spermatozoal transit times also indicate that they are functionally quite different to the ductuli efferentes. Spermatozoa spend much longer in these ducts than in the ductuli and so the region provides some storage of spermatozoa available for ejaculation. Further, because they are concentrated as they enter the connecting ducts the composition of their *milieu* can be rapidly regulated. This latter feature is correlated with reports that spermatozoa mainly develop their 'mature' pattern of motility in this region (Clulow & Jones, 1982) a feature which seems to enhance their capacity to ascend the female reproductive tract to the site of fertilisation (Howarth, 1983).

SUMMARY

Stereological studies of the spermatic ducts of the quail were carried out for comparison between different parts of the system and those of other species, and to provide a basis for future physiological studies. Duct length, surface areas and volumes of various components of the ducts were determined. Values were subsequently used to calculate net fluxes of fluid across the duct epithelium, spermatozoal velocity and the distribution of spermatozoa throughout the system.

It was concluded that the extratesticular spermatic ducts are divided into 2 main parts: (1) the ductuli efferentes where spermatozoa spend a brief period (8 minutes) and which are adapted for considerable net fluid reabsorption ($100 \mu\text{l}/\text{cm}^2/\text{h}$), and (2) the connecting ducts, ductus epididymidis and ductus deferens where spermatozoa spend a longer period (24 hours) and which are involved in little net fluid transport ($0.14\text{--}2.1 \mu\text{l}/\text{cm}^2/\text{h}$). Most spermatozoa (92.3%) are located in the ductus deferens. The velocity of spermatozoal transport is much the same through the quail spermatic ducts (0.37 mm/min) as through the mammalian epididymis, the difference between classes in the duration of spermatozoal transport being due to differences in the distance that they travel.

In a comparison between estimates of spermatozoal concentration using stereological methods and direct counts of spermatozoa in samples collected using micropuncture procedures it was concluded that both methods gave similar results.

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