THE UNIVERSITY OF MANITOBA

HISTOLOGICAL CHANGES IN THE TESTES OF THE SHARP-TAILED GROUSE (*Pedioecetes phasianellus* Linnaeus) IN RELATION TO DANCING GROUND SIZE AND ORGANIZATION.

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ABSTRACT

Histological Changes in the Testes of the Sharp-tailed Grouse (Pedioecetes phasianellus Linnaeus) in Relation to Dancing Ground Size and Organization.

Wayne Michael Nitchuk

The testes of 64 Sharp-tailed Grouse (Pedioecetes phasianellus Linnaeus) were collected from 20 dancing grounds near Hodgson, Manitoba. Testis volume, stage of spermatogenesis, maximum diameters of seminiferous tubule lumina, testis vascularity, incidence of mitochondria in interstitial cells, and interstitial cell level of cholesterol were measured to determine if histological changes during the breeding season varied with age, dancing ground size and social organization.

The levels of cholesterol and testis vascularity were maximal early in the display period and declined thereafter. Testis volume, spermatogenesis, seminiferous tubule diameters, and mitochondria incidence increased early in the season and were sustained until sampling ceased.

Comparisons between adults and juveniles, and between males from large and small dancing grounds revealed no

significant differences in body weight or testis histology. On large dancing grounds, the testes of high-dominance central males showed significantly greater levels of cholesterol, and stages of spermatogenesis than those of the low-dominance peripheral males.

The results indicated that Sharp-tailed Grouse males were reproductively mature by about one year of age, and that age structure did not appear to constitute an important basis for dancing ground organization. The data provided no evidence that males from small and large dancing grounds differed as a result of different degrees of social stimulation. Within large dancing grounds, the greater levels of spermatogenesis and cholesterol found in the more dominant centrally-located and reproductively active males appeared to constitute important functional and causal correlates of dancing ground organization.

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INTRODUCTION

Although the display and mating behaviour of the male Sharp-tailed Grouse (Pedioecetes phasianellus Linnaeus) has been described by several authors (e.g. Bent, 1932; Johnson, 1934; Marshall and Jensen, 1937; Grange, 1940; Hart et al, 1950; Hamerstrom and Hamerstrom, 1960; Evans, 1961; Lumsden, 1965), detailed investigations of the histological or physiological correlates of display and mating behaviour were limited primarily to studies of the testicular cycle in other grouse species, particularly the Sage Grouse (Centrocercus urophasianus) (Eng, 1963) and Blue Grouse (Dendragapus obscurus) (Simard, 1964). A histological description of the testis cycle throughout the breeding season, and the interrelations between this cycle and various aspects of display behaviour in the Sharp-tailed Grouse have received only limited treatment (Evans, 1961). The present study was designed to provide a more detailed analysis of testis histology in this species. In particular, the hypothesis was examined that during the breeding season, testis development, spermatogenesis, and the interstitial cycle of Sharp-tailed Grouse are similar to that reported for the related genera of Sage Grouse and Blue Grouse. To further delineate possible

biological and behaviourial correlates of the testis cycle, the hypothesis that at least the main phases of the testis cycle vary systematically with age of males, dancing ground size, and position of males on the dancing grounds, was also investigated.

Eng (1963) and Simard (1964) reported that juvenile male Blue Grouse and Sage Grouse had smaller gonads, a slower recrudescence, a later peak in spermatogenesis, and a shorter breeding period than the adults. The possibility of a similar phenomenon occurring in Sharp-tailed Grouse was examined in the present study.

Hamerstrom and Hamerstrom (1955) noted that the probability of a female Prairie Chicken (Tympanuchus cupido pinnatus) being mated on a small ground, containing from one to 10 males, was less than that on a medium ground, containing 11 to 15 males. Darling (1938; 1952) hypothesized that display grounds that are too small may lack social stimulation and therefore be less suitable. The above studies suggested the possibility that both androgen levels and spermatogenesis may be less for birds on small than large grounds. This was investigated by comparing gonads of males collected from small dancing grounds with those of males from large dancing grounds containing more than 10 males.

Studies by Hamerstrom and Hamerstrom (1960), Evans (1961), and Lumsden (1965) on the Sharp-tailed Grouse, and studies of related communal species, including the Black Grouse (Lyrurus tetrix) by Höhn (1953) and Koivisto (1965), Prairie Chicken by Hamerstrom and Hamerstrom (1960), and the Sage Grouse by Simon (1940), Scott (1942), Eng (1964), and Lumsden (1968), have shown that most matings are done by centrally located males on the lek. Koivisto (1965) and Lumsden (1965) also suggested that the more centrally located males are dominant to those whose territories lie at the periphery of the lek. These studies suggest that the centrally located males have a greater androgen output and achieve a greater reproductive potential than the peripherally located males of the same lek. The possibility that these differences may be reflected in the physiology of the gonads was tested by comparing the more dominant of the central males, which occupy territories surrounded by other males, and the less dominant of the peripheral males, which occupy territories at the periphery of the ground.

A preliminary survey of Sharp-tailed Grouse dancing grounds in the Interlake Region of Manitoba in 1967, indicated the presence of sufficient dancing grounds of various sizes to permit the required collections without severely reducing the male population.

REVIEW OF LITERATURE

Displays and Social Organization of Grouse

Eighteen recognized species of grouse, some with numerous subspecific forms, comprise the family Tetraonidae (Thomson, 1964). As reviewed by Hjorth (1967), the Tetraonidae are noted for elaborate and often highly ritualized courtship and mating displays by the males. Early descriptions of courtship and mating behaviour in the 10 North American species (American Ornithologists Union Check-List, 1957) were presented in Bent (1932). More detailed accounts of male displays for all North American Tetraonidae species have been compiled by Wing (1946). Hjorth (1967) provided an extensive resumé of the reproductive behaviour in male grouse of North American and Eurasian members of the family.

Although elaborate displays are characteristic of all Tetraonidae, social organization as illustrated by the spacing of displaying males, differs widely within the group. The males of some species, such as the Spruce Grouse (Canachites canadensis) and, to a lesser extent, the Blue Grouse and Ruffed Grouse (Bonasa umbellus), tend to disperse and display singly, on individual and often widely dispersed

territories. Others, including the Sharp-tailed Grouse, characteristically display in groups on communal display grounds, or "leks" (Hamerstrom and Hamerstrom, 1960; Lumsden, 1965). In addition to the Sharp-tailed Grouse, communal display grounds are used by the other three so-called "prairie grouse" species of North America; the Sage Grouse, Greater Prairie Chicken (Tympanuchus cupido), and the Lesser Prairie Chicken (Tympanuchus pallidicinctus), and two European species; the Black Grouse and Capercaillie (Tetrao urogallus). Detailed descriptions of the courtship and mating behaviour of these lek species include accounts by Simon (1940), Scott (1942), and Lumsden (1968) on the Sage Grouse; by Johnson (1934), Grange (1940), and Hamerstrom and Hamerstrom (1960) on the Prairie Chicken; by Höhn (1953), Hamerstrom and Hamerstrom (1960), and Koivisto (1965) on the Black Grouse, and by Lumsden (1961) and Palmer (1963) on the Capercaillie.

Displays and Social Organization of Sharp-tailed Grouse

Descriptions of the various displays and social organization of male Sharp-tailed Grouse were reported by Hamerstrom and Hamerstrom (1960), Evans (1961), and Lumsden (1965). Bent (1932), Marshall and Jensen (1937), Grange (1940), Hart et al (1950), and Scott (1950) quoted a number

of older accounts. The following resumé, based on the above cited studies, includes a general description of displays and social organization of Sharp-tailed Grouse during the spring breeding season.

Displays

The displays of male Sharp-tailed Grouse function in territorial defense, courtship, as well as attracting females to the lek (Lumsden, 1965; Hjorth, 1967; Robel, 1967). The "flutter-jump" display, in which the males jump into the air, flutter their wings and return to the ground, is characteristic of territorial males when females are nearby, and presumably functions primarily as an advertising display (Lumsden, 1965). "Cooing" vocalizations, which become frequent shortly after males arrive in the morning, are evoked primarily in aggressive situations between males; according to Lumsden (1965) they are not to be considered courtship displays, although they appear to serve the purpose of advertising the location of dancing grounds to females. A low-pitched gutteral "lock-a-lock" call, used in aggressive and fighting situations, may also serve to advertise dancing ground locations.

Agonistic behaviour most typically occurs at territory

boundaries between adjacent males. When approaching a rival, males may erect the feathers on their neck and point their tail upward. In more aggressive situations, they may walk or run parallel to one another with their heads and tails up. At high intensity, there is much calling, advancing, and retreating. Actual fighting may occur early in the display season, but is largely replaced by more ritualized threats as the season advances (Hamerstrom and Hamerstrom, 1960; Lumsden, 1965).

The major courtship display of male Sharp-tailed Grouse is referred to as the "dance" or "tail-rattling" display. It has been described as "one of the most remarkable performed by any Galliform" (Lumsden, 1965: p.43). In the display, males "dance" with rapid stamping or short quick steps, and rapidly vibrating rectrices, hence the term "dancing ground" for the communal display ground in this species. Like "flutter-jumps", the "tail-rattling" display is especially pronounced when females are present. Copulation, which is initiated in response to the crouched posture characteristic of the female "pre-copulatory" display, is typically preceded by periods of intense "tail-rattling". Detailed descriptions of body positions, movements, and sounds in these and other displays are included in the study by Lumsden (1965).

Dancing Ground Size and Organization

Sharp-tailed Grouse leks may accommodate one to more than thirty males. Each morning, and usually in the evenings during the spring display period, males come to the same lek which may be used annually for a period of many years (Lumsden, 1965).

Like Prairie Chicken and other lek grouse, Sharp-tailed Grouse exhibit well-developed territorial behaviour on the lek. This is evidenced by the regularity with which males occupy the same area each morning, coupled with occurrence of aggressive interactions between neighbours along territorial boundaries (Lumsden, 1965; Evans, 1969). As is characteristic of territorial avian species, male Sharp-tailed Grouse typically expell other males that intrude on their territory. On occasion, however, even apparently established males may be permanently expelled from their territories (Evans, pers. com.). Hamerstrom and Hamerstrom (1960) noted that hard fighting during territorial disputes occurs mainly at the beginning of the display season, and is then replaced largely by ritualized fighting or threats.

According to Lumsden (1965), male Sharp-tailed Grouse occupying territories on typical, or "classical" leks, are organized into a hierarchy of dominance in which the more

dominant males tend to defend territories near the center of the lek. Similar interpretations have also been advanced for this species and the other prairie grouse of North America by Scott (1942; 1950), and for the Black Grouse in Europe (Koivisto, 1965). These same authors noted that when females arrive on the lek, they tend to move towards the center, where most copulations occur. The radiating dominance hierarchy in males, coupled with the selectivity exhibited by females, appears to ensure that the majority of females are mated by a limited number of centrally-located, more dominant males. Subordinate males, restricted to the periphery of the lek, leave few, if any, offspring. In addition to providing a basis for such selective mating, territories are also thought to function in reducing disturbance during courtship (Scott, 1942, Hamerstrom and Hamerstrom, 1960; Koivisto, 1965).

Little is known concerning the organization of small dancing grounds containing one to 10 males. Such grounds apparently do not possess any obviously centrally-located males, although some males do appear to be more dominant than others (Lumsden, 1965). There is thus little direct evidence concerning the absence or presence of a radiating dominance hierarchy. There is evidence that small grounds may be less

stable, in that they may shift location from year to year and disappear in years when population densities are low (Lumsden, 1965).

Endocrines and Avian Reproductive Behaviour

Reviews by Witschi (1935), Sturkie (1954), Nalbandov (1958), Marshall (1961), and Barrington (1963) indicated that the release of avian sex hormones is closely correlated with development of the reproductive organs, secondary sexual characters, some sexually dimorphic characters, as well as behavioural patterns. Eisner (1960) described in detail the relationship of hormones to the reproductive behaviour of birds, referring especially to parental behaviour. Lehrman (1959; 1964) provided further information on the influence of endocrines upon reproductive behaviour, and cited evidence that not only does hormone secretion affect this behaviour, but that behaviour affects hormone secretion. In addition, field observers noted that the singing and posturing of the male bird stimulates nest-building behaviour on the part of the female of many species (Blanchard, 1941). Craig (1911; 1913) and Burger (1942) similarily reported how behaviour is important in influencing hormone secretion with resultant structural changes and behavioural

modifications conducive to reproduction in many species. It is also likely that many environmental changes affect hormone levels and reproduction in wild birds by influencing some critical behavioural interaction (Rogers, 1962).

The hormones primarily involved in avian reproduction are those of the anterior pituitary gland and the gonads. The first experimental evidence of the endocrine function of the testis was obtained as long ago as 1762 when John Hunter described the effects of transplantation of the testis of a domestic cock (Marshall, 1961). It was not until 1929, however, that Benoit, by use of Rontgen-radiation, was able to show that male hormone was produced somewhere in the inter-tubular tissue. Marshall (1949a) in describing the function of the interstitium of the testis, localized the endocrine function to secretory cells 'A' and 'B'.

In the male, both sexual and agonistic behaviours are greatly influenced by androgen (Bullough, 1945; Beach, 1948; Selinger and Bermant, 1967). Experiments by Selinger and Bermant (1967) on the hormonal control of aggressive behaviour in Japanese Quail (Coturnix coturnix japonica) indicated that gonadectomy resulted in a marked reduction in both aggressive and sexual behaviour. If the particular bird was high in the established dominance hierarchy, gonadectomy also

resulted in displacement to a lower position. Such evidence indicates that dominance and aggressiveness in birds are influenced by androgen levels. In addition, seasonal changes in secondary sexual characters also may depend upon these same hormones and the gonadotrophins. In the Weaver Finch (Pyromelana franciscana) for example, condition of the plumage correlates with that of the gonads (Rollo and Domm, 1943). Similarily, in the domestic fowl, characteristic male vocalizations are stimulated by androgen (Nalbandov, 1958). Robinson (1956) found that the seasonal development of song patterns in the Australian Magpie (Gymnorhina dorsalis, Campbell) could also be correlated with changes in the state of the testis. The available evidence thus suggests that during the spring reproductive period, characteristic behaviour patterns such as vocalizations, displays, fighting, the setting up of territories, and dominance hierarchies are significantly influenced by androgen released by the testes (Eisner, 1960). These internal stimuli are of course operating in conjunction with stimuli from the environment and, as Lehrman (1959) discussed more fully; the behaviour itself probably results in an intensification of the hormone secretion.

The Annual Breeding Cycle

The avian breeding cycle consists of reproductive and non-reproductive phases, with or without intervening migration. The breeding cycle of the North Temperate species commonly shows an annual periodicity (Lack, 1950; Thomson, 1950), which is reflected in behaviour. Thus the males of many species, including Sharp-tailed Grouse, become aggressive towards other males of the species during the spring breeding season, while at other times they associate with few agonistic interactions (Höhn, 1953; Lehrman, 1959; Hamerstrom and Hamerstrom, 1960; Lumsden, 1965). The breeding cycle is also reflected in the striking changes in size and activity of the gonads. The testes in the Gambel Sparrow (Zonotrichia leucophrys gambeli), for example, increase in volume by about 125 times while going from non-breeding to breeding condition (Blanchard and Erickson, 1949). In the Anna Hummingbird (Calypte anna) the increase may only be 10 times greater than the minimum volume (Williamson, 1956).

Gross changes in testis size are associated with histological changes, and both have been used as criteria for separating the avian gonad cycle into stages. Rogers (1962) divided the cycle into the following three general stages:

Refractory Phase

This stage is referred to as 'refractory' because the gonads do not respond to light treatment (Wolfson, 1952). At this period, usually mid-summer, the testes shrink rapidly to their minimum size. The secretory products of the interstitial cells are exhausted during the refractory period, and the cytoplasm of the Sertoli cells and germ cells of the testes tubules is converted into a mass of cholesterol positive lipid material lying in the lumen of the shrinking tubules (Marshall, 1949a). Sexual behaviour practically ceases and many species gather in flocks. A post-nuptial moult characteristically ensues.

Acceleration Phase

The acceleration phase follows the refractory phase beginning in late summer or early autumn. Having reached their minimum size by the end of the refractory phase, the testes then begin to grow and the last remnant of lipids disappear from the tubules. The newly formed interstitial cells are already lipoidal and the new tubule epithelium contains spermatogonia (Marshall, 1949a). Typically, there is a corresponding increase in sexual activity, with resultant autumn displaying (Marshall, 1952), a behaviour also

characteristic of the Sharp-tailed Grouse (Lumsden, 1965; Evans, 1969). However, apparently no autumn matings have been recorded in species inhabiting the temperate regions, nor do the gonads begin to increase in overall size until early January. The duration of this phase varies between species. For example, in those that reach this stage in late summer and early autumn, it appears to be prolonged by the adverse environmental conditions of autumn and winter. This is thought to prevent progression to full breeding condition at this unfavorable time of the year (Marshall, 1952; Rogers, 1962).

Culmination Phase

Spermatogenesis reaches its height during the culmination phase. The greatly enlarged tubules of the testes are filled with spermatozoa. With expansion of the tubules the interstitial cells are compressed, scattered and nearly obscured. During this period, display and mating are completed. As these activities are concluded the birds once again enter the refractory phase.

A more detailed analysis of the avian testis cycle has been presented by Johnson (1956) for the California Gull (Larus californicus). As described below, Johnson (1956) divides spermatogenesis into eight stages.

Stage 1. Stage 1 is the inactive winter condition. The testes attain their minimum size, and the tunica albuginea its maximum thickness. There is merely one basal layer of spermatogonia and Sertoli cells resting on the basement membrane. Lumina are almost non-existant. "Inactive" primary spermatocytes are present.

Stage 2. Primary spermatocytes are in synapsis, with their chromosomes lying to one side of the nucleus. There is still basically one layer of spermatogonia and Sertoli cells. Lumina are filled with detritus.

Stage 3. An increase in the number of primary spermatocytes in synapsis occurs forming two or more layers adjacent to the lumen. Tubules commence to enlarge, and the tunica albuginea becomes thinner.

Stage 4. There is a predominance of primary spermatocytes in synapsis along with the first appearance of secondary spermatocytes. The tubules increase considerably in size. A large empty lumen is present.

Stage 5. Most of the spermatids present are bordering the lumen except those that are metamorphosing are moving from the lumen toward the Sertoli cells. When compared to the number of primary spermatocytes, spermatids are few in number. Only rarely are mature spermatozoa present.

Stage 6. This stage is referred to as the breeding condition. Spermatozoa are found in bundles spaced around the tubule. Testes and tubules attain their maximum size. Tunica albuginea is thinnest.

Stage 7. This stage differs from the preceding one in that the majority of sperm bundles have been shed into the center of the lumen of the tubule.

Stage 8. After spermatozoa are shed into the lumen a casting off, in succession, of spermatids, spermatocytes, spermatogonia and Sertoli cells occurs. This is thus the regression stage. Tubules collapse and become smaller, approaching the inactive winter condition.

The Control of Avian Breeding Cycles

As defined by Baker (1939), Lack (1950), and Thomson (1950), two types of causes are involved in the control of breeding seasons: ultimate and proximate factors. Proximate causes, in turn, may either be primarily endogenous, or due to the influence of the environment on particular physiological processes.

Ultimate Factors

Ultimate factors are those which are thought to operate through natural selection to achieve a correlation between

reproduction and optimum ecological conditions, especially the availability of food for the young (Lack, 1950; Thomson, 1950; Seel, 1968). For instance, the diet of young Sharp-tailed Grouse is 95% insects, decreasing with age, 8.5% at twelve weeks (Hart et al, 1950; Kobriger, 1965; Bernhoft, 1967). The need for sufficient insect food for the young may therefore be one of the most important ultimate factors necessitating that reproduction occurs in the early summer.

Proximate Factors

Proximate factors are those which operate through the physiology of the gonads to bring the birds into breeding condition at the biologically appropriate season (Lack, 1950). To function effectively during the appropriate season, it is apparent that activity of the gonads must be controlled by some timing mechanism, either internal or external, so that gonad recrudescence occurs before the onset of optimum ecological conditions.

The Internal Rhythm of Breeding Cycles

At the present time there is no general agreement as to the importance of an internal rhythm in regulating avian reproductive cycles. The probable existence of an internal

rhythm, modifiable by external factors, has been accepted by a number of workers (Bissonette, 1937, Blanchard, 1941; Burger, 1949).

Marshall (1949a) believed an anatomical basis for an internal physiological rhythm may have been shown in his investigation of the seasonal cycle of the interstitium of the testes of the Fulmar (Fulmarus glacialis). There is also some evidence that such a rhythm may become established and persist in its characteristic periodicity even when environmental factors, such as photoperiod, are neutralized or reversed (Thomson, 1950). Baker and Ranson (1938), among others, have shown that some birds native to the southern latitudes, like the Gouldian Finch (Poephila gouldiae), when artificially removed to northern latitudes, retained a tendency to breed at the same date which would have been appropriate had they not been transported. Other species, including the Western Rosella Parrot (Platyecrcus icterotis), in like circumstances, adapt more readily to the seasonal cycle of the new environment (Thomson, 1950). Thomson (1950: p.184) pointed out, however, "that where an inherent annual rhythm exists, to keep the physiological and environmental cycles in step there must be one event in the former which is directly linked to some point in the latter".

Environmental Factors and Breeding Cycles

Since endogenous rhythms, even if present, are not in themselves sufficient to produce the necessary degree of correlation between breeding cycles and optimum ecological conditions (Thomson, 1950), exogenous factors that correlate in time with the appropriate endogenous conditions have been assumed to be of primary importance. The classic experiments of Rowan (1925) on the Slate-coloured Junco (Junco hyemalis) focused attention on light as one such exogenous proximate factor. Rowan and subsequent experimenters demonstrated that upon exposing male birds of various species to increased amounts of artificial light in winter, the gonads increased in size and spermatogenesis occurred (Rowan, 1925; Bissonette, 1937; Berger, 1949; Kirkpatrick, 1955; Threadgold, 1960; Lofts and Coombs, 1965; Lofts et al, 1967; Farner, 1967, Wilson, 1968). These observations provide abundant evidence for increased daylength to be an effective proximate factor promoting gonad recrudescence. As such, it presumably acts merely as a timing mechanism and need not be supposed to have some other, more fundamental ultimate effect on avian reproduction (Lack, 1950). In addition to light, other factors such as air temperature (Marshall, 1949b) and precipitation (Lack, 1950) may also act as proximate factors, modifying the

effects of light so that breeding is timed to coincide with optimum local conditions.

Physiological Control of Avian Breeding Cycles

According to evidence reviewed by Farner (1967), the precise photoperiodic mechanisms that have been developed by avian species of the mid and high latitudes constitute the primary basis for the control of breeding cycles in these species. The core of this control system in birds, as in other higher vertebrates, includes the hypothalamus, anterior pituitary gland and gonads. External stimuli, particularly light, activate exteroceptors which transmit information about the stimuli to the so-called "higher centers" of the central nervous sytem. Impulses are then transmitted from these centers to the hypothalamus, where the production of neuro-hormones, produced by neurosecretory cells, is stimulated (Guyton, 1964). Neuro-hormones are then transported to the pituitary gland through a system of portal veins and affect the secretion of gonad stimulating hormones, the gonadotrophins (Farner, 1967), which are produced in the anterior pituitary gland. Lehrman (1959) and Rogers (1962) think it probable that all other external factors that affect the gonads, such as temperature, rainfall, and stimuli from

other individuals, also operate by activating neural discharges which are relayed to the hypothalamus where they modify the activity of the neurosecretory cells.

