Features of spermatogenesis in the laughing dove *Streptopelia senegalensis*

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Spermatogenesis in the testis of the laughing dove *Streptopelia senegalensis*, a non-seasonal breeder, differs markedly from that in seasonal breeding birds. The testes probably never regress fully after reaching the mature stage and the tubules are kept in a development/regression equilibrium which allows mature spermatozoa to be produced throughout but also leaves some parts of the tubules in a resting condition. Spermatogenic development in the longitudinal as well as the horizontal level of each tubule can range from primary spermatocytes to mature spermatozoa.

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Spermatogenese in die testis van die rooibors duifie *Streptopelia senegalensis*, 'n voël wat dwarsdeur die jaar broei, verskil grootliks van dié van seisoenbroeiende voëls deurdat die testis waarskynlik nooit weer na 'n algehele onaktiewe toestand terugkeer nadat volwassenheid bereik is nie. Elke buisie word gehou in 'n ontwikkelings/rustende ewewig waartydens spermatozoa in een deel van die buisie geproduseer word terwyl ander dele in 'n rustoestand verkeer. In 'n enkele dwarssnit deur 'n buisie is verskeie ontwikkelingstadia gewoonlik sigbaar wat kan wissel van primêre spermatosiete tot volwasse spermatozoa.

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There have been few studies on the reproductive physiology of birds in southern Africa. The gonadal cycles of male and female laughing doves *Streptopelia senegalensis* throughout a single year were investigated as part of a study on the ecology and population dynamics of the laughing dove in the Barberspan area of the western Transvaal (Dean 1977, 1979a, 1979b, 1980). Breeding was recorded in every month of the year (Dean 1980) as were individuals with testes in full spermatogenesis (Dean 1979b). The stages of spermatogenesis in the testes of the laughing dove were not discussed in detail in previous papers. Spermatogenic features of the testes of the laughing dove differ from those of seasonal breeding bird species such as the Cape white-eye *Zosterops pallidus*, black-eyed bulbul *Pycnonotus barbatus*, yellow-eyed canary *Serinus mozambicus* (Earlé 1981) and zebra finch *Taeniopygia guttata* (Sossinka 1970) and differ from the general descriptions of annual reproductive cycles in birds. This paper presents data on spermatogenesis and the annual cycle of the laughing dove.

Material and Methods

Laughing doves were collected on Klippan, Barberspan area (26°32′S, 25°41′E), in an isolated patch of *Acacia karroo* woodland in an intensively farmed area. In all, 79 male specimens were collected from July 1976 to June 1977. Except for samples in the first three months, all the birds were dissected in the field and the gonads removed and fixed in Bouin's Fluid or formol-saline within 10 min of shooting. The testes were then dehydrated, embedded, sectioned at 10 μm and stained with Ehrlich's haematoxylon and eosin or Mallory's Triple Stain. By microscopical examination of the sections, developmental stages were determined on the basis of the state of the tunica albuginea and the presence and relative amount of different spermatogenic cells. Although spermatids were already present from stage 2, spermatid differentiation was not used as the main criterion for staging (*cf.* Clermont 1958) because the asynchronous development within a single tubule (see Discussion) gave significantly different spermatid counts at different levels of the tubule.

Results

Five developmental stages of the laughing dove testes were recognized.