The influence of the gonadotrophins upon the testis governs the elaboration of the male sex hormones, androgens. Androgens, along with the gonadotrophins, result in the development of a mature, physiologically reproductive testis. The appearance of secondary sex characteristics and associated reproductive behaviour are also a result of the elaboration of androgen and in some cases gonadotrophins (Witschi, 1935; Sturkie, 1954; Nalbandov, 1958; Marshall, 1960).

Testis Cycle of Grouse

Detailed histological studies of grouse testes have been limited to two species. The Sage Grouse was investigated by Eng (1963). More recently, Simard (1964) analyzed the testis cycle of the Blue Grouse (Dendragapus obscurus fuliginosus) and its relationship to age, breeding behaviour and migration.

The criteria of the stages of spermatogenesis employed by Simard (1964) were those defined by Johnston (1956: p.155) as described above. As noted by Johnston (1956), the broad

features of spermatogenesis are in close agreement for all the species examined whether they breed in their first or subsequent years. The Fulmar (Marshall, 1949a) is a non-passerine which does not begin to breed until older than one year. On the other hand, the Ring-necked Pheasant (Phasianus colchicus) (Hiatt and Fisher, 1947), breeds by the end of its first year. The Sharp-tailed Grouse, along with most of the Tetraonidae, also breed by the end of the first year.

Both Eng (1963) in his study of Sage Grouse, and Simard (1964) in his study of Blue Grouse, noted that the gonads of the juveniles, birds about one year old, were smaller, and did not reach the maximum size attained by the gonads of the adults. Both studies revealed that the juvenile testes contained mature spermatozoa and hence, the birds were presumably physiologically capable of breeding, but observations indicated that few, if any, females were actually inseminated by juveniles. In addition, the juveniles tended to be subordinate to adult males in territorial encounters. In summary, both studies revealed that the juveniles had smaller testes, a slower recrudescence, a later peak in spermatogenesis, a shorter breeding period and therefore an earlier winter stage. The subordinate status and reduced reproductive potential of

juveniles on the breeding range could therefore be explained at least in part, by the reduced development of their testes compared to those of the adults. Similar published data for Sharp-tailed Grouse are apparently lacking.

MATERIAL AND METHODS

Study Area

Observations and collections took place within a 19-mile radius of Hodgson in the Interlake region about 125 miles north of Winnipeg, Manitoba (Fig. 1a). This Interlake region may be classified, on the basis of economic standards, as "non-agricultural" (Weir, 1960). However, the study area was primarily a belt of cultivated land interspersed by forests, consisting of a grass-woodland transition with black-grey wooded soil predominating. Associated soils are black, dark grey and peaty meadow (Weir, 1960). The natural tree cover in the area consists of mixed st^ands of broad leaf and coniferous species, chiefly aspen, (Populus tremuloides) and spruce, (Picea mariana). Peat bog and marsh are also prevalent. Observations and collections were conducted over an area of approximately 20 square miles, containing 26 dancing grounds; dancing ground positions are indicated in Fig. 1b.

Locating Dancing Grounds

Dancing grounds were located by listening for the sounds of displaying males. From shortly before sunrise to about one to one and one-half hours later, on clear, cool, calm mornings, was found to be the best time for finding dancing

Fig. 1. a) Map of the province of Manitoba showing the Hodgson study area. b) Map of the Hodgson study area showing location and number assigned to each Sharp-tailed Grouse dancing ground from which observations and collections were made.

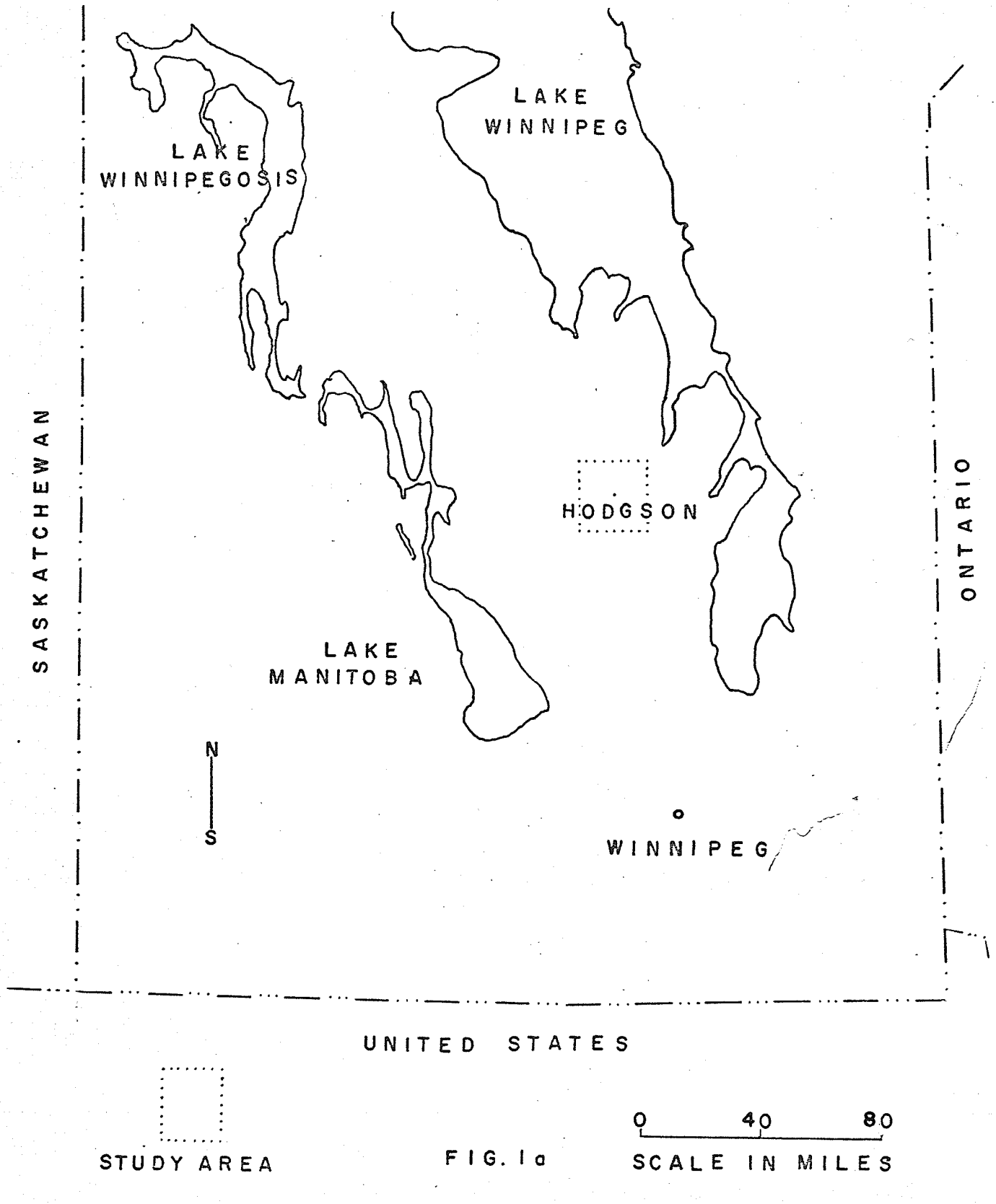

LAKE
WINNIPEGOSIS
LAKE
WINNIPEG
HODGSON
LAKE
MANITOBA
SASKATCHEWAN
ONTARIO
N
S
WINNIPEG
UNITED STATES
STUDY AREA
0 40 80
SCALE IN MILES

FIG. 1a

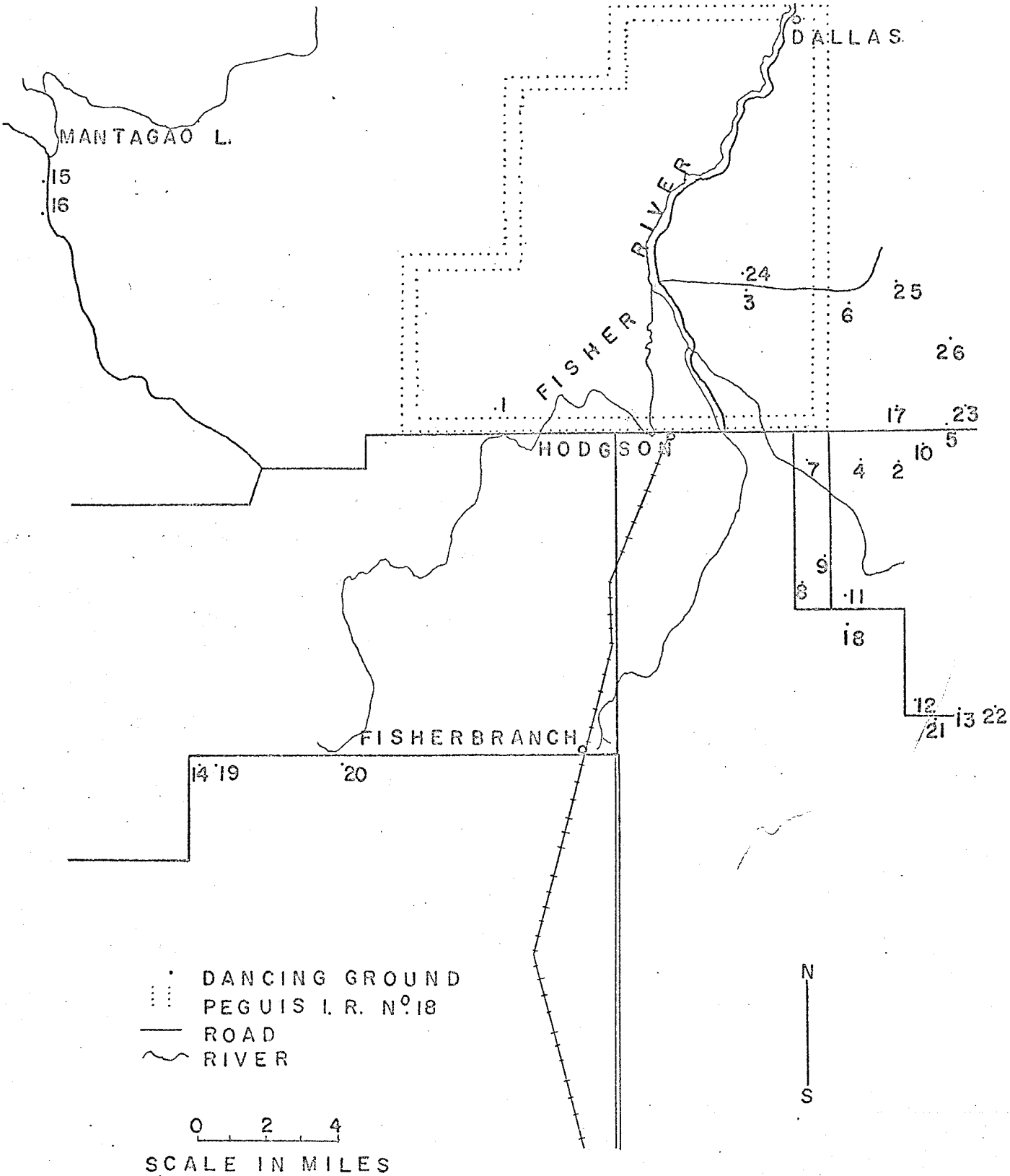

DALLAS
MANTAGAO L.
FISHER RIVER
HODGSON
FISHERBRANCH
DANCING GROUND
PEGUIS I. R. N°18
ROAD
RIVER
0 2 4
SCALE IN MILES
N
S

FIG. 1b

grounds. Under these conditions, displaying Sharp-tailed Grouse can typically be heard a mile away (Lumsden, 1965). Each dancing ground was located by observing displaying males, or finding fresh droppings and shed feathers that characterize active dancing grounds during the spring display period.

During the afternoons preceding days on which detailed observations or collections were made on any given dancing ground, a blind consisting of burlap hooked over a 3' X 4' X 4' board frame was erected on the edge of the dancing ground, approximately 25 yards from the center of the display area. The blind was placed so that at sunrise the sun would not rise directly in front of or behind the blind.

Observations and collections were carried out primarily during the morning display. Equipment and observer were hidden in the blind before the birds arrived.

Census and Observations

The maximum numbers of males and females using each ground were counted from the blind during early May through June in 1967, and during early April through early June in 1968. The sexes were distinguished by differences in both behaviour and morphology (Evans, 1961; Lumsden, 1965). In collecting 64 birds, a female was never mistaken for a male.

Each dancing ground was observed at least once before collection to determine the relative locations of males and females, and to determine ranks within the dominance hierarchy. Copulations and clumping of females on a given territory were noted, and used as indicators of dominance in the males. Indirect evidence of dominance in a particular male included the observation that the bird would be located near or on a slight elevation when this was present (Lumsden, 1965), and that it was particularily active, and highly successful in defending its territory boundaries (Lumsden, 1965).

Collections

Male birds only were collected, 25 from May to June in 1967, and 39 from April to June in 1968. Four males were collected each week, two from a large and two from a small dancing ground.

Following sufficient observations to determine the number of birds and the approximate position of each male, each ground was classified as small or large. Small dancing grounds at no time contained more than 10 males, while large grounds possessed 11 or more males. The figures chosen, although in part arbitrary, have been useful in comparisons between small and large grounds in the closely-related Prairie

Chicken (Hamerstrom and Hamerstrom, 1955).

Two males were collected from small dancing grounds each week; in no case was the entire male population removed. A random sampling technique was employed to determine which male from a given small dancing ground was to be collected. Two males were collected each week from large dancing grounds, one male whose territory was located near the center, and one from the periphery. Where possible an attempt was made to collect central males exhibiting high dominance status and, peripheral males exhibiting low dominance status. Collections were not undertaken if this would reduce numbers of males to 10 or less.

Only five of the 19 central males collected were known to have mated. However, the central location of these birds indicated that they would rate relatively high in the hierarchial system of the dancing ground (Koivisto, 1965; Lumsden, 1965).

Males were shot with a .22 calibre rifle, fitted with a 3X telescopic sight and fired from the blind. Collected males were numbered, weighed, and information recorded on a data sheet (Appendix I). In 1967, the right testis was removed and its volume measured to the nearest tenth of a milliliter by measuring the observable quantity of water displaced when

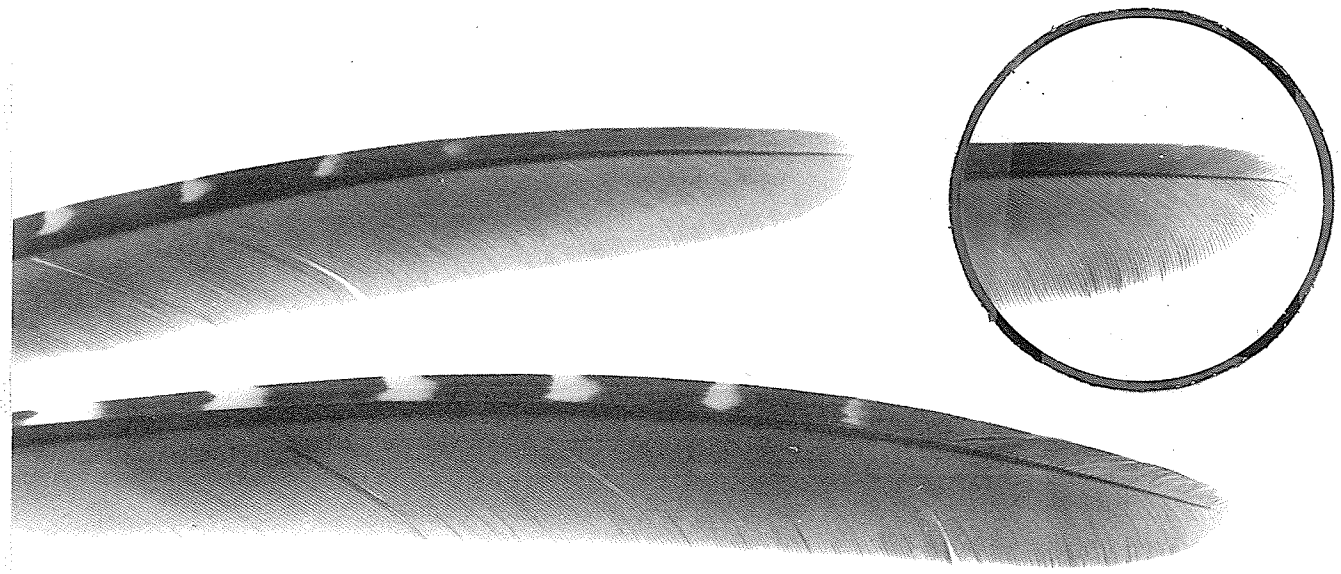
the testis was immersed in a partially filled 10-ml graduated cylinder. In 1968 volumes of both testes were measured.

Determination of Age

The central rectrices and one wing segment containing the primaries were preserved for age determination. In the present study, the age of each collected male was determined first according to the shape, wear, and fading of primaries 9 and 10 (Dwight, 1900; Leopold, 1939; Petrides, 1942; Ammann, 1944; Evans, 1960; Zwickel and Martinsen, 1967; Ellison, 1968) (Fig. 2).

The total length of one central rectrice was then measured to the nearest millimeter. The external diameter of the shaft of one ninth primary was measured at the point where the first central barbs come off the shaft on the underside of the feather. This was measured, using a calibrated stage micrometer, to the nearest .02 mm. Studies by Dorney and Holzer (1957) and Evans (1960), with grouse of known age, have shown that when rectrice length is plotted against ninth primary diameters, plotted values for adults lie upwards and to the right of values for juveniles. When the rectrice length was plotted against the ninth primary diameter for the males collected in 1967, and a line drawn between the values

Fig. 2. Adult (a) and juvenile (b) primaries, 9 (lower) and 10 (upper), of male Sharp-tailed Grouse illustrating the sharper point and greater wear of juvenile primaries.



A.

B.

FIG. 2

of adults and juveniles whose age was determined on the basis of feather shape, wear, and fading, complete separation of points was obtained (Fig. 3). A similar treatment of the 1968 data produced a similar result.

Histological Preparations

Collection of Tissue Specimens

Histological sections were prepared from the right testis in 1967 and from both testes in 1968. Since Johnston (1956) did not note any significant differences in the histological appearance of left and right testes, data from both were pooled.

Within 10 minutes after the body weight and testis volume of a freshly-collected male were obtained, one-third of each testis was placed into one of three fixatives; Bouin's, digitonin, and Zenker-formol. Scott and Middleton (1967: p.80) found "no striking histological differences between apical and central transverse sections" in testes of Brown-headed Cowbirds (Molothrus ater), hence, no attempt was made to standardize the location of tissue specimens within the testes in the present study.

Fig. 3. A scatter diagram illustrating the plotted values of central rectrice length and diameter of the ninth primary for adult and juvenile Sharp-tailed Grouse collected at Hodgson, Manitoba, in 1967 and 1968. The plotted values for adults fall to the right of the line and the juveniles to the left.

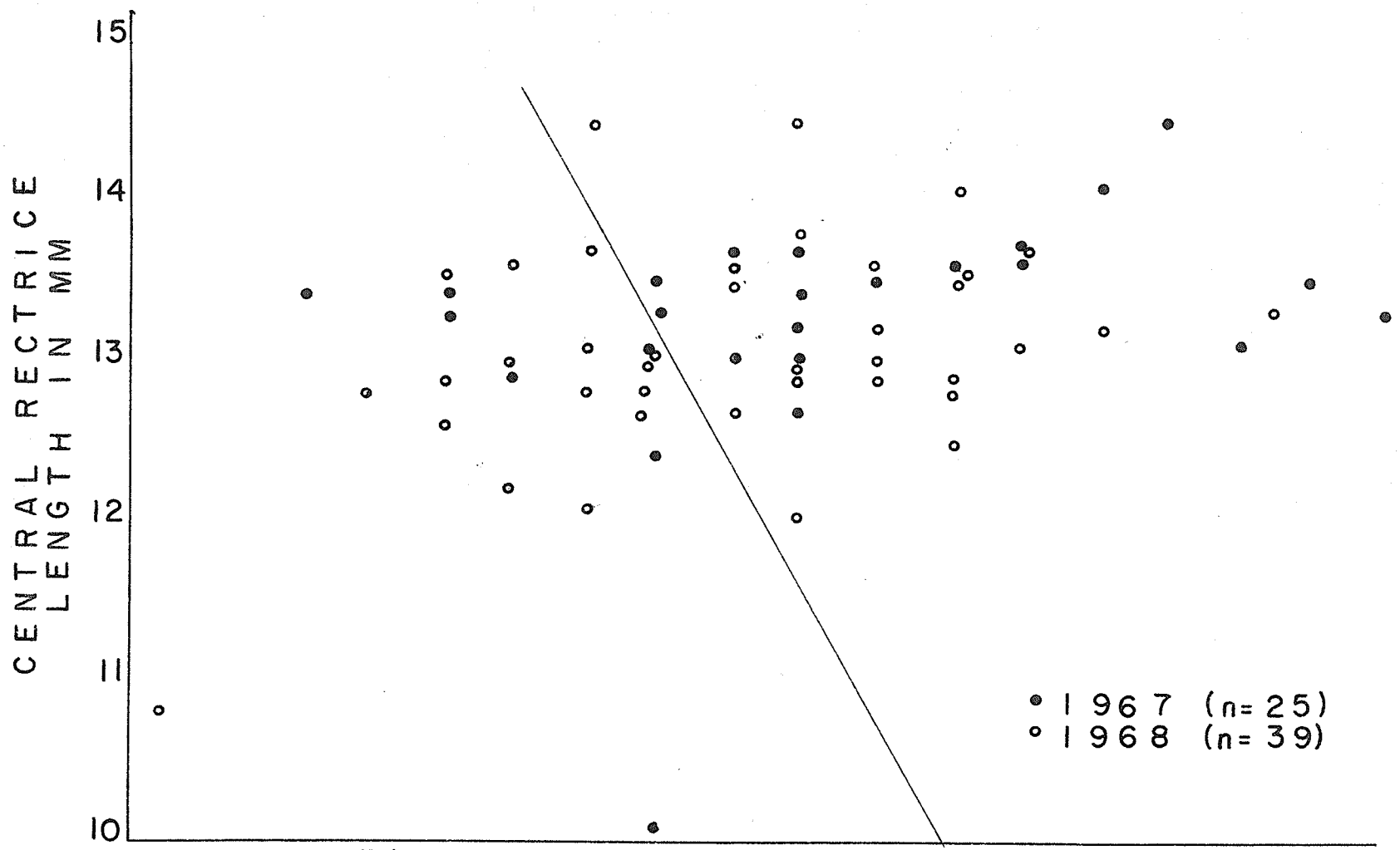

CENTRAL RECTRICE LENGTH IN MM
15
14
13
12
11
10
3.0
3.1
3.2
3.3
3.4
3.5
3.6
3.7
DIAMETER OF NINTH PRIMARY IN MM
● 1967 (n=25)
○ 1968 (n=39)

FIG. 3

Fixation and Staining

Subsequently, the tissue was transferred into 70% alcohol until embedded (Appendix II). The tissue specimens were embedded in paraplast (57-59° C), and sectioned at 7μ. Sections were then stained by Masson's trichrome technique (Culling, 1963) with modifications as outlined in Appendix III. These preparations were used for assessing spermatogenic stages (Blanchard and Erickson, 1949; Marshall, 1949a; Lewin, 1963; Scott and Middleton, 1967).

For the determination of cholesterol, a lipid compound from which testosterone is derived (Harrow and Mazur, 1962; Harper, 1967), the tissue was fixed in digitonin for 36 hours. Digitonin precipitated cholesterol, which was detected by the bismuth trichloride method (Culling, 1963).

The third tissue specimen was fixed in Zenker-formol fluid to demonstrate the minute filamentous or granular mitochondria scattered throughout the cytoplasm of the Leydig cells (Culling, 1963). Altmann's acid fuchsin-picric acid technique was employed to stain the mitochondria (Culling, 1963). This technique also demonstrated the presence of red and white blood cells.

Quantitative Determination of Testis Cycle and Cholesterol Levels

The seasonal pattern of the avian testis cycle, as described earlier, has been divided into stages, each representing a particular level of intratesticular development (Blanchard and Erickson, 1949; Johnston, 1956; Williamson, 1956; Johnson, 1961; Lewin, 1963; Simard, 1964; Scott and Middleton, 1967). The particular stage of development attained by each tissue specimen was noted and used as an index of testis development.

For greater accuracy, the method of Chalkley (1943), was employed as follows. An eyepiece was fitted with 5 pointers, 4 being used for recording and a short fifth one for focusing (Fig. 4). Any structures at the tips of the 4 main pointers were recorded as "hits" after focusing at the end of the short pointer. The procedure was repeated by throwing the field out of focus, moving the stage a short distance along a zigzag course through the section, and then bringing the preparation back into focus. The procedure was repeated 175 times, this being sufficient to give statistical reliability to the data (Eschenbrenner et al, 1948; Roosen-Runge, 1956). The relative frequency of "hits" on any particular cell type or other structure indicated the relative volume occupied by

Fig. 4. Positions of pointers used for the Chalkley technique, in which an eyepiece was fitted with 5 pointers, 4 being used for recording and a short fifth one for focusing. Masson's trichrome technique. X 1250.

Fig. 5. Transverse section of Sharp-tailed Grouse testis: Spermatogonia (1); Spermatocytes, primary (2); Spermatocytes, secondary (3); Spermatozoa (4); Basement membrane (5). Masson's trichrome technique. X 500.

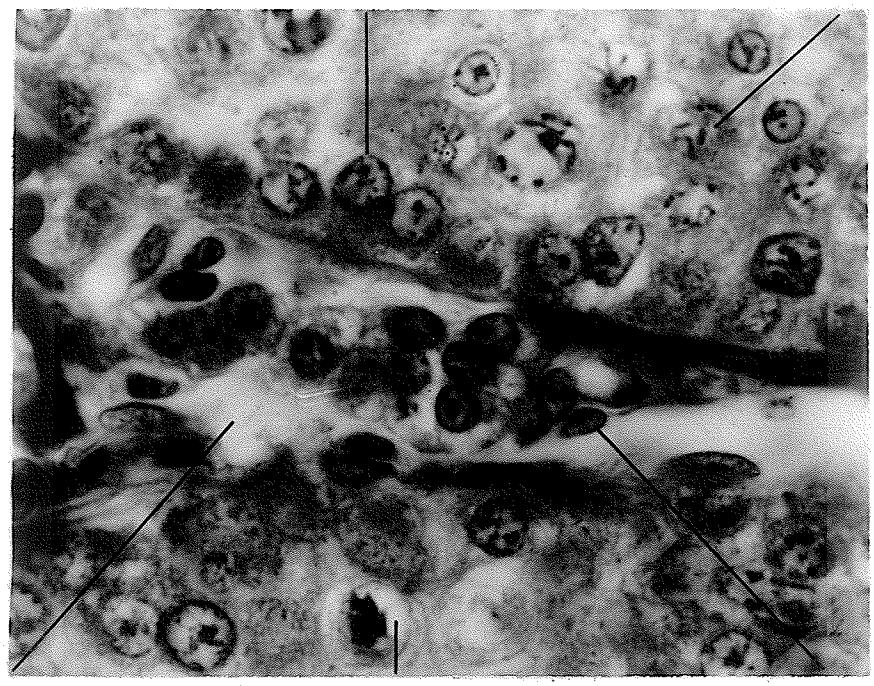


FIG. 4

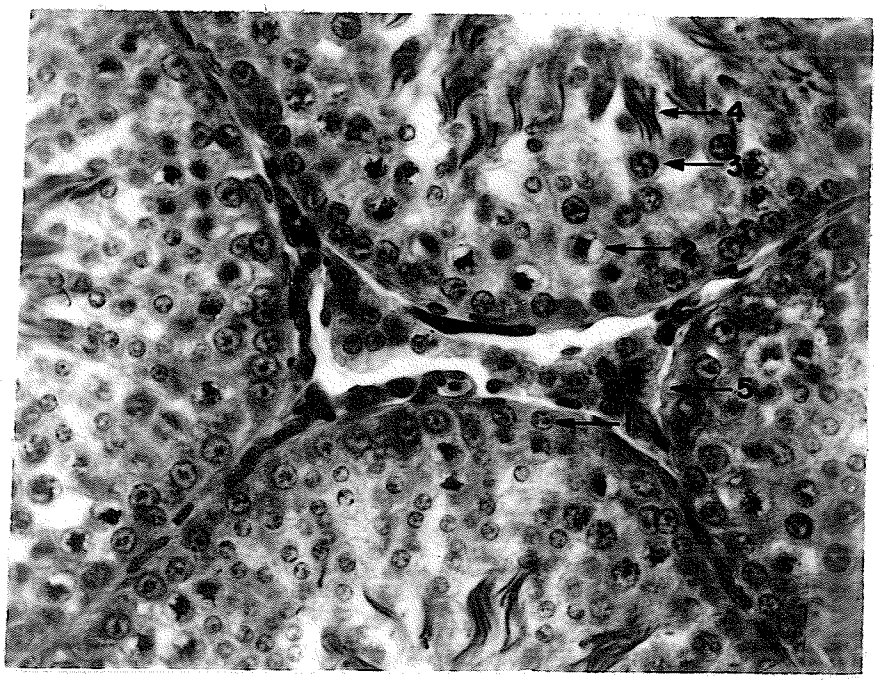


FIG. 5

all cells or structures of this type. All determinations were made under oil-immersion (100X) with a 10 X eyepiece.

The successful use of Chalkley's method required an accurate and consistent identification of the structures recorded. The following characteristics, as defined by Roosen-Runge (1956), Simard (1964), and Johnson (1966), were used:

Spermatogonia: These cells are located in the most peripheral layer on the basement membrane of the tubule with a fine network of chromatin with 2 or 3 chromocenters (Fig. 5).

Spermatocytes: (Primary and secondary) Primary spermatocytes have a clear pole and a tangled mass of threads at the other pole. Secondary spermatocytes have 1 to 3 large chromatin condensations with a scattering of smaller granules along the nuclear membrane. Both are larger than spermatids and possess more distinct chromatin patterns (Fig. 5).

Spermatids and Spermatozoa: These are very similar and were not separated. Spermatids may be found in any layer of the tubule, although they usually were observed in groups near the lumen (Fig. 5).

Sertoli Cells: The pyramidal, clear nuclei with large spherical nucleoli characterized the Sertoli cells. Using a trichrome stain, their cytoplasm was distinguished from that of the surrounding cells by its fine fibrous appearance.

Space: In this case the pointer was located either on cytoplasm of unknown cell type or in open spaces between the cells of the seminiferous epithelium.

Lumen: This denotes the space bounded by seminiferous epithelium. The lumen often contains cells and a fine coagulum. These cells were recorded similar to those in their natural positions. Presence of coagulum was recorded as lumen.

Basement Membrane: This consists of the well organized connective tissue sheath encircling each seminiferous tubule (Fig. 5).

Interstitial Tissue: This included all structures or space outside the seminiferous tubules with the exception of Leydig cells, basement membrane, and tunica albuginia.

Leydig Cells: As described by Marshall (1949a), Leydig cells are polygonal, epitheloid cells located in groups between the tubules (Fig. 6).

To measure cholesterol, the Chalkley method was employed to tissues fixed by digitonin and treated with a bismuth trichloride reagent. As described by Culling (1963), the cholesterol appeared as a shapeless dark brown mass between the seminiferous tubules (Fig. 7). The percentage of "hits" by the four pointers in 175 random fields was recorded from each section.

Fig. 6. Transverse section of Sharp-tailed Grouse testis illustrating Leydig cells (arrows) between the seminiferous tubules. Altmann's acid fuchsin-picric acid technique. X 1250.

Fig. 7. Transverse section of Sharp-tailed Grouse testis illustrating the presence of cholesterol (arrows) as a dark mass between the seminiferous tubules. Bismuth trichloride method. X 95.

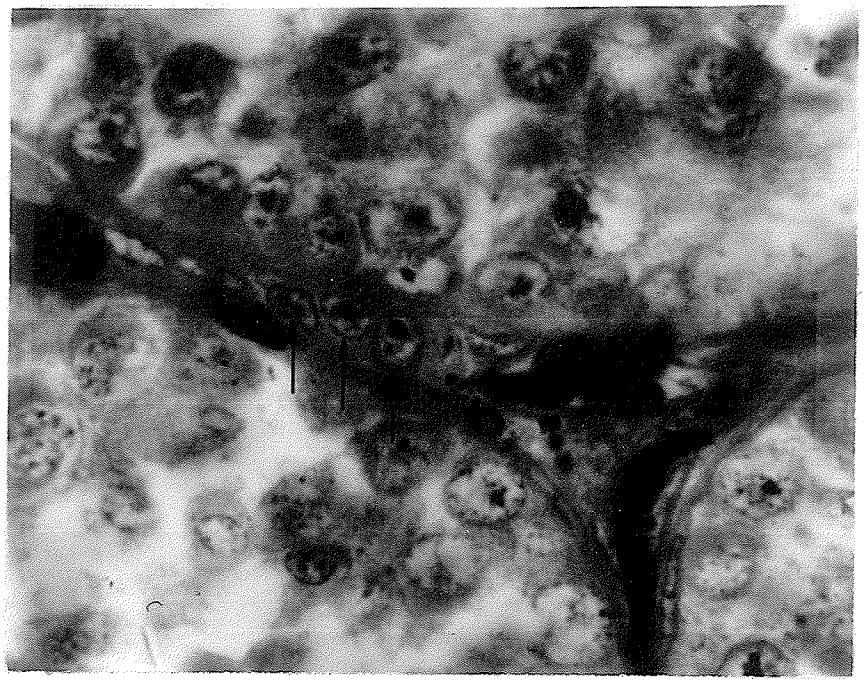


FIG. 6

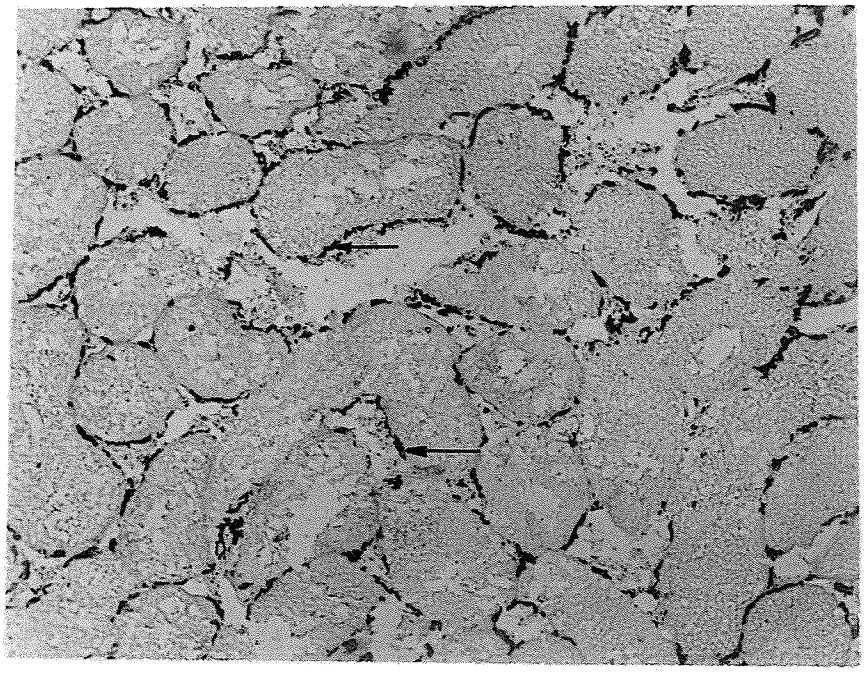


FIG. 7

Mitochondria and Blood Cell Incidence

A qualitative analysis was applied for assessing the incidence of mitochondria, for when stained by Altmann's acid fuchsin-picric acid technique, the nuclear material also took up the stain, making it difficult to determine, under oil immersion, whether mitochondria (Fig. 8) or nuclear material were observed. However, assuming the amount of nuclear material was constant from section to section (Bloom and Fawcett, 1962), variations in staining can presumably be primarily attributed to variations in mitochondria. By studying only the interstitial tissue and using the seminiferous tubules for orientation, an assessment of changes in relative density of mitochondria could therefore be obtained. Relative incidence of mitochondria was estimated subjectively by assigning to each specimen a number from 1 to 8 to describe the amount of mitochondria it possessed relative to the minimum, 1, and maximum, 8, observed in the entire population.

This method also stained red and white blood cells (Fig. 9). Although not an initial objective, blood cell incidence or vascularity was measured to investigate changes correlating with the testis cycle. The Chalkley technique was employed for these determinations.

Fig. 8. Transverse section of Sharp-tailed Grouse testis illustrating the presence of mitochondria (arrows) in the Leydig cells. Altmann's acid fuchsin-picric acid technique. X 1250.

Fig. 9. Transverse section of Sharp-tailed Grouse testis illustrating the presence of blood cells (arrows) in the interstitium. Altmann's acid fuchsin-picric acid technique. X 650.

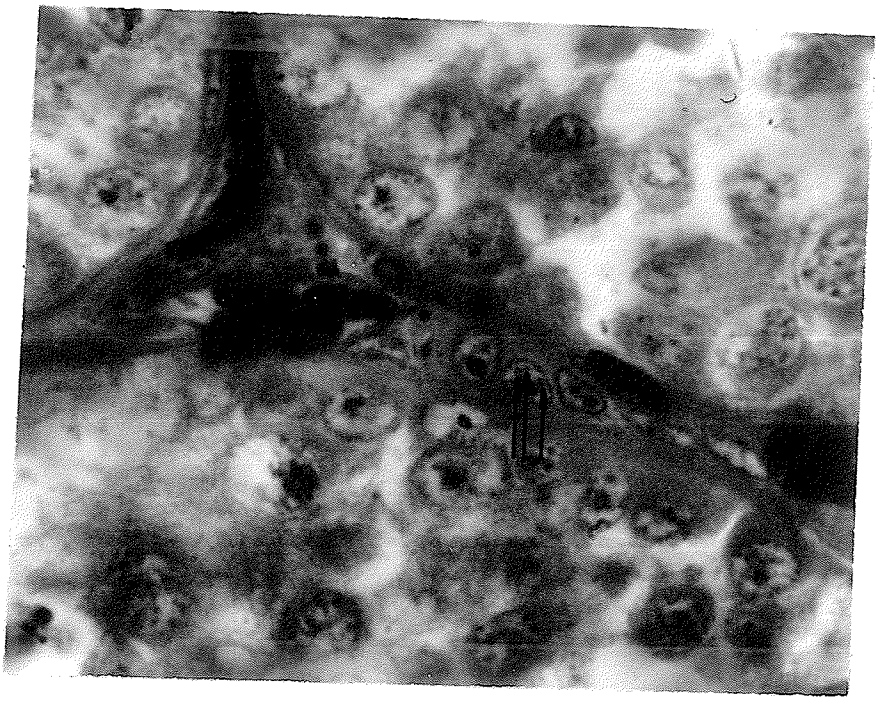


FIG. 8

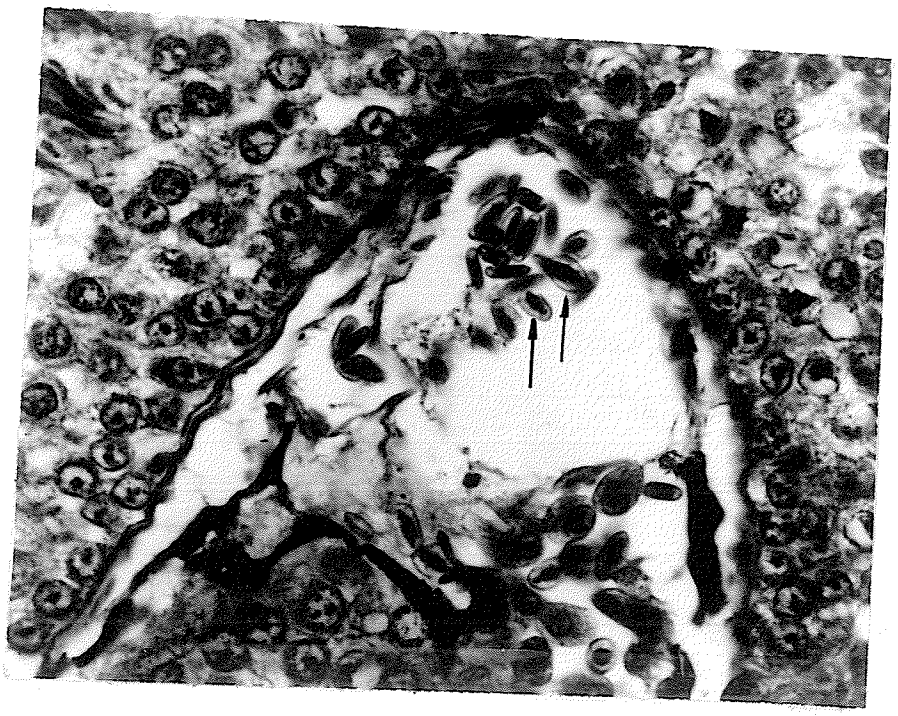


FIG. 9

Lumen Diameter

To determine if any changes in the maximum of lumen internal diameters occurred that might correlate with the testis cycle, a quantitative analysis was employed. The maximum internal lumen diameter present on each tissue section was recorded to the nearest .02 mm for tissues fixed in Bouin's and stained by Masson's trichrome technique.

RESULTS

In 1967, the first male Sharp-tailed Grouse was collected on May 7, which was well into the spring display period. Collections terminated on June 21, after which date the males failed to re-appear on the dancing grounds. In 1968 collections commenced on April 11, and concluded on June 12, the last day of the spring display period. Consequently, collections covered the entire breeding season in 1968, compared to only the last one and one-half months in 1967. Over the two years a total of 64 males were collected, 23 juveniles and 41 adults. Testes of two birds, one juvenile and one adult, were so badly damaged during collection that volume measurements were not obtainable; tissue specimens for all but one male were secured and preserved for histological analysis.

Census

A summary of the number of dancing grounds of various sizes, and the maximum number of males and females in attendance, reveals that the total male population increased in 1968 on the 20-square-mile area that was studied (Table I). The number of dancing grounds also increased, from 6 to 9, for large grounds, but decreased from 10 to 9 for small grounds.

TABLE I

Summary of the total number of dancing grounds, and maximum numbers of males and females on the dancing grounds for 1967 and 1968. (Small dancing grounds: 1 - 10 males; Large dancing grounds: more than 10 males).

	YEAR							
	1967				1968			
	Total	Avg.	Median	Range	Total	Avg.	Median	Range
Large dancing grounds	6				9			
Females	30	5	3	3-20	27	3	2	1-7
Males	117	20	17	14-30	141	17	16	12-21
Small dancing grounds	10				9			
Females	11	1	0	0-4	23	2	1	1-5
Males	62	6	7	3-10	74	8	9	5-10

These differences are reflected in the average dancing ground sizes, which decreased from 20 to 17 for large dancing grounds, and increased from 6 to 8 for small grounds (Table I). Taken together, these changes indicate a trend towards more dancing grounds of intermediate size in 1968 (Fig. 10).

An increase in the total number of females observed on the dancing grounds was also noted between 1967 and 1968, especially on small grounds. However, the result did not necessarily reflect a change in female population levels, since census data are lacking for the earliest part of the display period in 1967.

The attendance of females on the dancing grounds during the 1967 and 1968 display period, expressed as a percentage of the total attendance by both sexes, is illustrated in Fig. 11. In 1967, female attendance reached 24 per cent of the total population in early May, but after one week, their number declined to approximately 10 per cent of the total population until both sexes failed to return in the third week of June. In 1968 the females fluctuated from 10 per cent to 20 per cent of the total population in April, then remained at approximately 10 per cent of the total number until dancing ground activity ceased for both sexes during the last week of June.

Fig. 10. Frequency distribution of five Sharp-tailed Grouse dancing ground size classes in 1967 and 1968. Classes based on maximum number of males in attendance.