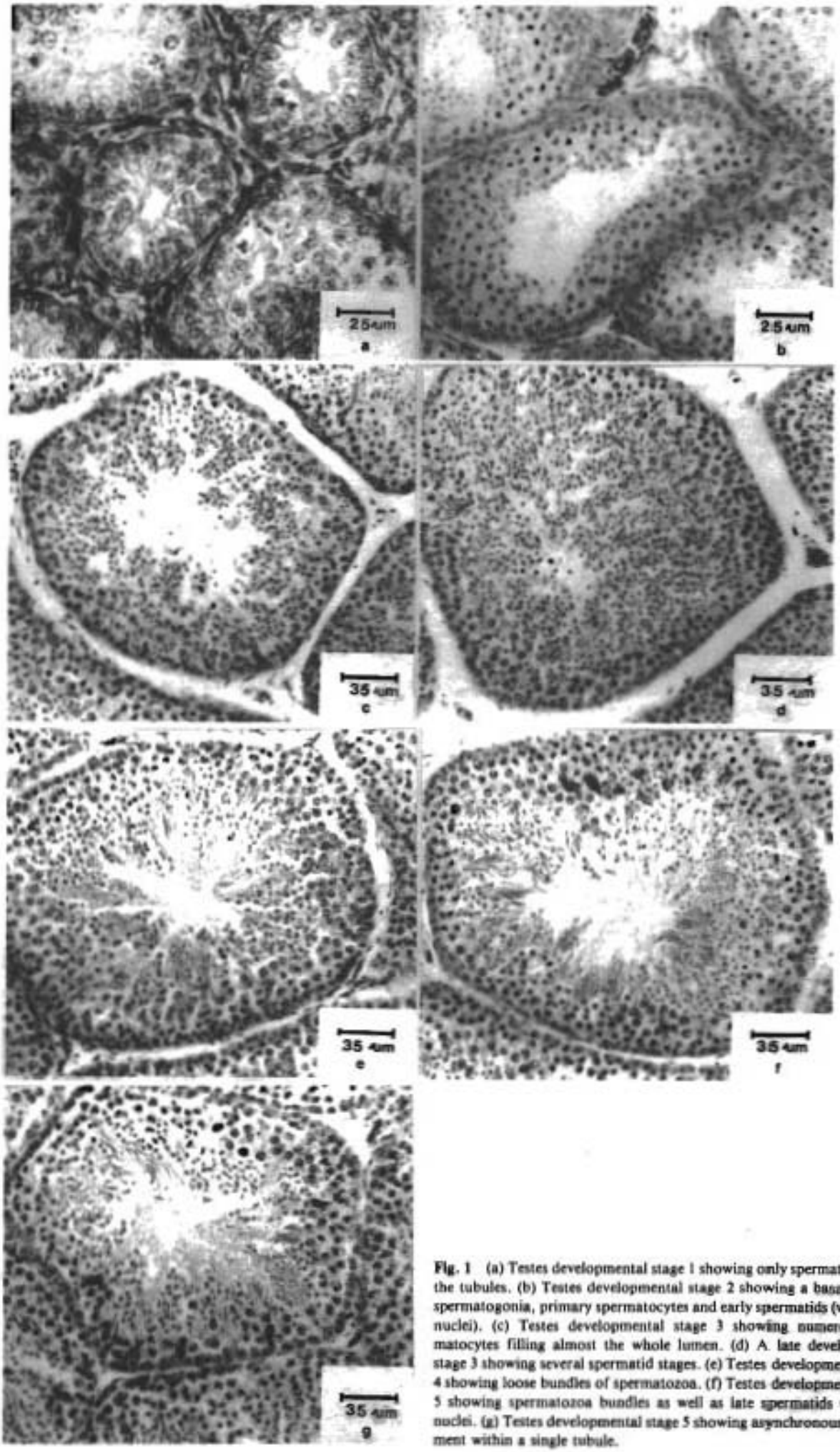

Fig. 1 (a) Testes developmental stage 1 showing only spermatogonia in the tubules. (b) Testes developmental stage 2 showing a basal layer of spermatogonia, primary spermatocytes and early spermatids (with small nuclei). (c) Testes developmental stage 3 showing numerous spermatocytes filling almost the whole lumen. (d) A late developmental stage 3 showing several spermatid stages. (e) Testes developmental stage 4 showing loose bundles of spermatozoa. (f) Testes developmental stage 5 showing spermatozoa bundles as well as late spermatids with oval nuclei. (g) Testes developmental stage 5 showing asynchronous development within a single tubule.