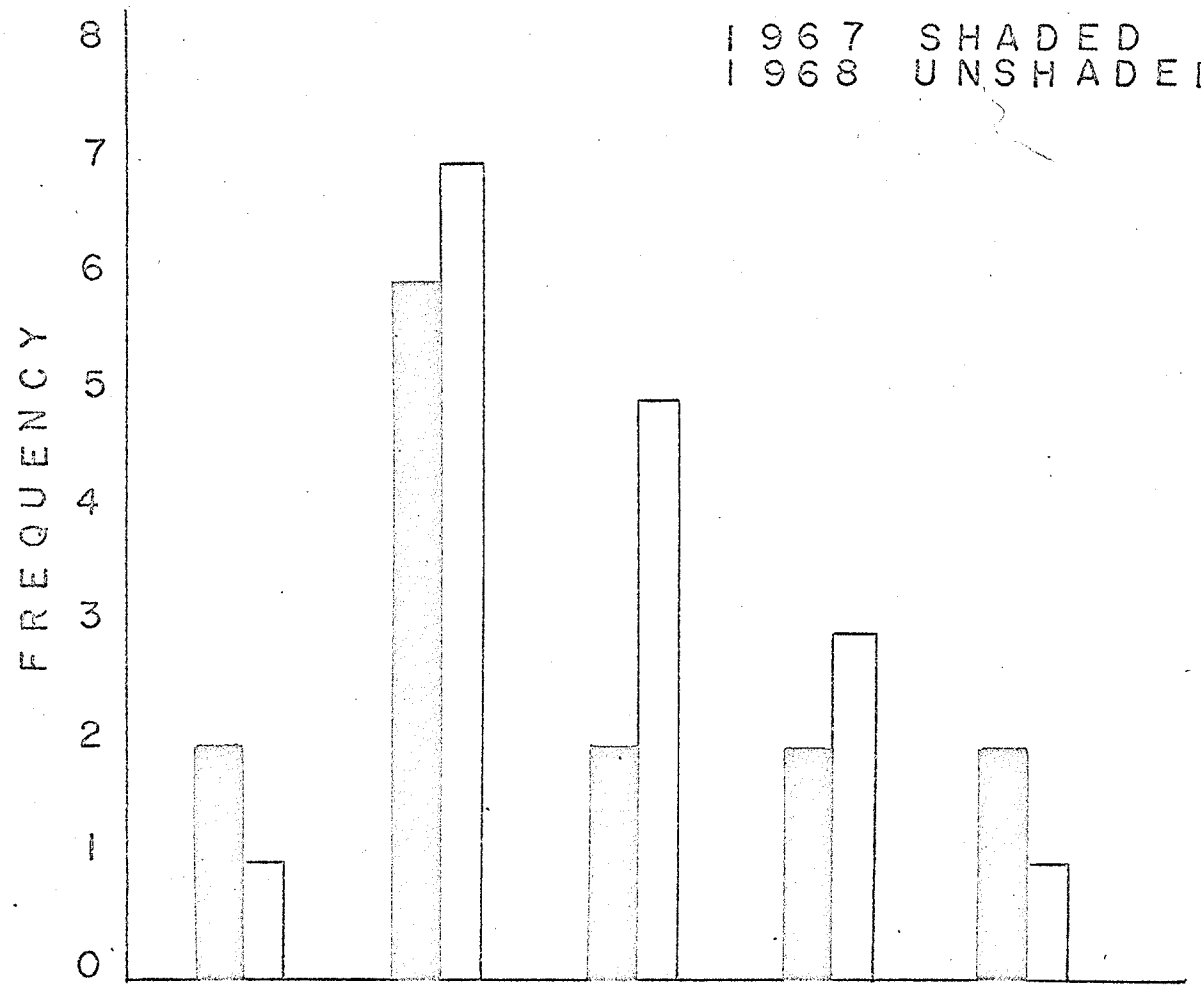

1967 SHADED
1968 UNSHADED
FREQUENCY
0
1
2
3
4
5
6
7
8
1-5
6-10
11-15
16-20
>20
DANCING GROUND SIZE CLASS

FIG. 10

Fig. 11. Weekly average occurrence of females, (as a per cent of the total birds) on the dancing grounds in 1967 and 1968.

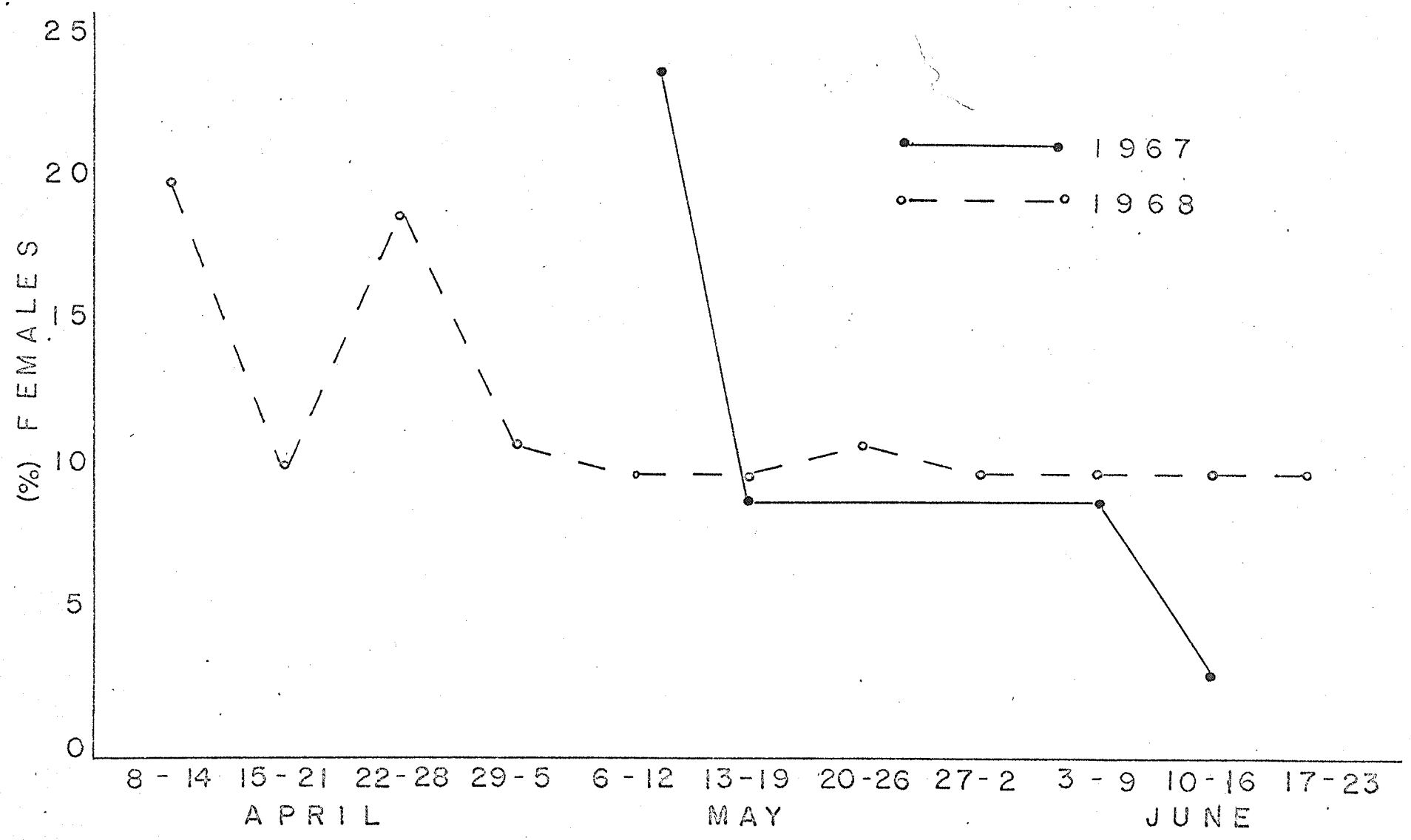

25
20
15
10
5
0
(%) FEMALES
1967
1968
8 - 14
15 - 21
22 - 28
29 - 5
6 - 12
13 - 19
20 - 26
27 - 2
3 - 9
10 - 16
17 - 23
APRIL
MAY
JUNE

FIG. 11

Except on the periphery of large grounds in 1968, adult males outnumbered juvenile males for both large and small dancing grounds in both years (Table II). There were no significant changes ($X^2 = 1.12$, $.75 > P > .50$) in the ratio of adults to juveniles between 1967 and 1968. On large dancing grounds, the incidence of adults was similar for the center and periphery ($X^2 = 0.67$, $.75 > P > .50$). Similarily, differences were not present between large and small dancing grounds ($X^2 = 0.12$, $.50 > P > .25$). These findings suggested that dancing ground size as well as social organization, as reflected by central as opposed to peripheral positions, were independent of the age composition of the males present.

Mean Body Weight of Males

Body weight of males ranged from 737 to 964 g in 1967, and 730 to 1075 g in 1968. The mean body weight of both adult and juvenile age classes was greater in 1968 than in 1967 (Fig. 12). Analysis of the data by the paired-t-test indicated, however, that mean weights did not differ significantly between the years for either age class (Table III, A).

Age

In both years of the study, the heaviest males, which ranged up to 964 g in 1967 and 1075 g in 1968, were adults

TABLE II

Total number of adult and juvenile males collected from large and small dancing grounds in 1967 and 1968.

Date	Sample Size	Large Ground				Small Ground		Total	
		Central		Periphery		Random			
		Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
1967	25	5	3	7	0	6	4	18	7
1968	39	7	4	5	7	11	5	23	16
Total	64	12	7	12	7	17	9	41	23
Per cent		63	37	63	37	65	35	66	34

TABLE III

Summary of paired-t-tests between body weights of males of different age classes and collection years.

	Date	Classification	df	t (P=0.05)	t	Significance
A.	67-68	Adult-Adult	4	± 2.78	0.46	N.S.
	67-68	Juvenile-Juvenile	5	± 2.57	0.47	N.S.
B.	1967	Adult-Juvenile	5	± 2.57	1.45	N.S.
	1968	Adult-Juvenile	8	± 2.31	1.35	N.S.

Fig. 12. Comparison of body weight between adult and juvenile Sharp-tailed Grouse in 1967 and 1968. (ends of vertical lines = range; ends of blackened rectangle = standard deviation; wide horizontal lines = mean. (Numbers in parenthesis indicate sample size).

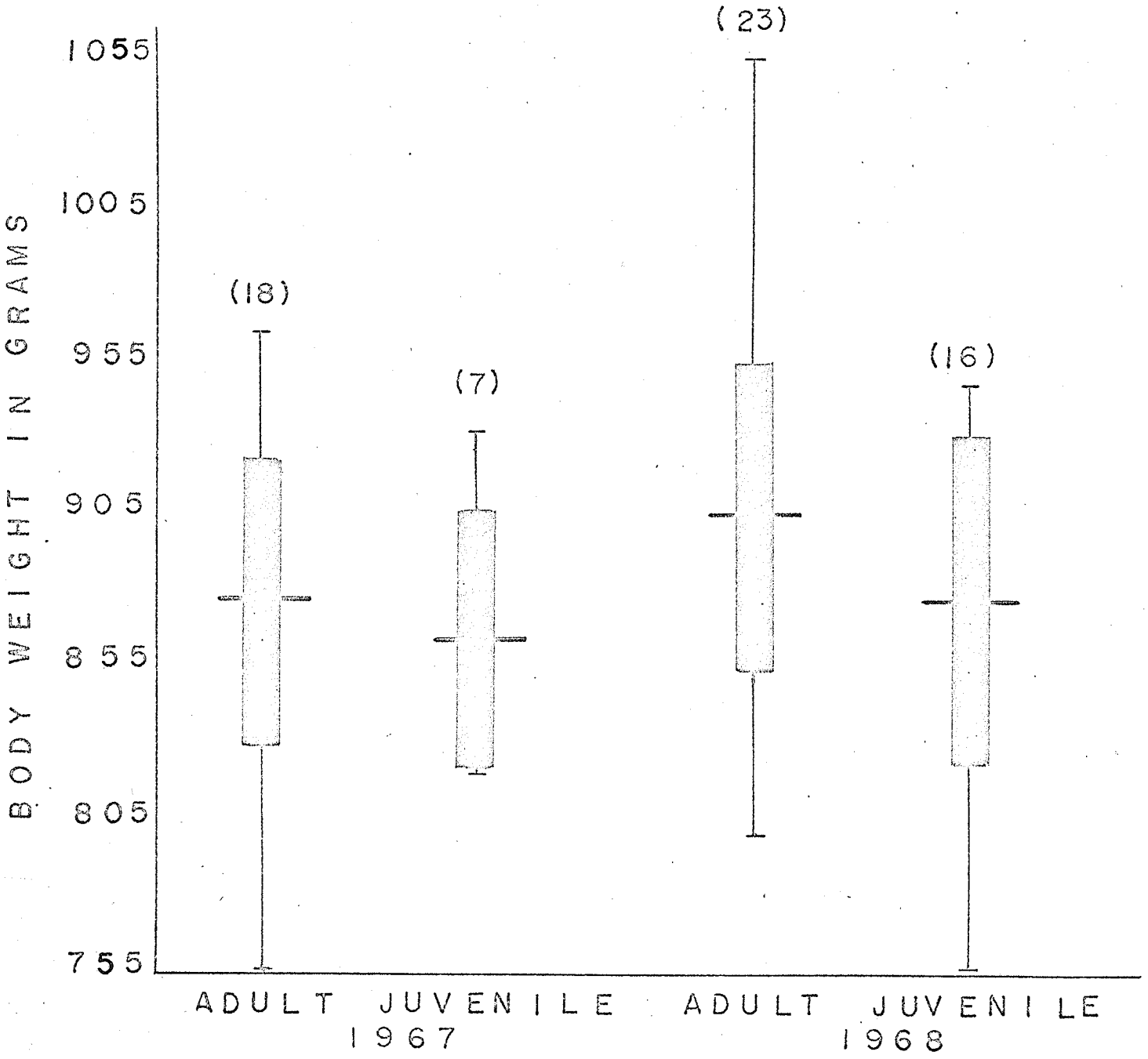

BODY WEIGHT IN GRAMS
1055
1005
955
905
855
805
755
(18)
(7)
(23)
(16)
ADULT
JUVENILE
ADULT
JUVENILE
1967
1968

FIG. 12

(Fig. 12). The mean weights of the adults were also greater than those of the juveniles in both 1967 and 1968. Overlap between the age classes was large (Fig. 12), however, and analysis of the data by the paired-t-test revealed no significant differences ($P > 0.05$) in the mean weight of the two age classes in either year (Table III, B).

Position on the Dancing Ground

In both 1967 and 1968 the central males, collected from large dancing grounds, had a greater mean body weight than either those from the periphery of large grounds or those collected randomly from small dancing grounds (Fig. 13). The mean weight of randomly-collected males, in turn, was greater than that of the peripheral males, which had the smallest mean body weight of any group. However, a considerable amount of overlap between the weights of the three positions existed and, as summarized in Table IV, there were no significant

TABLE IV

Summary of the results from the randomized complete-block design for analysis of variance for three treatments; body weight vs. positions in 1967 and 1968.

Date	df	F (P=0.05)	F	Significance
1967	2 and 12	19.41	1.09	N.S.
1968	2 and 16	19.43	1.95	N.S.

Fig. 13. Comparison of body weight between central (C), peripheral (P), and random (R) Sharp-tailed Grouse males in 1967 and 1968. (Symbols as in Fig. 12).

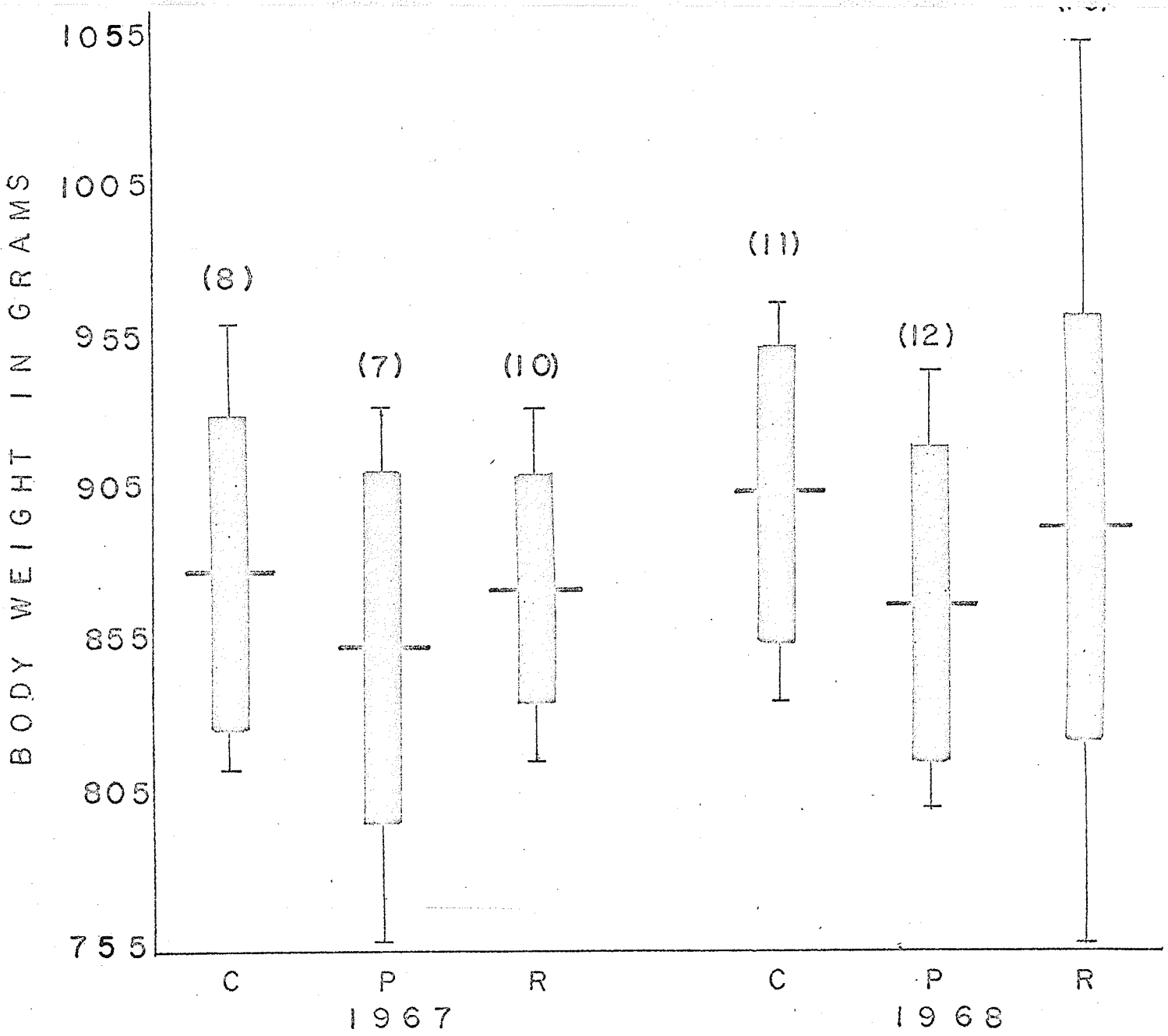

BODY WEIGHT IN GRAMS
1055
1005
955
905
855
805
755
(8)
(7)
(10)
(11)
(12)
C
P
R
C
P
R
1967
1968

FIG. 13

differences in weights between the three positions in either year of the study. The values shown in Fig. 13 indicated further, that mean body weights of males were greater in 1968 than in 1967 for each of the three positions, but these differences, when analyzed by the paired-t-test, were also not significant ($P \geq 0.05$) (Table V).

TABLE V

Summary of paired-t-tests between years for body weight of the males on each of the three positions in 1967 and 1968.

Date	Position	df	t (P=0.05)	t	Significance
67-68	Central	3	± 3.18	0.07	N.S.
67-68	Peripheral	5	± 2.57	1.50	N.S.
67-68	Random	5	± 2.57	-0.21	N.S.

Testis Volume

Comparison Between Left and Right Testes.

Of the 35 males for which the volumes of both testes were obtained, there were 14 (40 %) in which the left testis was larger; 8 (23 %) in which the right testis was larger, and 13 (37 %) in which both testes were equal in volume (Table VI, A). The percentages listed in Table VI, A indicate, further, that the tendency for more males to possess

TABLE VI

Summary of the volumes of the left and right testes. A. Percentages of instances in which left testes was greater, less than, or equal to the right testes. B. Volume (ml) of left and right testes.

		Classification					
		Age		Position			
		Adult	Juvenile	Central	Periphery	Random	Total
A. Sample size		21	14	11	11	13	35
Left > right testes		43%	36%	45%	45%	31%	40%
Left < right testes		24%	21%	27%	18%	23%	23%
Testes equal		33%	43%	28%	37%	46%	37%
B. Left testes:	Mean	1.0	0.8	0.9	0.8	1.0	0.9
	Range	1.5-0.6	1.0-0.4	1.5-0.6	1.2-0.4	1.2-0.8	1.5-0.4
	SD	0.2	0.1	0.3	0.3	0.1	0.2
Right testes:	Mean	0.9	0.8	0.9	0.8	1.0	0.9
	Range	1.4-0.4	1.0-0.5	1.2-0.4	1.0-0.5	1.2-0.8	1.4-0.4
	SD	0.2	0.2	0.2	0.2	0.2	0.2

a larger left testes was consistent for both adult and juveniles, and for central, peripheral, and random males. Similarily, the average volume of left testes (.93 ml) for all 35 males combined was somewhat greater than the right (.88 ml). This trend also occurred in both age classes and for both central and peripheral males (Table VI, B). Random males were the only exception, and then, the right mean testes volume exceeded the left mean testes volume by only .01 ml. However, differences between the volumes of the left and right testes were small, and not significant ($P > 0.05$) when tested by a paired-t-test ($t=1.12$, $t.95$ $(34df) = \pm 2.04$).

Testis Volume and Age

No consistent relationship between testis volume and age was found (Fig. 14). In 1967 the mean volume of the juvenile testes was .95 ml, compared to a mean of only .83 ml for the adult testes. This relationship was reversed in 1968, when the juveniles had a mean testes volume of .83 ml compared to a mean volume of .97 ml for the adults. Lack of any consistent relationship between age class and testis volume was substantiated by a lack of statistical significance between adult and juvenile testes volumes in both 1967

Fig. 14. Comparison of testis volume between adult and juvenile Sharp-tailed Grouse in 1967 and 1968. (Symbols as in Fig. 12).

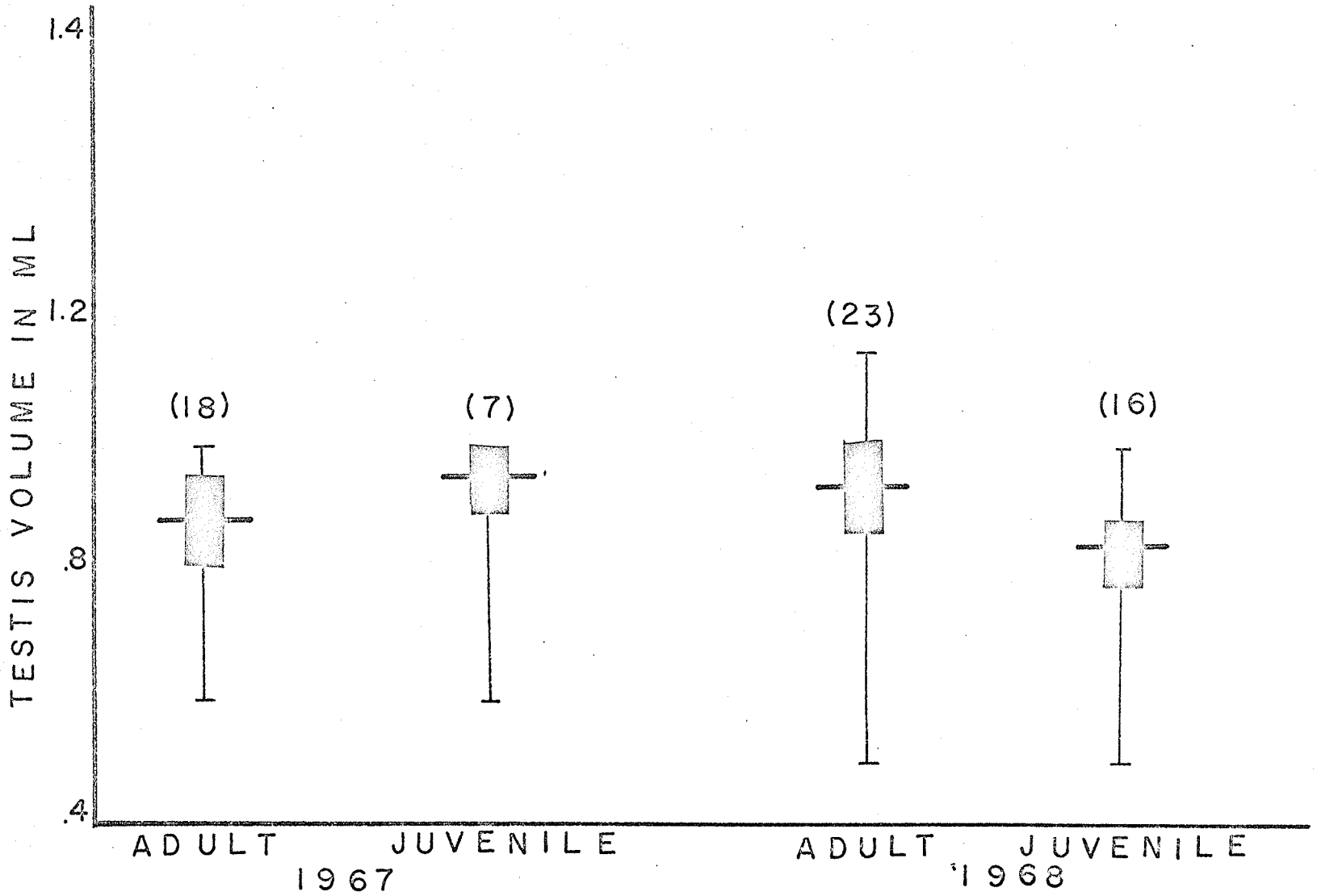

1.4
1.2
.8
.4
TESTIS VOLUME IN ML
(18)
(7)
(23)
(16)
ADULT
JUVENILE
ADULT
JUVENILE
1967
1968

FIG. 14

($P>0.05$) and 1968 ($P>0.05$) (Table VII).