Stage 1: The testes were usually very small (4 – 6 mm in length). At first only one layer of spermatogonia lined the tubules. Mitoses could be seen in a large number of spermatogonia and in the latter stages two layers of spermatogonia lined the tubules (Figure 1a). No cells occurred in the lumen centre. Between the tubules great numbers of active interstitial cells could be seen. The tunica albuginea was still thick and the nuclei of these cells rounded.

Stage 2: The testes were about 10 mm in length and a basal layer of spermatogonia lined the tubules. A primary spermatocyte layer of four to seven cells was also present (Figure 1b). Few spermatids, with very small nuclei, appeared on the lumenid side of the primary spermatocytes. In most of the tubules the lumen was still present. Few interstitial cells were present. The tunica albuginea was very thin and no individual cells could be recognized.

Stage 3: The testes were 10,5 – 16 mm in length. Spermatocytes filled almost the whole lumen (Figure 1c). A late stage 3 section showed several spermatid stages but no spermatozoa (Figure 1d). Very few interstitial cells were visible and the tunica albuginea was a very thin layer with no recognizable individual cells.

Stage 4: The testes were 13 – 21 mm in length (one of 7,1 mm). Long spermatozoon heads were now visible usually in loose bundles of three to eight (Figure 1e). In less than 10% of the tubules could free spermatozoa be seen in the lumen. Only one or no spermatozoa bundles were present in each of the tubules.

Stage 5: The testes were now 14 – 25 mm in length. This stage only differed from stage 4 in that two to ten spermatozoa bundles, where the spermatozoa heads were tightly packed, were present in all the tubules (Figure 1f). Free spermatozoa could be seen in more than 40% of the tubule lumina.

In total, 82% ($n = 64$) of all the specimens collected, had testes in either developmental stage 4 or 5 and were considered to be capable of breeding. However, none of these testes showed synchronous development in any one tubule and in Figure 1f and 1g almost all the spermatozoon developmental stages can be seen in a single tubule section.

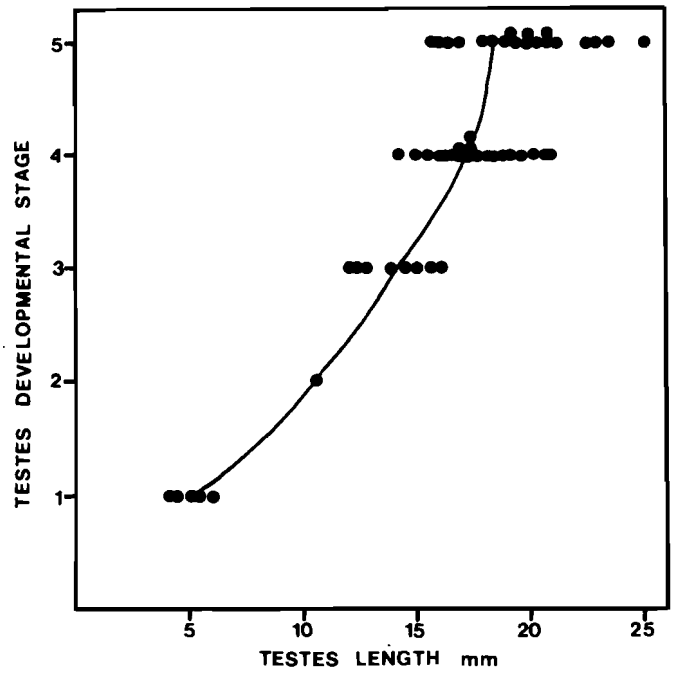

Fig. 2 The length of the larger testes of male laughing doves collected at Barberspan given against the developmental stage for each testis. The line indicates the mean length of all testes measured.

The developmental stage of each testis is given against the length of the larger testis of each specimen in Figure 2. The mean testis length in stage 4 was 17,2 mm ($n = 58$) and in stage 5 it was 18,4 mm ($n = 53$). November was the only month in which no specimens with testes in developmental stage 4 were found (Figure 3) with the majority regressed to developmental stage 3. November was the month of peak moult (Figure 3, Dean 1979b).