TABLE VII

Summary of paired-t-tests between testis volumes of adults and juveniles in 1967 and 1968.

Date	Age	df	t (P=0.05)	t	Significance
1967	Adult-Juvenile	6	± 2.45	-1.35	N.S.
1968	Adult-Juvenile	9	± 2.26	1.70	N.S.

Testis Volume and Position on the Dancing Ground

In 1967, the testes volumes of central males were high by the second week of May and then declined gradually (Fig. 15A). Testes volumes of central males in 1968 (Fig. 15B) were more variable, with no consistent seasonal trends. Testes volumes of peripheral and random males did not reach levels equal to those of central males at the start of the season in 1967, but in 1968 and by the middle of the third week in May in 1967 the 3 groups were similar. In 1967, and to a lesser extent in 1968, testis volume of peripheral males appeared to decline less rapidly than that of central males during the latter portion of the breeding season. These results suggested a possible delay in the seasonal cycle of peripheral males relative to central males.

Fig. 15. Testis volume for central, peripheral, and random males for successive weekly intervals during the breeding season of (A) 1967 and (B) 1968. (Numbers in parenthesis indicate total sample size).

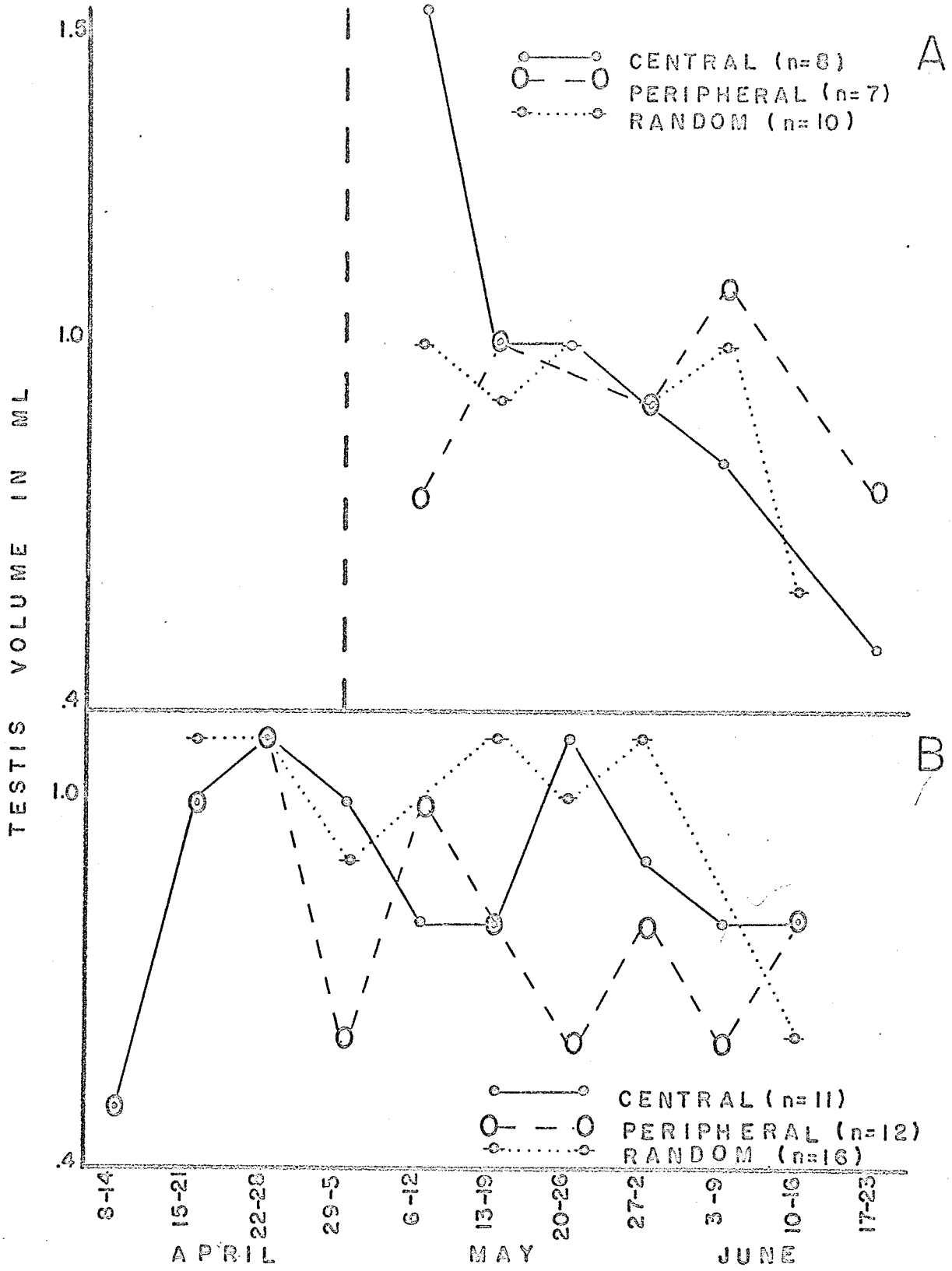

A
CENTRAL (n=8)
PERIPHERAL (n=7)
RANDOM (n=10)
1.5
1.0
.4
B
1.0
.4
CENTRAL (n=11)
PERIPHERAL (n=12)
RANDOM (n=16)
TESTIS VOLUME IN ML
8-14
15-21
22-28
29-5
6-12
13-19
20-26
27-2
3-9
10-16
17-23
APRIL
MAY
JUNE

FIG. 15

A comparison of the average testis volumes over the entire collection period indicated that in both 1967 and 1968 the range of values for testis of central males achieved a greater maximum value than either the peripheral males, which were collected from the same large dancing grounds, or the birds collected randomly from small grounds (Fig. 16). In 1967, the central males also had the largest mean testis volume, but in 1968 the mean volume of the testis from random males was greater than that for either central or peripheral males. However, as summarized in Table VIII, differences in the testes volumes between central, peripheral or random males were not significant in either year of the study ($P>0.05$). Except for the randomly-collected males, the mean volumes for 1967 tended to be greater than their counterparts

TABLE VIII

Summary of paired-t-tests between testis volumes of central, peripheral, and random birds in 1967 and 1968.

Date	Position	df	t (P=0.05)	t	Significance
1967	Central-Peripheral	6	± 2.45	0.19	N.S.
1967	Central-Random	6	± 2.45	0.36	N.S.
1967	Peripheral-Random	6	± 2.45	0.78	N.S.
1968	Central-Peripheral	8	± 2.31	1.37	N.S.
1968	Central-Random	8	± 2.31	-0.73	N.S.
1968	Peripheral-Random	8	± 2.31	1.45	N.S.

Fig. 16. Comparison of testis volume between central (C), peripheral (P), and random (R) Sharp-tailed Grouse males in 1967 and 1968. (Symbols as in Fig. 12).

FIG. 16

in 1968, but these differences were also small (Fig. 16), and not significant ($P>0.05$).

Testis Volume and Body Weight

As illustrated in Fig. 17, some evidence was obtained that the gonads of the heavier birds tended to be larger than those of the lighter birds. However, correlation coefficients calculated for testis volume and body weight in 1967 and 1968, approached, but did not reach statistically significant values ($P>0.05$) (Table IX).

TABLE IX

Summary of correlations between body weight and testis volume.

Date	Sample Size	r (P=0.05)	r	Significance
1967	25	0.38	0.29	N.S.
1968	37	0.32	0.24	N.S.

Cholesterol Levels

Cholesterol levels obtained for 39 males in 1968, dropped rapidly during April, from 24 per cent at the beginning of the display season, to 11 per cent to 12 per cent by the end of April and the first week in May (Fig. 18A). Variation between subsequent levels was less pronounced, and a level of 11 per cent was again present at the end of the season.

Fig. 17. Relationship between testis volume and body weight of Sharp-tailed Grouse in 1967 and 1968. (Numbers in parenthesis indicate sample size).

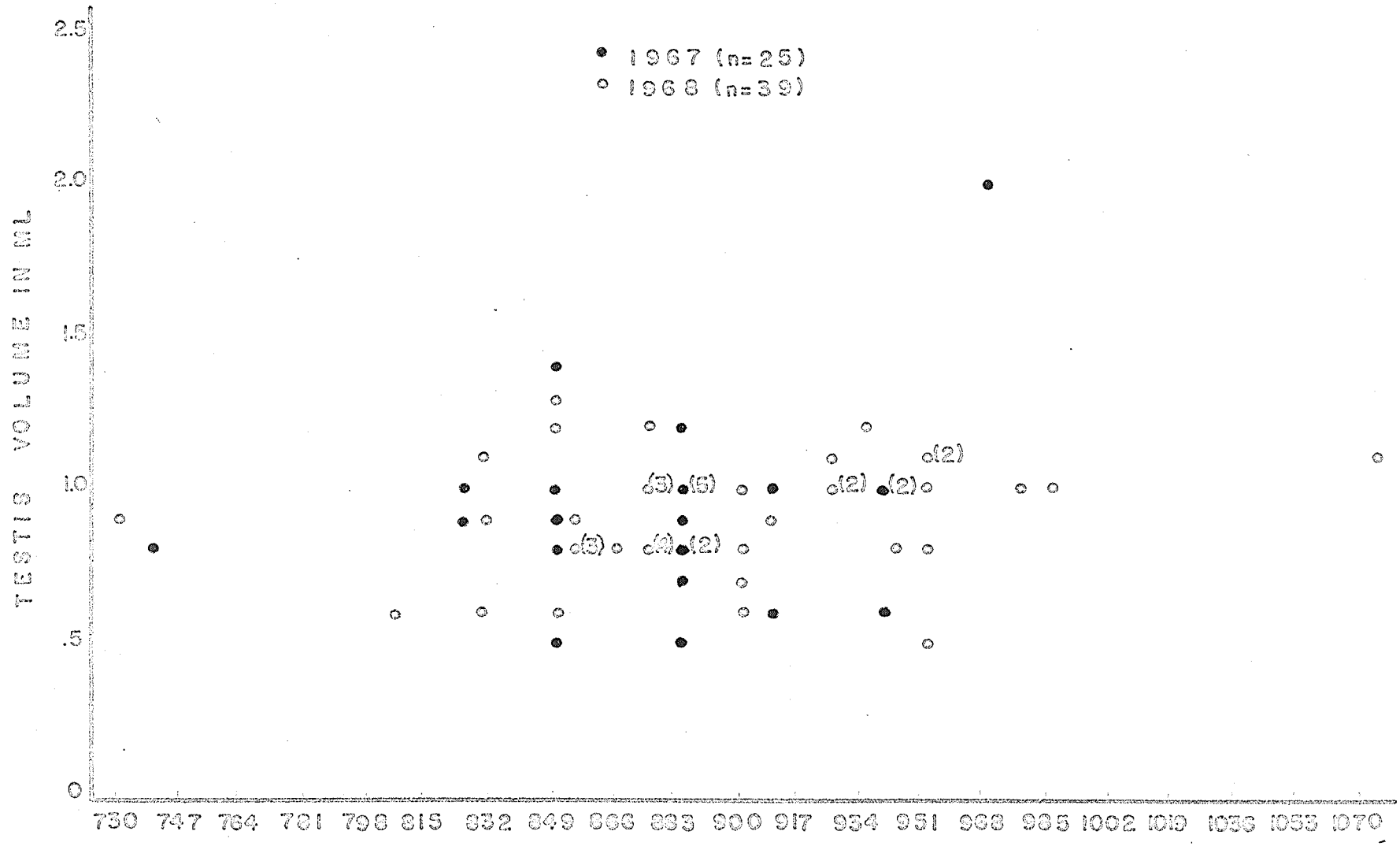

1967 (n=25)
1968 (n=39)
TESTIS VOLUME IN ML.
2.5
2.0
1.5
1.0
.5
0
730 747 764 781 798 815 832 849 866 883 900 917 934 951 968 985 1002 1019 1036 1053 1070
WEIGHT IN GRAMS

FIG. 17

Fig. 18. Level of cholesterol in Sharp-tailed Grouse testes at successive weekly intervals during the 1968 breeding season. (A) Total sample; (B) adults and juveniles; (C) central, peripheral, and random males. (Numbers in parenthesis indicate sample size).

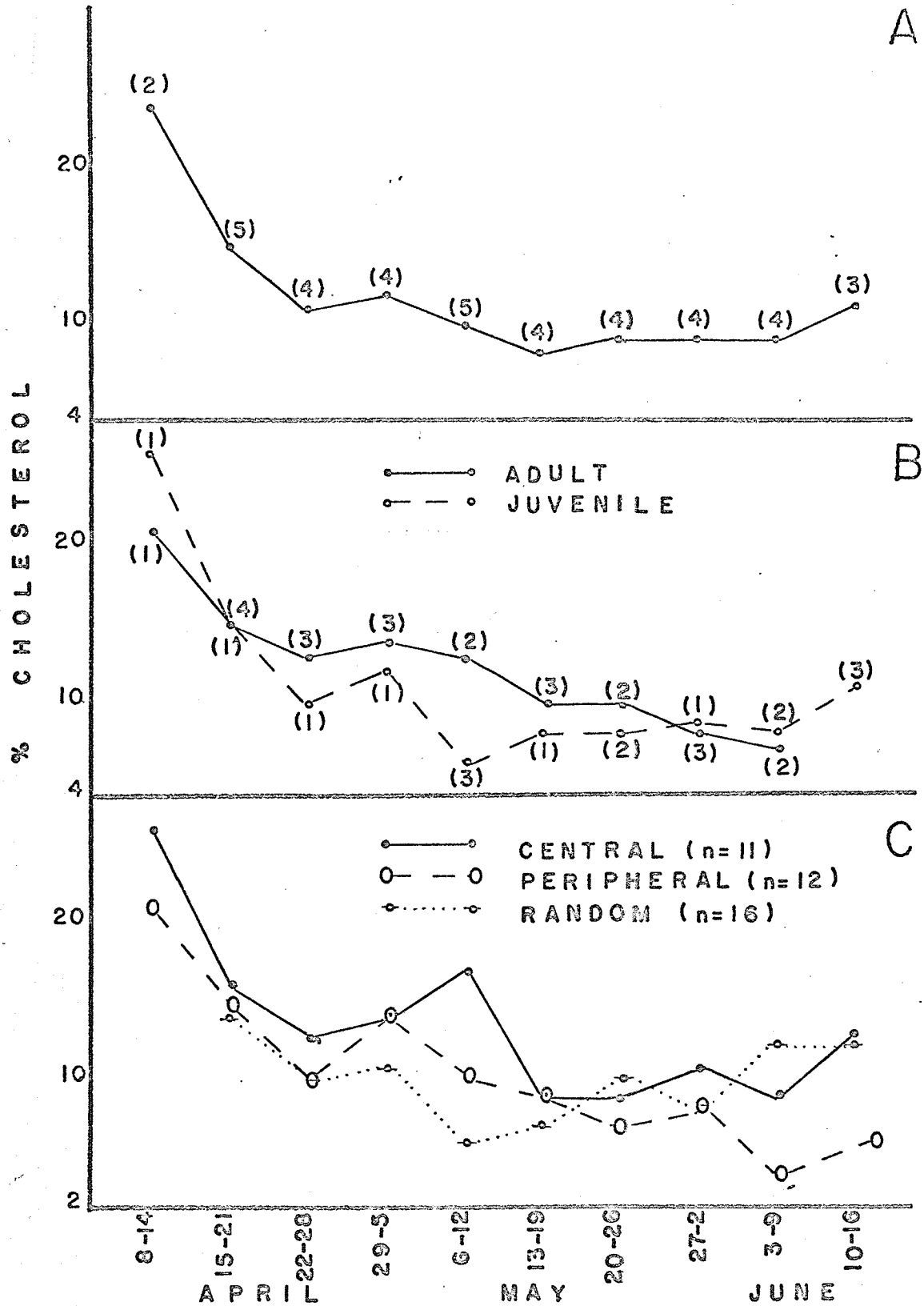

A
B
C
% CHOLESTEROL
20
10
4
2
ADULT
JUVENILE
CENTRAL (n=11)
PERIPHERAL (n=12)
RANDOM (n=16)
8-14
15-21
22-28
29-5
6-12
13-19
20-26
27-2
3-9
10-16
APRIL
MAY
JUNE

FIG. 18

For the entire collection period in 1968, the relationship between level of cholesterol and season was found to be significant when tested by a rank correlation coefficient ($r = -0.44$, $P < 0.05$).

Cholesterol Levels and Age

The significant seasonal decrease in testis cholesterol level in 1968 applied to both adults and juveniles when tested separately (Fig. 18B, Table X). The similarity between adults and juveniles is further indicated by values for

TABLE X

Summary of rank correlations between cholesterol level and season, for adult and juvenile age classes.

Age Class	df	r (P=0.05)	r	Significance
Adults	17	0.41	-0.53	0.05
Juveniles	14	0.46	-0.51	0.05

mean volume of cholesterol, which did not differ significantly between adults and juveniles ($t = -0.69$, $t.95(8df) = \pm 2.31$).

Cholesterol Levels and Position on the Dancing Ground

The seasonal decrease in cholesterol levels was especially pronounced in peripheral males (Fig. 18C). The ran-

dom birds appeared to lag behind birds from the center and periphery of large grounds until late in the display season, when they either equalled or exceeded both central and peripheral birds. This condition is reflected in the values of rank correlation coefficients, calculated for cholesterol levels over the season, which indicate a significant decline with season for both central ($r = -0.73$, $P < 0.01$) and peripheral ($r = -0.82$, $P < 0.01$) birds, but not for random birds ($r = -0.18$, $P > 0.05$). It also appears from Fig. 18C, that late in the season both random and central males maintained more or less constant levels of cholesterol, whereas birds collected from the periphery of large grounds exhibited a more consistent decrease in quantity of cholesterol levels as the display period progressed. If not ascribable to chance, this result suggests that of the three groups, peripheral males are least able to maintain consistent levels of androgen output during the latter phases of the breeding season.

As illustrated in Fig. 19, the central males achieved a greater maximum and average quantity of cholesterol than peripheral or random males. Cholesterol levels of central males also tended to be greater than that of peripheral males throughout the entire breeding season (Fig. 19). Comparisons between

Fig. 19. Cholesterol levels in testes of central, peripheral, and random Sharp-tailed Grouse in 1968. (Symbols as in Fig. 12).

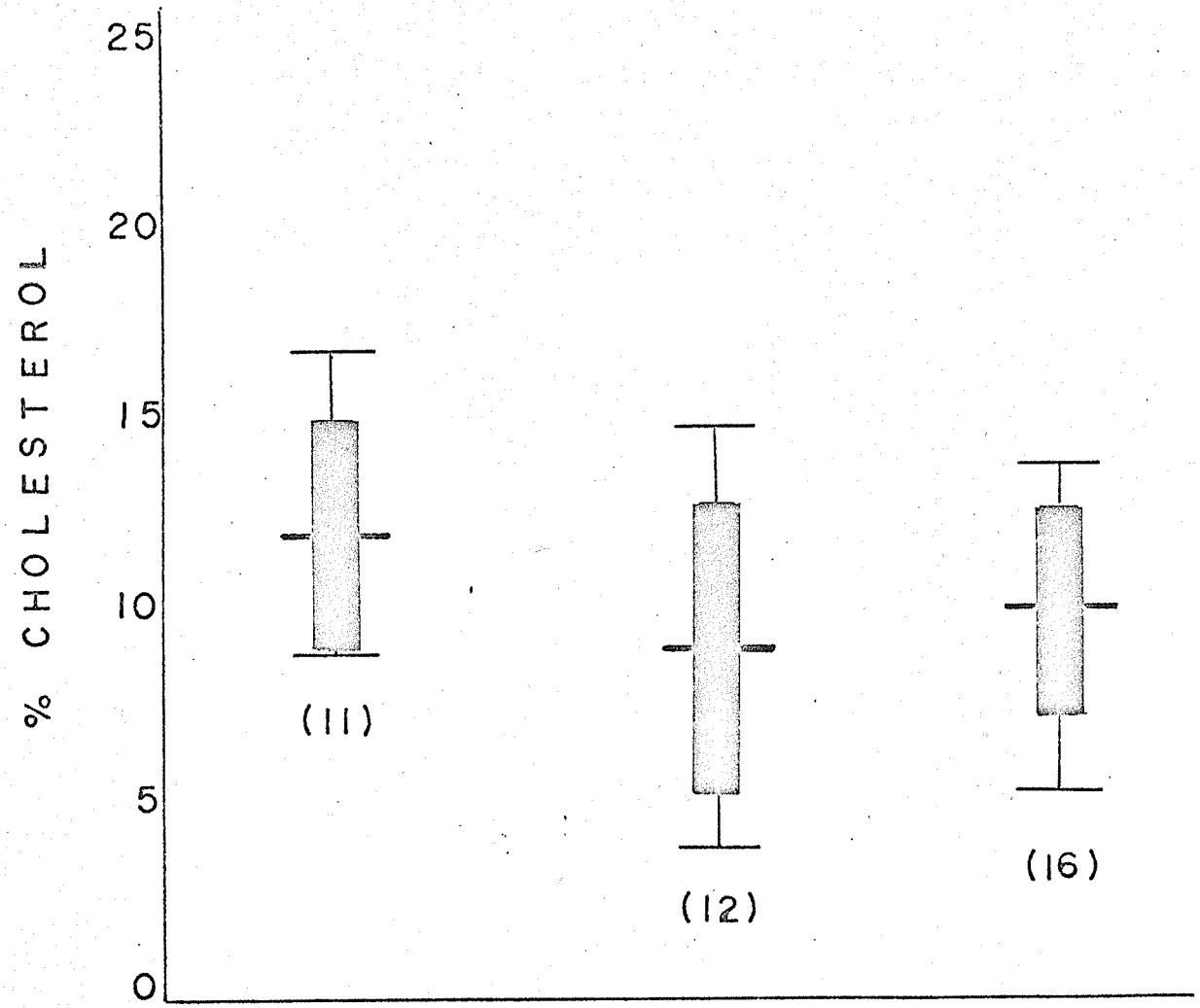

25
20
15
10
5
0
% CHOLESTEROL
(11)
(12)
(16)
CENTRAL
PERIPHERAL
RANDOM

FIG. 19

10 pairs of central and peripheral birds showed that in 9 pairs, central males had a greater level of cholesterol than peripheral males ($X^2 = 4.3$, $P < 0.05$). A comparison between 9 pairs of central and random males, and 9 pairs of random and peripheral males, revealed no significant difference ($P > 0.05$).

Further support for significant differences between central and peripheral males was provided by an analysis of the data by the paired-t-test, which signified that central males had a significantly greater quantity of cholesterol than peripheral males ($t = 3.19$, $t.95(8df) = \pm 2.31$). Differences between peripheral and random males ($t = -0.06$, $t.95(8df) = \pm 2.31$) and central and random males ($t = 1.78$, $t.95(8df) = \pm 2.31$) were not significant.

Degree of Spermatogenesis

Spermatogenesis and Age

On the basis of the presence of mature spermatozoa in the seminiferous tubules, both age classes appeared to be physiologically capable of breeding (Fig. 20). In both 1967 and 1968, juveniles appeared to achieve the same levels of spermatogenesis as adults. The mean volume of spermatozoa was actually greater in juveniles than adults

Fig. 20. Cross section through a seminiferous tubule of an adult (A) and juvenile (B) Sharp-tailed Grouse. Arrows indicate mature spermatozoa. Masson's trichrome technique. X 300.

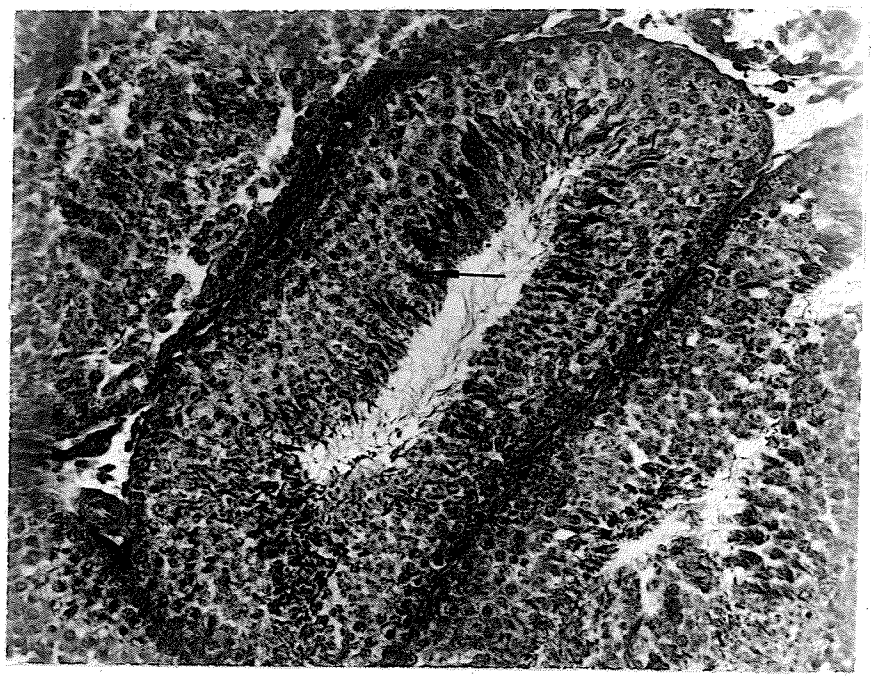


FIG. 20A

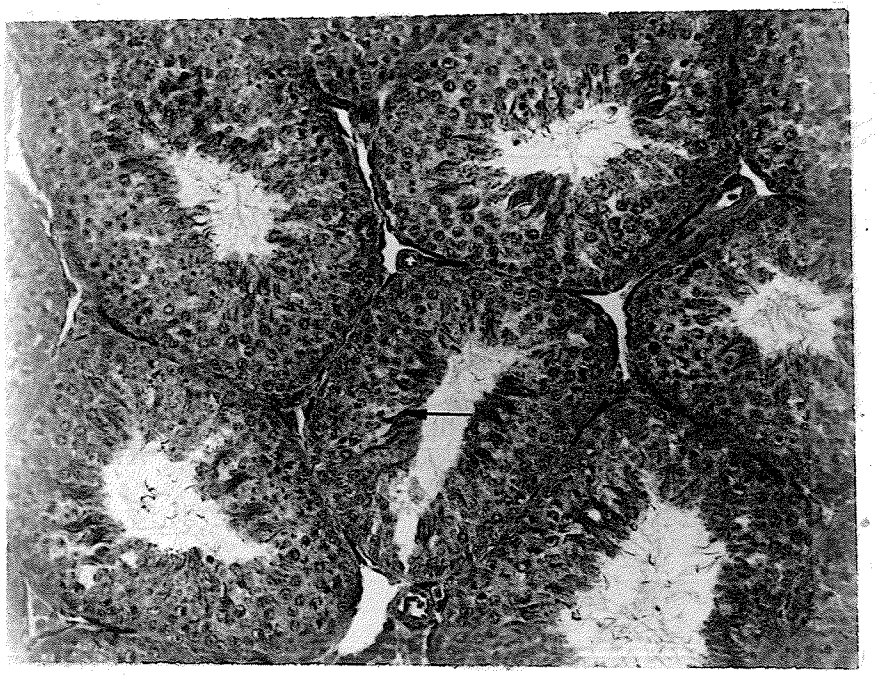


FIG. 20B

in both years (Fig. 21), but analysis of the data by paired-t-tests revealed no significant differences ($P > 0.05$) between the age classes (Table XI, A). Both age classes possessed a greater mean volume of spermatozoa in 1967 than did the corresponding age classes of 1968, but these differences were also not significant ($P > 0.05$; see Table XI, B).

TABLE XI

Summary of paired-t-tests between levels of spermatozoa of males in two age classes for 1967 and 1968.

	Date	Age	df	t (P=0.05)	t	Significance
A.	1967	Adult-Juvenile	5	± 2.57	-1.64	N.S.
	1968	Adult-Juvenile	8	± 2.31	-0.41	N.S.
B.	67-68	Adult-Adult	4	± 2.78	-0.17	N.S.
	67-68	Juvenile-Juvenile	4	± 2.78	0.15	N.S.

Spermatogenesis and Position on the Dancing Ground

As noted in the previous section, all birds appeared to be physiologically capable of breeding. Significant differences did occur, however, in the level of spermatogenesis reached by the males collected from each of the three positions on the dancing grounds.

In 1967 and 1968 centrally-located males possessed a significantly greater mean level of spermatozoa than did the

Fig. 21. Levels of spermatozoa for adult and juvenile Sharp-tailed Grouse for 1967 and 1968. (Symbols as in Fig. 12).

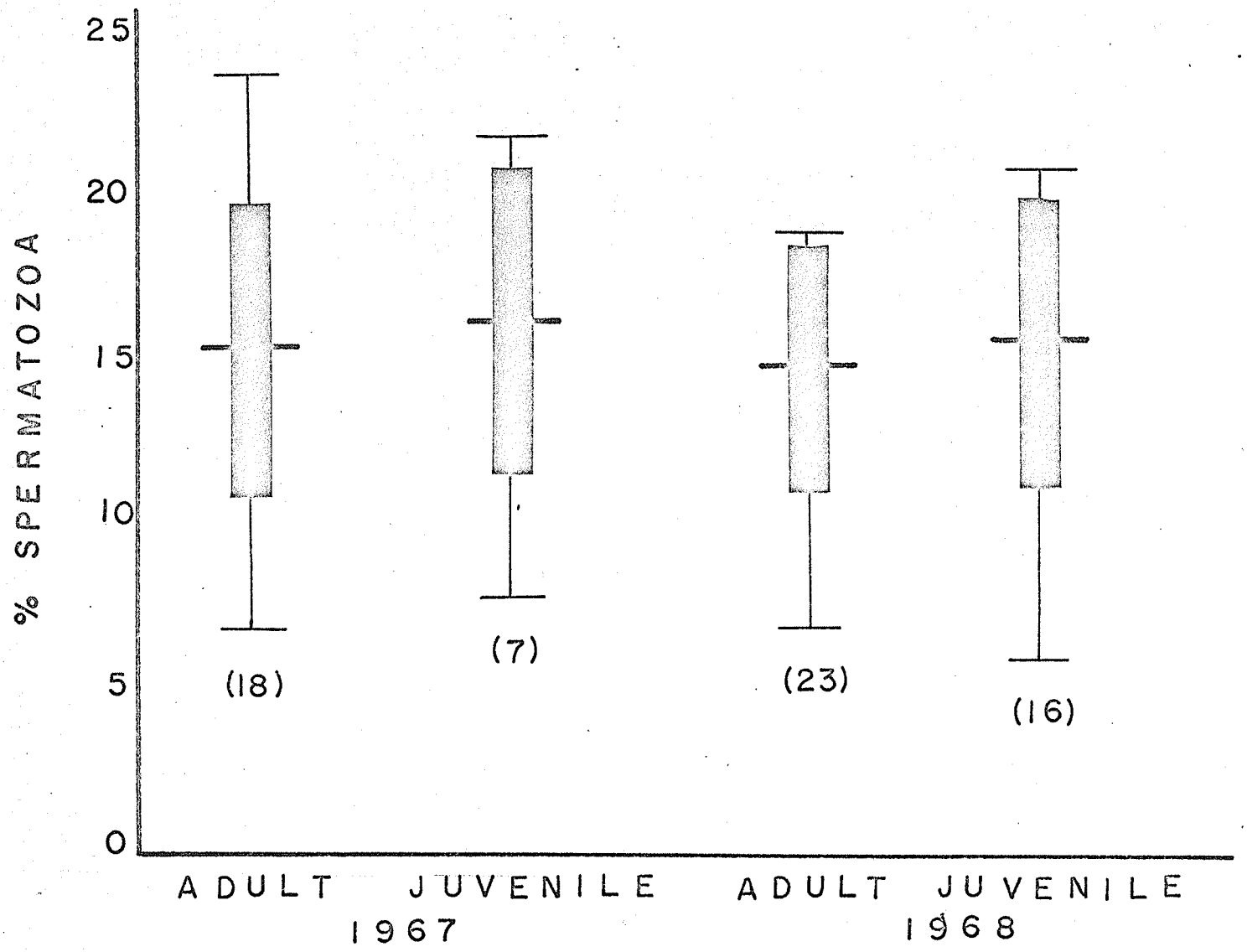

25
20
15
10
5
0
% SPERMATOZOA
(18)
(7)
(23)
(16)
ADULT
JUVENILE
ADULT
JUVENILE
1967
1968

FIG. 21

peripheral birds (Fig. 22 and Table XII). In 1967, the level of spermatozoa of random males was also significantly greater than that of peripheral males ($P<0.05$). The differences between random and peripheral males in 1968 approached significant levels ($P<0.10$). Differences between random and central birds, although present in both years (Fig. 22) were not significant ($P>0.05$).

TABLE XII

Summary of paired-t-tests between the levels of spermatozoa for males from each of three positions on the dancing grounds.

Date	Position	df	t (P=0.05)	t	Significance
1967	Central-Peripheral	4	± 2.78	3.31	$P<0.05$
1967	Central-Random	5	± 2.57	0.86	N.S.
1967	Peripheral-Random	5	± 2.57	-3.86	$P<0.05$
1967	Large-Small Grounds	5	± 2.57	-1.02	N.S.
1968	Central-Peripheral	8	± 2.31	5.46	$P<0.05$
1968	Central-Random	8	± 2.31	1.91	N.S.
1968	Peripheral-Random	7	± 1.90	-2.24	$.10>P>.05$
1968	Large-Small Grounds	7	± 2.36	-0.59	N.S.

In both 1967 and 1968, the quantities of spermatozoa in both central and random males were greater than those of the peripheral males throughout the entire breeding season (Figs. 23 A and B). The number of instances in which central and random males were greater than peripheral males

Fig. 22. Levels of spermatozoa for central, peripheral, and random Sharp-tailed Grouse for 1967 and 1968. (Symbols as in Fig. 12).

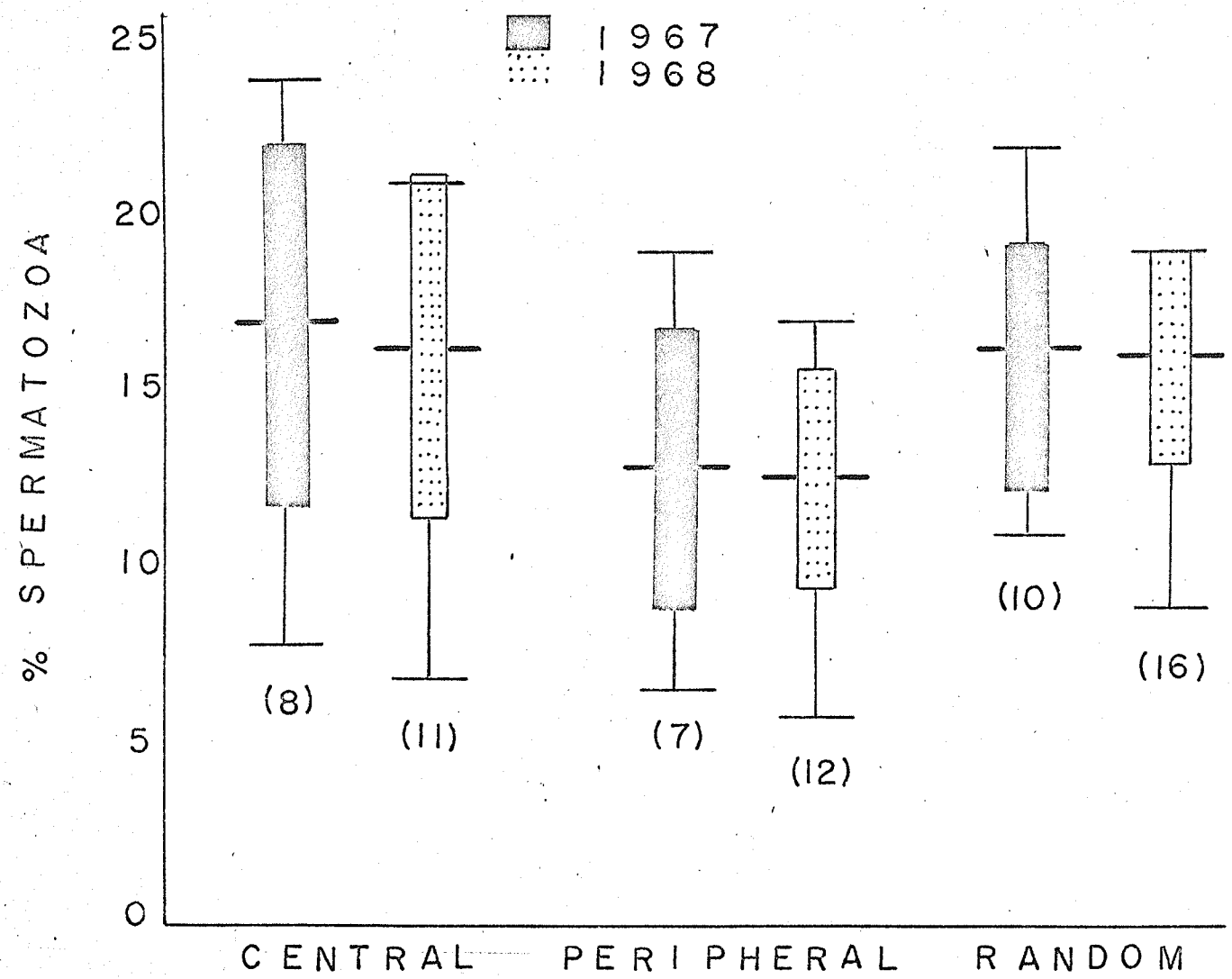

1967
1968
% SPERMATOZOA
25
20
15
10
5
0
(8)
(11)
(7)
(12)
(10)
(16)
CENTRAL
PERIPHERAL
RANDOM

FIG. 22

Fig. 23. Levels of spermatozoa in testes of central, peripheral, and random Sharp-tailed Grouse at successive weekly intervals during the (A) 1967 and (B) 1968 breeding seasons. (Numbers in parenthesis indicate total sample size).

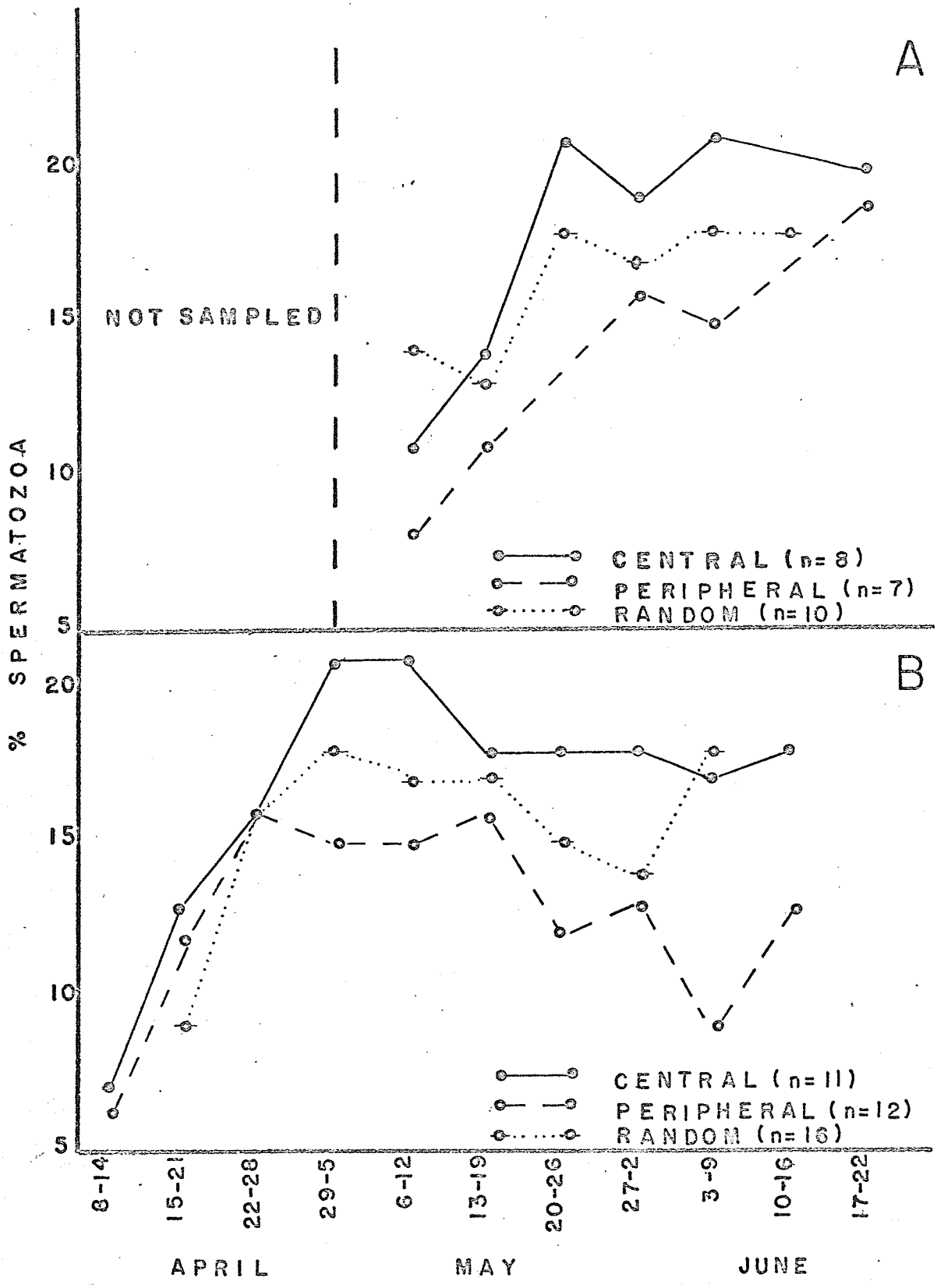

A
B
NOT SAMPLED
% SPERMATOZOA
20
15
10
5
CENTRAL (n=8)
PERIPHERAL (n=7)
RANDOM (n=10)
CENTRAL (n=11)
PERIPHERAL (n=12)
RANDOM (n=16)
8-14
15-21
22-28
29-5
6-12
13-19
20-26
27-2
3-9
10-16
17-22
APRIL
MAY
JUNE

FIG. 23

collected in the same week, is listed in Table XIII. In both years, these proportions departed significantly from random, thereby providing further evidence that spermatozoa levels of both central and random males exceeded peripheral males throughout the season. Differences between central and random males were not significant ($P > 0.05$) in either year.

Differences in the timing of spermatogenesis were also present between males collected from the different sized dancing grounds and between central and peripheral males. This is illustrated in Figs. 24 and 25, where the levels of spermatozoa and their progenitors, the spermatocytes, are plotted against time for males from each position. In 1967 and 1968 (Figs. 24 and 25) levels of spermatozoa exceeded levels of spermatocytes earlier in the season for central males than for peripheral males from the same dancing grounds. In 1967 a similar trend was also recorded between central males and random males. In 1968, both the random and central males achieved the peak reproductive condition in the third week of April, but the random males failed to maintain this condition consistently. Comparison between parts A, B, and C, of Figs. 24 and 25 indicates that, in general, neither peripheral nor random males consistently maintained the peak re-

TABLE XIII

Summary of data from X^2 tests of differences in levels of spermatozoa between central, peripheral, and random males in 1967 and 1968 combined.

Date	Position and Relation tested	Number of pairs	Number of instances positive	X^2 (P=0.05)	X^2	Significance
67-68	Central > Peripheral	16	16	3.84	16.0	0.001
67-68	Random > Peripheral	13	12	3.84	9.4	0.01
67-68	Central > Random	16	11	3.84	1.2	N.S.

Fig. 24. Levels of spermatocytes and spermatozoa in testes of central (A), peripheral (B), and random (C) Sharp-tailed Grouse at successive weekly intervals during the 1967 breeding season. (Numbers in parenthesis indicate sample size).