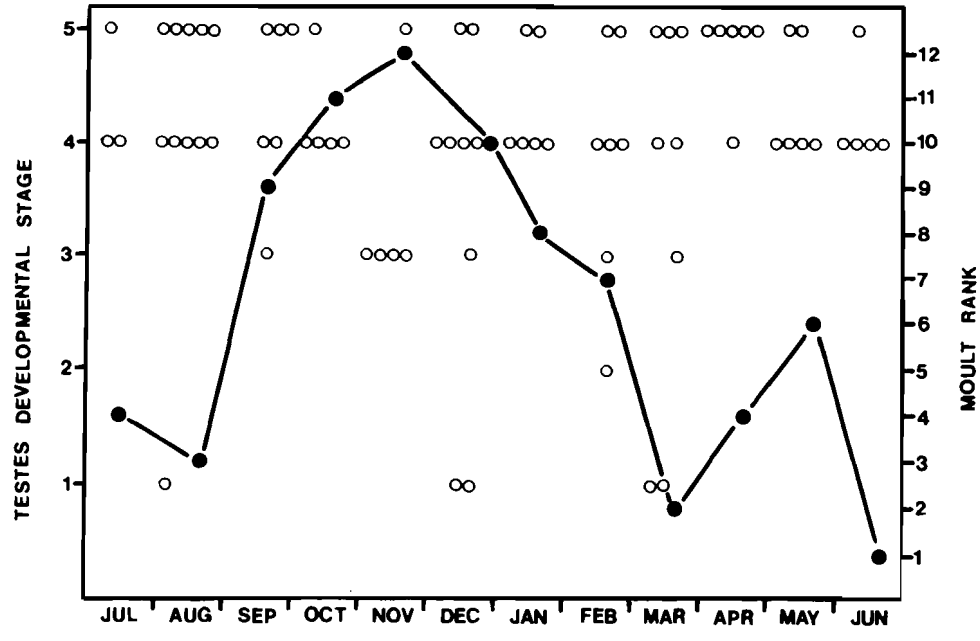

Fig. 3 A scattergram of the developmental stages of all testes of male laughing doves collected at Barberspan. The graph represents the percentage of adult laughing doves in moult ranked in order from the month of least activity (= 1) to the month of highest moult activity (= 12).

Discussion

The testes of the laughing dove probably never regress fully after reaching the mature stage. This is supported by the fact that only one (1,3%) of the males collected had testes in developmental stage 2 and that at least two of the five (and probably all) specimens collected with testes in stage 1, were juvenile birds. However, in the month of peak moult and minimum breeding, November (Dean 1979b, 1980), the testes did regress to stage 3 in most individuals (Figure 3). Frith, Mackean & Braithwaite (1976) found 16,3% ($n = 129$) of all the collected laughing dove males in Australia, with testes in a state of degeneration and thus not capable of breeding. This is very similar to the 18% birds not capable of breeding found in the present study.

A non-seasonal breeder such as the laughing dove does not follow the seasonal annual pattern of development and regression of the testes as described by Lofts & Murton (1973) but probably has the testicular tubules in some development/regression equilibrium which would allow mature spermatozoa to be produced throughout the year but would also have some parts of the tubules in a resting condition. It has been established in mammals that the spermatogenic condition of the germinal epithelium is not synchronous throughout the length of any given tubule but shows a longitudinal progression in the form of a wave of development along the length of the tubule (Lofts & Murton 1973). It seems as if there is an even greater asynchronization in the testes of the laughing dove in that spermatogenic development in the longitudinal as well as the horizontal level of each tubule can range from primary spermatocytes to mature spermatozoa (Figure 1g). Marshall's (1961) statement that in bird species with a protracted breeding season, spermatozoa are released in waves seems to be particularly true for the laughing dove with an all-year-round breeding season. This process, whereby mature spermatozoa are produced continuously at presumably a slower rate than maximum, is probably not too energy demanding and does take place simultaneously with other physiological energy demanding processes such as moult (*cf.* Dean 1979b).

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