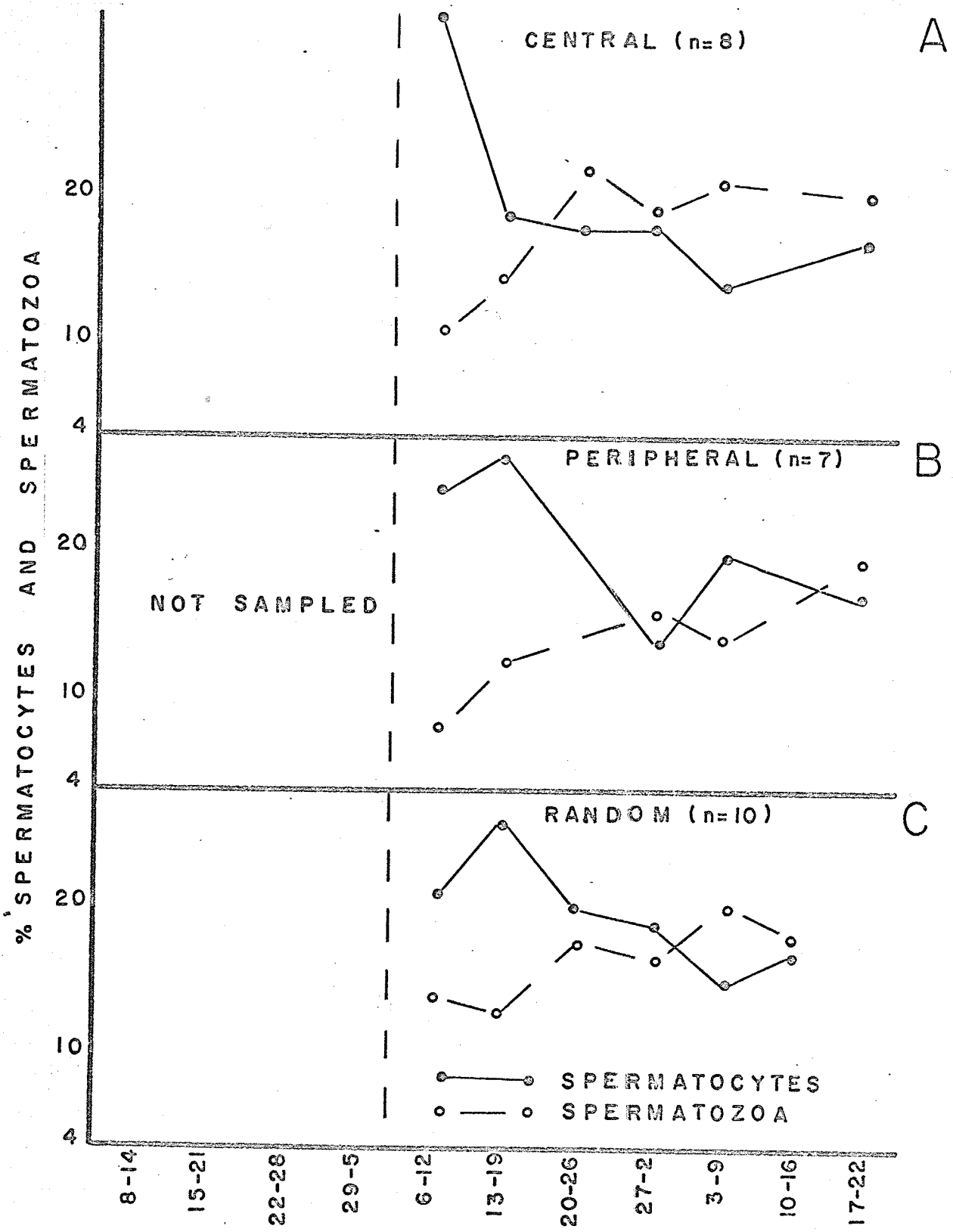

CENTRAL (n=8)
A
20
10
4
PERIPHERAL (n=7)
B
NOT SAMPLED
20
10
4
RANDOM (n=10)
C
20
10
4
% SPERMATOCYTES AND SPERMATOZOA
SPERMATOCYTES
SPERMATOZOA
8-14
15-21
22-28
29-5
6-12
13-19
20-26
27-2
3-9
10-16
17-22
APRIL
MAY
JUNE

FIG. 24

Fig. 25. Levels of spermatocytes and spermatozoa in testes of central (A), peripheral (B), and random (C) Sharp-tailed Grouse at successive weekly intervals during the 1968 breeding season. (Numbers in parenthesis indicate sample size).

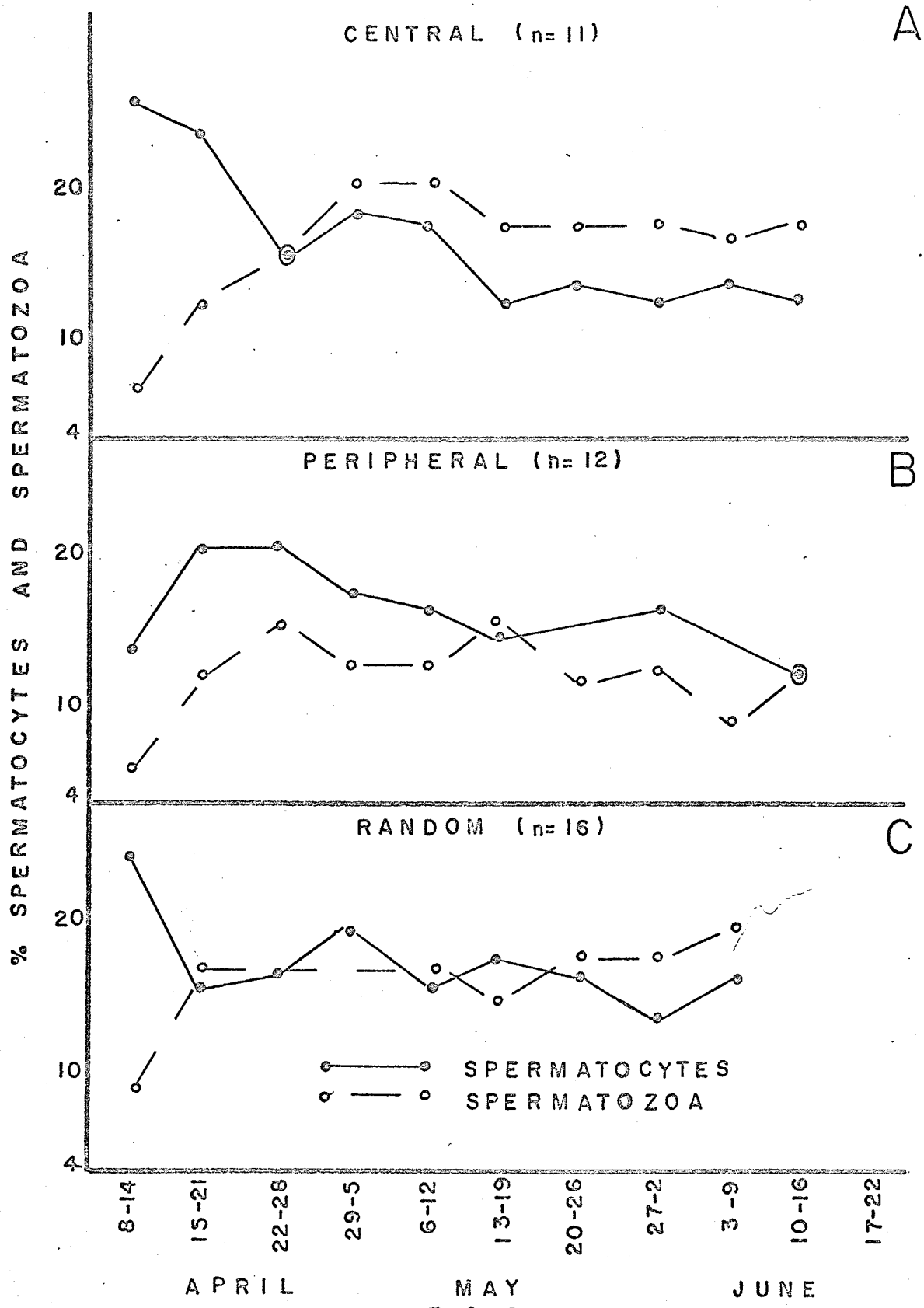

CENTRAL (n= 11)
A
PERIPHERAL (n= 12)
B
RANDOM (n= 16)
C
% SPERMATOCYTES AND SPERMATOZOA
20
10
4
SPERMATOCYTES
SPERMATOZOA
8-14
15-21
22-28
29-5
6-12
13-19
20-26
27-2
3-9
10-16
17-22
APRIL
MAY
JUNE

FIG. 25

productive condition achieved by the central males.

Comparison between Figs. 24 and 25 also reveals that regardless of position, males collected in 1968 consistently achieved the peak breeding condition before each of their counterparts in 1967.

Incidence of Mitochondria

Rank correlation coefficients indicated a significant increase in mitochondria incidence with time for the total sample ($r = 0.84$, $P < 0.01$); adults ($r = 0.85$, $P < 0.01$): and juveniles ($r = 0.81$, $P < 0.01$) (Figs. 26 A and B). However, the distributions for adults and juveniles did not differ significantly ($X^2 = 0.02$, $.25 > P > .10$).

Similarily, rank correlation coefficients indicated a significant increase in mitochondria incidence with time for central, peripheral, and random collected males (central $r = 0.85$, $P < 0.01$; peripheral $r = 0.83$, $P < 0.01$; random $r = 0.69$, $P < 0.05$). The distributions between central and peripheral, central and random, and random and peripheral males were not consistently greater for any particular group (Fig. 26C).

Vascularity of Testis

Rank correlation coefficients indicated a significant

Fig. 26. Incidence of mitochondria present in Sharp-tailed Grouse testis interstitial tissue during successive weeks of the 1968 breeding season. (A) Total sample; (B) adults and juveniles; (C) central, peripheral, and random males. (Numbers in parenthesis indicate sample size).

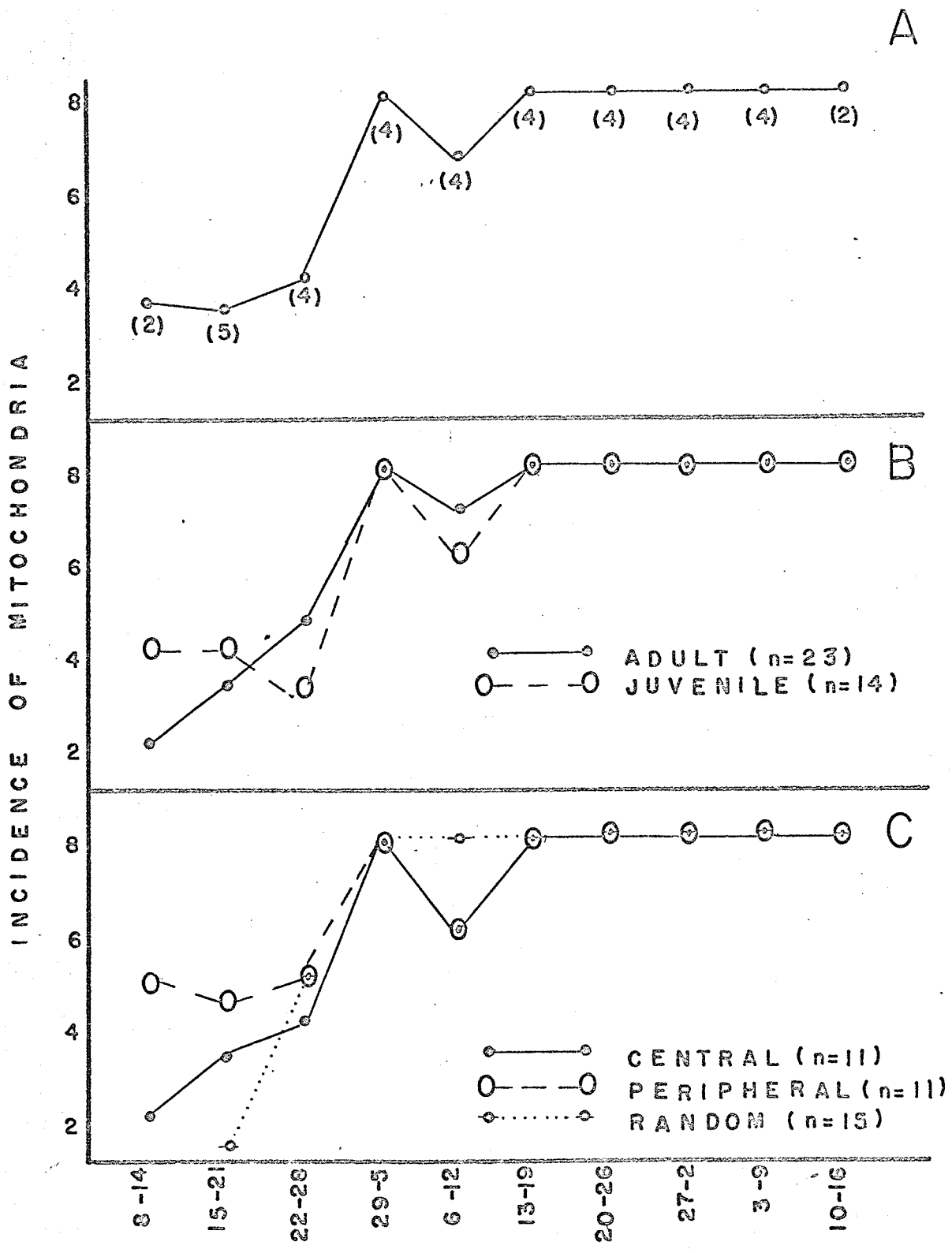

A
B
C
INCIDENCE OF MITOCHONDRIA
8
6
4
2
(2)
(5)
(4)
(4)
(4)
(4)
(4)
(4)
(4)
(2)
ADULT (n=23)
JUVENILE (n=14)
CENTRAL (n=11)
PERIPHERAL (n=11)
RANDOM (n=15)
3-14
15-21
22-28
29-5
6-12
13-19
20-26
27-2
3-9
10-16
APRIL
MAY
JUNE

FIG. 26

increase in vascularity with time for the total sample ($r = -0.82$, $P < 0.01$); adults ($r = -0.77$, $P < 0.01$); and juveniles ($r = -0.68$, $P < 0.05$) (Figs. 27 A and B). However, differences in vascularity between adults and juveniles when analyzed by the paired-t-test, were not significant ($t = 0.14$, $t.95(6df) = \pm 2.45$). Differences in vascularity between the males collected from each of the positions in 1968, when analyzed by the paired-t-test, were not significant ($P > 0.05$) (Table XIV).

TABLE XIV

Summary of paired-t-tests between vascularity in the testes of males from three dancing ground positions in 1968.

Position	df	t (P=0.05)	t	Significance
Central-Peripheral	7	± 2.36	0.17	N.S.
Central-Random	7	± 2.36	-0.75	N.S.
Peripheral-Random	6	± 2.45	-0.03	N.S.

Lumen Diameter

Maximum internal lumen diameters tended to increase up to maximum levels by mid May, then declined (Fig. 28). Rank correlation coefficients indicated no consistent significant increase or decrease over the entire breeding season for the total sample (1967, $r = 0.43$, $P > 0.05$; 1968, $r = 0.42$,

Fig. 27. Vascularity in Sharp-tailed Grouse testes at successive weekly intervals during the 1968 breeding season. (A) Total sample; (B) adults and juveniles. (Numbers in parenthesis indicate sample size).

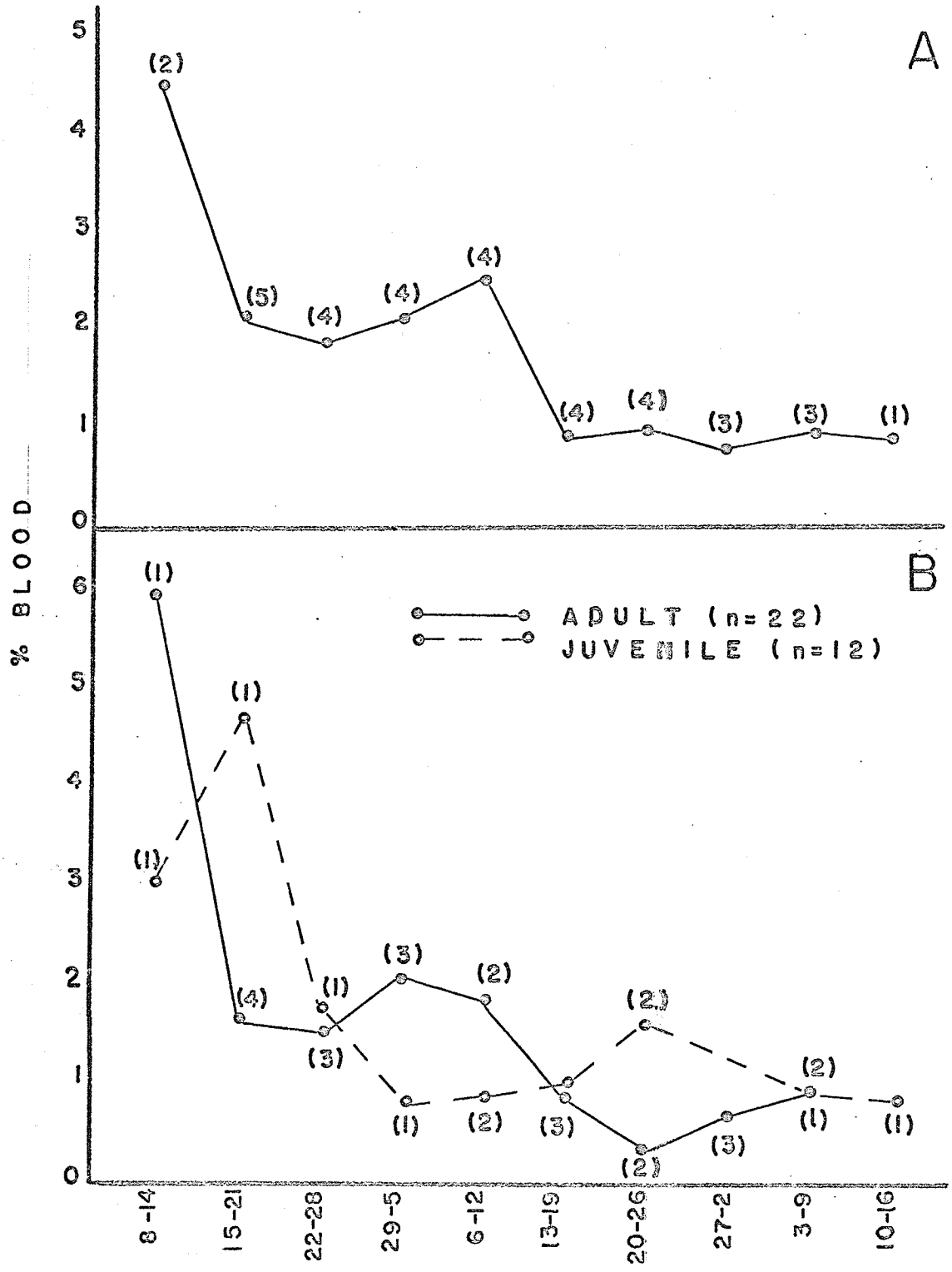

A
B
% BLOOD
ADULT (n=22)
JUVENILE (n=12)
8-14
15-21
22-28
29-5
6-12
13-19
20-26
27-2
3-9
10-16
APRIL
MAY
JUNE

FIG. 27

Fig. 28. Maximum internal lumen diameters of Sharp-tailed Grouse testes at successive weekly intervals in the 1967 and 1968 breeding seasons. (Numbers in parenthesis indicate sample size).

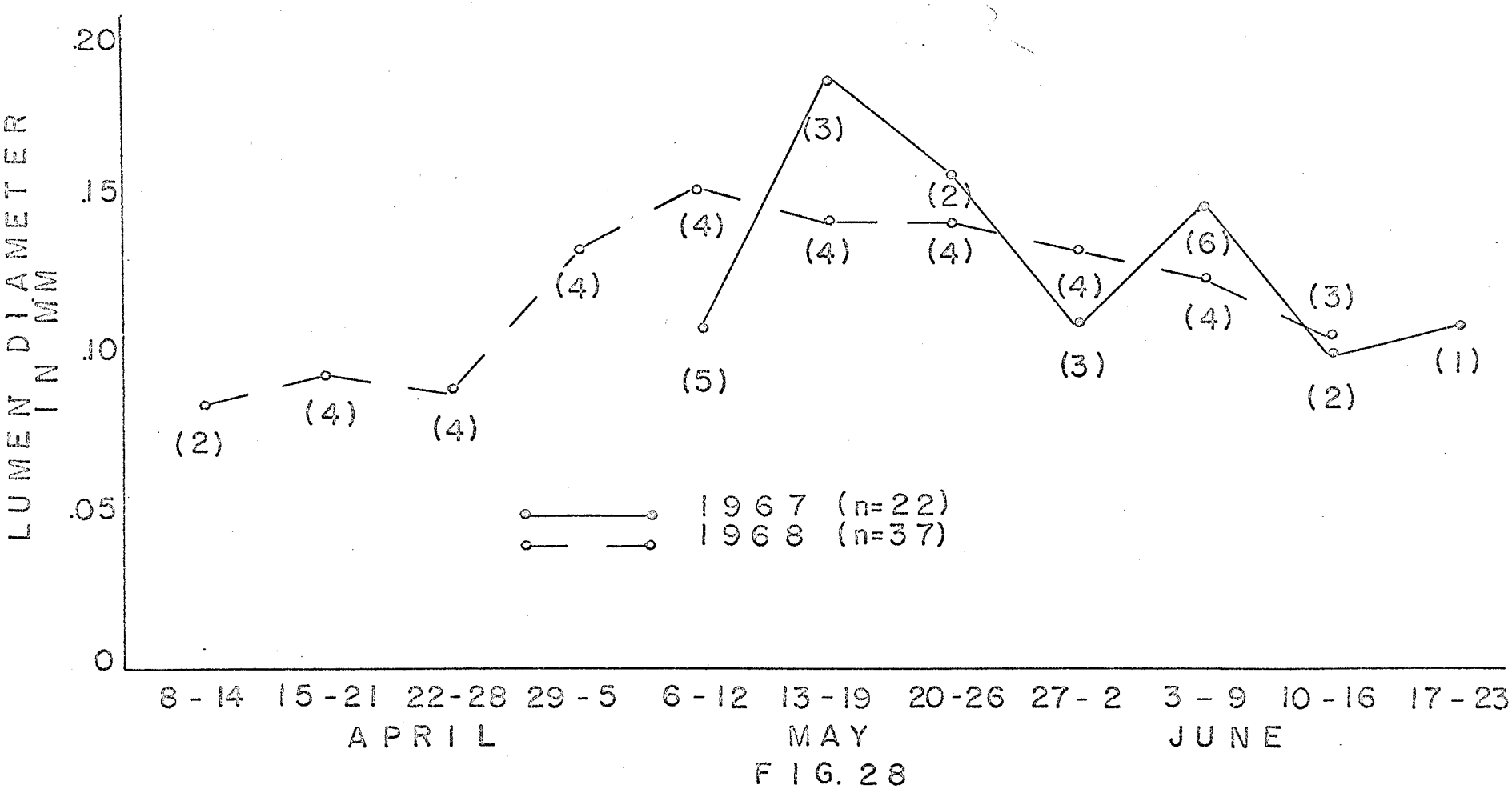

LUMEN DIAMETER IN MM
.20
.15
.10
.05
0
(2)
(4)
(4)
(4)
(4)
(5)
(3)
(4)
(2)
(4)
(4)
(3)
(6)
(4)
(3)
(2)
(1)
1967 (n=22)
1968 (n=37)
8-14
15-21
22-28
29-5
6-12
13-19
20-26
27-2
3-9
10-16
17-23
APRIL
MAY
JUNE

FIG. 28

$P > 0.05$) (Fig. 28). Analysis of the data by the paired-t-test indicated that in both years no significant differences occurred in maximum internal diameter of seminiferous tubule lumina between adults and juveniles ($P > 0.05$) (Fig. 29), or between males from the three dancing ground positions ($P > 0.05$; Table XV) (Fig. 30).

TABLE XV

Summary of paired-t-tests between the maximum internal diameter of testes lumina of males from three dancing ground positions in 1967 and 1968.

Date	Position	df	t (P=0.05)	t	Significance
1967	Central-Peripheral	4	± 2.78	-1.41	N.S.
1967	Central-Random	5	± 2.57	-1.55	N.S.
1967	Peripheral-Random	5	± 2.57	0.49	N.S.
1968	Central-Peripheral	9	± 2.26	1.73	N.S.
1968	Central-Random	8	± 2.31	0.58	N.S.
1968	Peripheral-Random	8	± 2.31	-2.06	N.S.

Lumen Diameter and Incidence of Mitochondria

The relationship between maximum internal diameters attained by the seminiferous lumina and the relative incidence of mitochondria is illustrated in Fig. 31. It appears from this figure that the incidence of mitochondria tended to increase as the maximum lumen diameter increased. A sig-

Fig. 29. Comparisons between maximum internal seminiferous lumen diameters of adult and juvenile Sharp-tailed Grouse in 1967 and 1968. (Symbols as in Fig. 12).

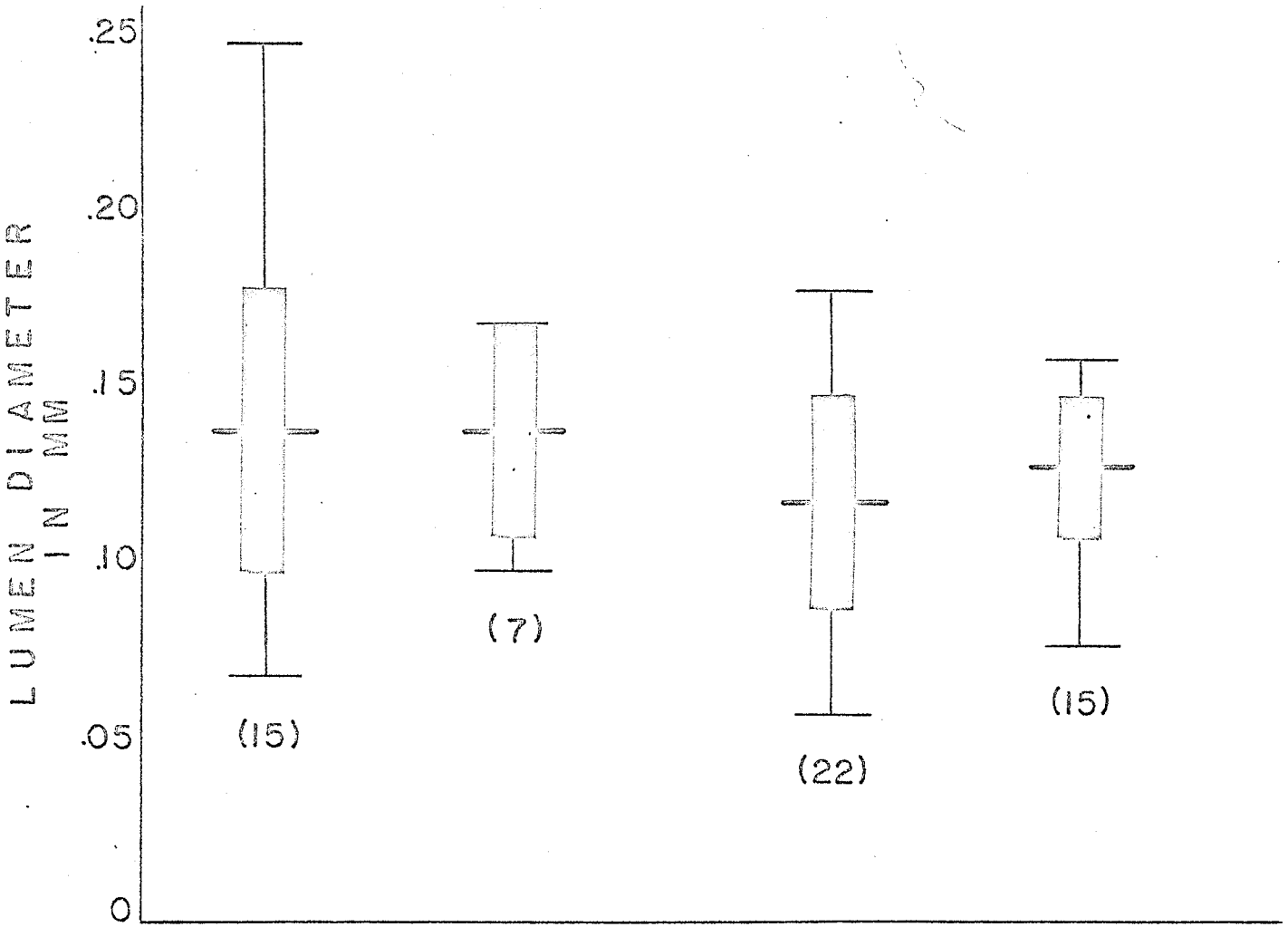

LUMEN DIAMETER IN MM
.25
.20
.15
.10
.05
0
(15)
(7)
(22)
(15)
ADULT
JUVENILE
ADULT
JUVENILE
1967
1968

FIG. 29

Fig. 30. Comparisons between maximum internal seminiferous lumen diameters of central (C), peripheral (P), and random (R) Sharp-tailed Grouse during the 1967 and 1968 breeding seasons. (Symbols as in Fig. 12).

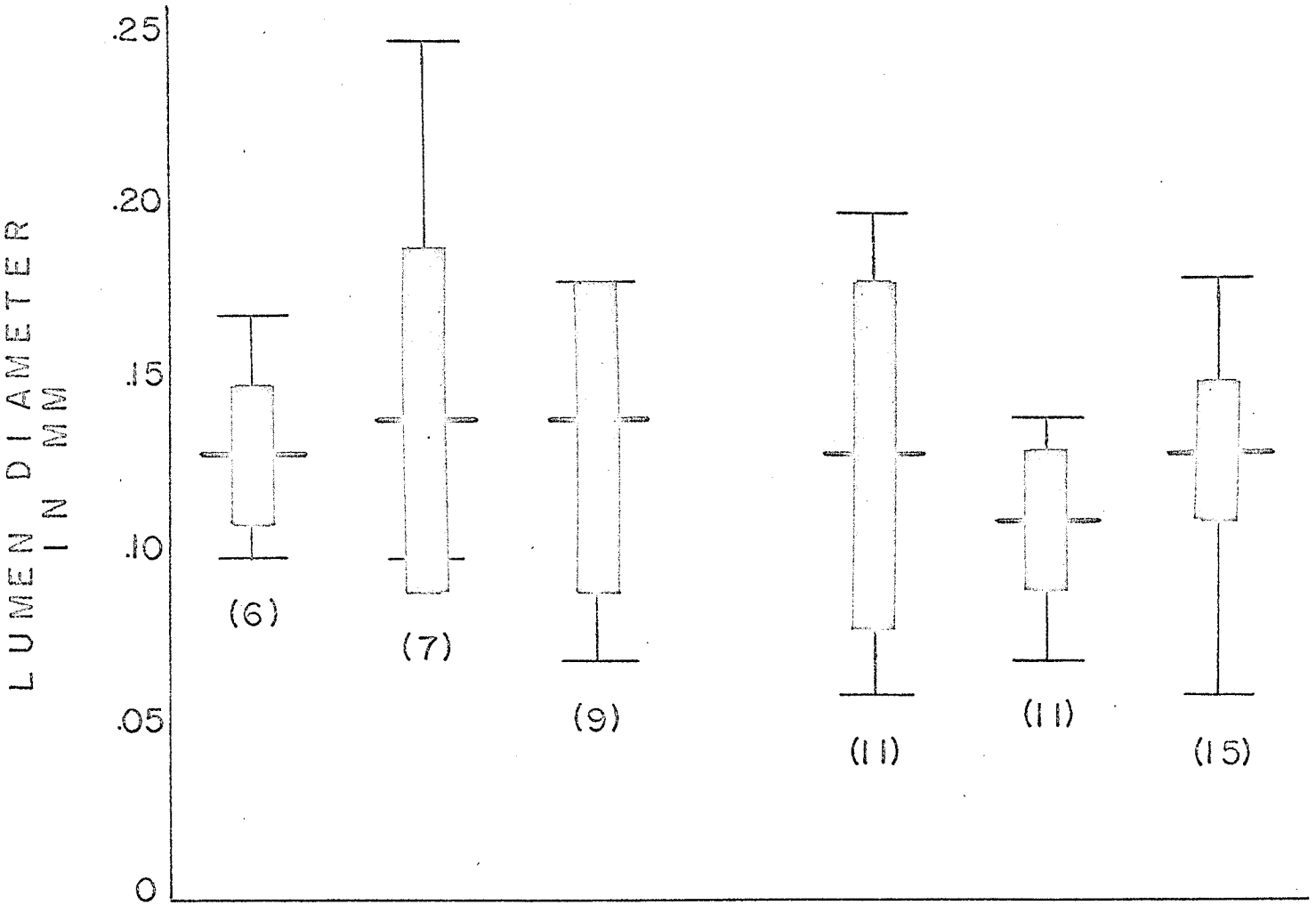

LUMEN DIAMETER IN MM
.25
.20
.15
.10
.05
0
(6)
(7)
(9)
(11)
(11)
(15)
C
P
R
C
P
R
1967
1968

FIG. 30

Fig. 31. Relationship between the incidence of mitochondria and maximum internal lumen diameter of Sharp-tailed Grouse testes in 1968. (Numbers in parenthesis indicate sample size.

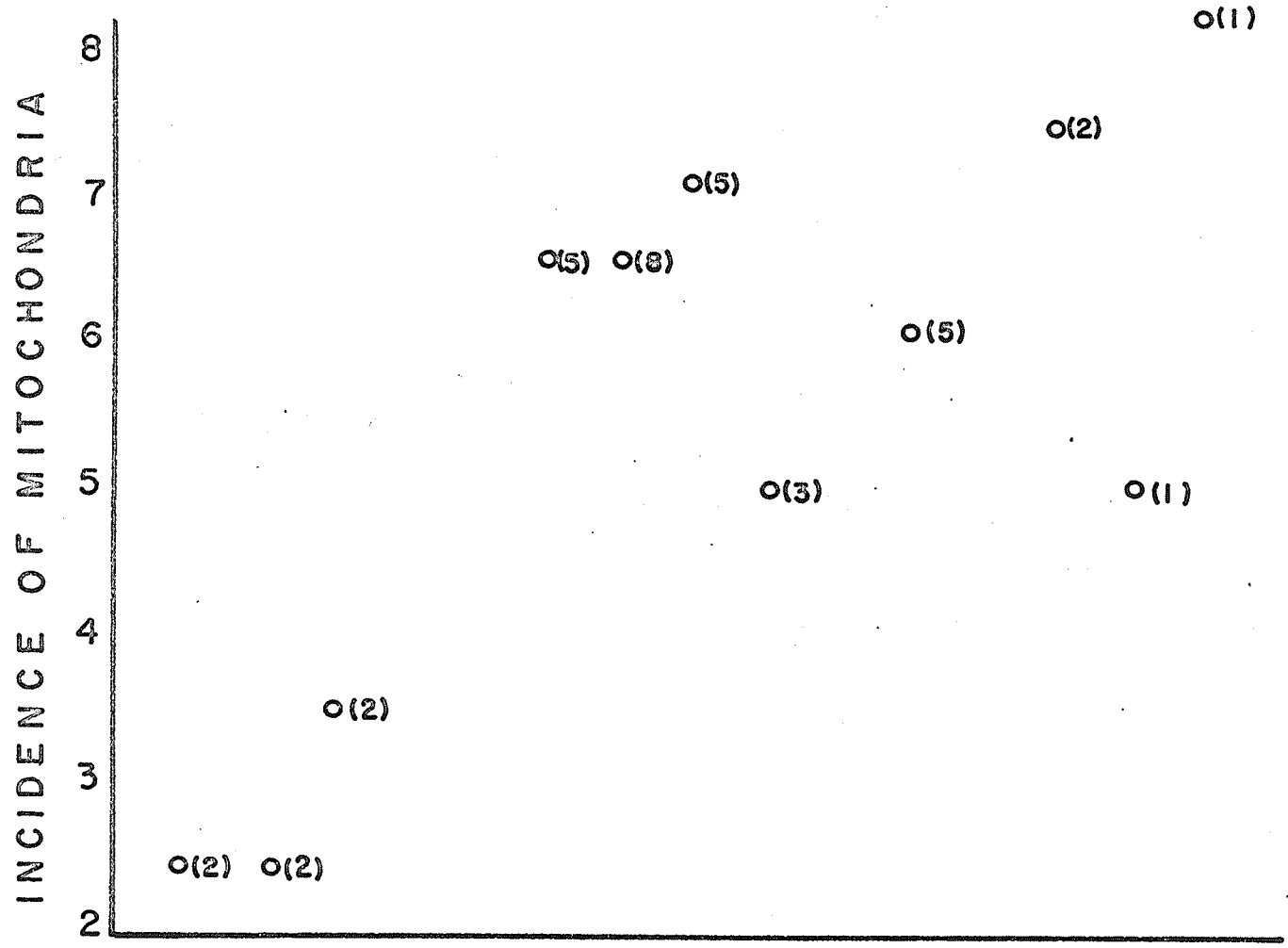

INCIDENCE OF MITOCHONDRIA
8
7
6
5
4
3
2
O(1)
O(2)
O(5)
O(5) O(8)
O(5)
O(3)
O(1)
O(2)
O(2) O(2)
.06 .07 .08 .09 .10 .11 .12 .13 .14 .15 .16 .17 .18 .19 .20
LUMEN DIAMETER IN MM

FIG. 31

nificant rank correlation calculated for these two variables supports this observation ($r = 0.55$, $P < 0.05$).

DISCUSSION

Dancing Ground Size and Stability

On the basis of field studies, Lumsden (1965) has suggested that social organization on small dancing grounds tended to be less stable than on large dancing grounds. At the Hodgson study area, the total number of males increased from 179 in 1967 to 215 in 1968. There was also an increase in the total number of dancing grounds from 16 to 18. In conjunction with this overall increase in Sharp-tailed Grouse numbers in 1968, there was an increase of from two to five in the number of dancing grounds of the intermediate size class containing 11 to 15 males. In contrast, one dancing ground in the "small" size class of one to 10 males disappeared and three others shifted up to one-half mile from their 1967 location. Such disappearances, or shifts in dancing ground locations, were not recorded for large grounds containing 11 or more males. These data are therefore in agreement with the suggestion of Lumsden (1965) that small dancing grounds tend to be less stable.

Dancing Ground Organization in Relation to Male Age and Body Weight

In Black Grouse, Kruijt (1962) noted that the most successful fighters among the males were located at the center of the lek and always had completely adult plumage indicating that they were at least two years old. Juveniles were apparently restricted primarily to the periphery of the lek, and thus contributed little, if anything, to the gene pool during their first year (Kruijt and Hogan, 1967). Similarily, there is evidence that yearling male Sage Grouse seldom held territories and did not display fully until after the peak of mating (Eng, 1963; Lumsden, 1968), and hence did not mate at that age. Lumsden (1965) suggested that in Sharp-tailed Grouse, only the adult males were able to achieve sufficient dominance over their competitors to hold a central territory where most copulations occurred, although he suggested that yearling males may, on occasion, be sufficiently vigorous to claim a central position.

Contrary to what has been recorded for both Black and Sage Grouse, the proportions of adults collected from the central portions of large Sharp-tailed Grouse dancing grounds at Hodgson did not differ significantly from those collected from the periphery. These data suggest that for this popu-

lation, whether a male was the best fighter or held a central as opposed to a peripheral territory was essentially independent of the age of the bird after attainment of sexual maturity at one year of age. Similarily, differences in the proportion of adults and juveniles were not present between large and small dancing grounds. This study suggests, therefore, that in Sharp-tailed Grouse, social organization on dancing grounds is not determined by age.

In the Sage Grouse, the most dominant, central males tended to be larger than the less dominant peripheral males (Eng, 1963). In Sharp-tailed Grouse, in which size differences between males and females was markedly less than in the Sage Grouse, Evans (1961) suggested that dominance may be less dependent on the size of the rival cocks, but rather may be based primarily on levels of agonistic behaviour exhibited by the various individuals. At Hodgson, significant differences were not found between body weights of central or peripheral males, or between body weight of males from large and small dancing grounds. These observations suggest that in male Sharp-tailed Grouse, the position in the dominance hierarchy is not significantly affected by the size of the attending males.

Histological Changes During the Breeding Season

The Sharp-tailed Grouse, like the Blue Grouse studied by Simard (1964), is an annual breeder, and appears to follow a spermatogenic cycle similar to that species. Although analysis of testes in the present study was done only during the breeding season, the spermatogenetic stages and cholesterol levels at that time correlated closely with the condition described by Simard (1964) for the Blue Grouse. Simard (1964) noted that when male Blue Grouse started to establish territories, the interstitial tissue was at its maximum volume, and hence hormone output was probably maximum. Similarily, Marshall (1949a) noted the appearance of "secretory cells", in the interstitial tissue of Fulmars, at the time when testes tubules were approaching the full breeding condition. At the time male Sharp-tailed Grouse appeared regularly on the dancing grounds at Hodgson during the spring display period, their gonads also had achieved the full breeding condition. This stage, which correlated with stage 6 of Simard, was maintained until the males left the dancing grounds in late spring or early summer, when regression, referred to as stage 8 in Simard's (1964) study, occurred.

Data from the present study are likewise in agreement

with the analyses of Simard (1964) and Marshall (1949a) in that maximum endocrine activity as judged by cholesterol levels and vascularity was achieved at the beginning of the breeding period and declined thereafter.

In the Fulmar, the incidence of mitochondria in the testes was found to be greatest when the seminiferous tubule diameters were at their maximum (Marshall, 1949a). The present data indicate a similar condition in Sharp-tailed Grouse testes during the latter phase of the breeding season. Since at this period a new generation of Leydig cells arises in the interstitium (Marshall, 1949a), it is likely that the increase in mitochondria may be correlated with an important increase in energy release.

Marshall (1949b) presented evidence that, in addition to light, other factors such as temperature and precipitation may act as proximate factors in modifying the effects of light on the breeding of Chaffinch (Fringilla coelebs), Great Tit (Parus major), Blue Tit (Parus coeruleus), and the Robin (Erithacus rubecula). Observations in the present study suggest that a similar interpretation may be valid for the Sharp-tailed Grouse. The spring of 1967 was colder and more extended, in comparison to 1968, as indicated by the mean monthly temperatures which, in 1967, were lower by 6.6° F

in April, and 2.0° F in May. The colder spring in 1967 was reflected in the later appearance of the full breeding condition of the testes in that year. Since daylength was presumably similar for both years, these data conform with the suggestions of Marshall (1949b) that factors such as temperature may modify the timing of breeding. Whether it had a direct, or indirect influence through food, was not investigated.

Histological Changes and Age

Eng (1963) and Simard (1964), in analyzing the testis histology of the Sage Grouse and Blue Grouse, found marked differences between adults and juveniles. They reported that juveniles had a smaller weight, smaller testis volume, delayed and slower testis recrudescence, a shorter breeding period, and an earlier and faster testis regression than did the adults. Both age classes possessed mature spermatozoa, but few, if any of the juveniles mated.

The present data agree with the studies of Eng (1963) and Simard (1964) in that mature spermatozoa were present in the testes of both age classes of Sharp-tailed Grouse. However, in contrast to the results obtained for the Sage and Blue Grouse, significant differences in either the total body weight, testis volume or spermatogenesis between adult

and juvenile Sharp-tailed Grouse were not detected. Males collected from their breeding grounds in successive weeks indicated, further, that adults and juveniles were similar in these respects and also in mitochondria incidence, vascularization, and lumen diameters throughout the entire breeding season.

The level of cholesterol, an index of testosterone production, indicated that adult and juvenile Sharp-tailed Grouse also did not differ significantly in testosterone output. The evidence available from various avian species, such as Japanese Quail, Weaver Finch, and Australian Magpie, suggested that the behaviour patterns characteristic of males in the spring reproductive period, including displays, fighting, the setting up of territories and dominance hierarchies, were controlled by the androgen released by the recrudescent testis (Eisner, 1960; Selinger and Bermant, 1967). The similarity in cholesterol levels between adult and juvenile Sharp-tailed Grouse therefore suggests that the two age classes would attain similar levels of reproductive and agonistic displays. The apparent independence of the location and age of attending males, discussed in an earlier section, is consistent with this interpretation.

In both the Sage Grouse (Eng, 1963) and Blue Grouse

(Simard, 1964) the adults consistently dominated the juveniles, suggesting that in these species, in contrast to the Sharp-tailed Grouse, testosterone levels may be greater in the adults than in the juveniles.

The above comparisons indicate consistent differences between Sharp-tailed Grouse and both Blue and Sage Grouse. In the populations studied, of both of the latter species, adults tended to attain a more advanced testis development than did juveniles. In contrast, for Sharp-tailed Grouse significant differences were not found between adults and juveniles in relation to body weight, state of spermatogenesis, cholesterol level, testis vascularity or mitochondria incidence. This suggests that the males of this species mature more rapidly than either the Sage and Blue Grouse males, in which age differences were found to be more marked (Eng, 1963; Simard, 1964).

Histological Changes and Dancing Ground Size and Male Position

According to the hypothesis put forward by Darling (1938, 1952) for the Black Grouse, small leks may provide sub-optimum levels of social stimulation, and therefore may be less suitable. Studies of the Greater Prairie Chicken by Hamerstrom and Hamerstrom (1955) demonstrated that on small

leks containing one to 10 males, the females had a lower probability of being mated on any given day than did females on medium-sized leks containing 11 to 15 males. Both these studies suggested the possibility that hormone and spermatozoa levels might be less on smaller dancing grounds. However, observations in the present study, did not support such a hypothesis for Sharp-tailed Grouse. Body weight, testis volume, levels of cholesterol and spermatozoa, incidence of mitochondria and vascularization of testis did not differ significantly between males from large and small dancing grounds. These results do not rule out the possibility that social facilitation, and hence reproduction or stability may be less on small dancing grounds.

On large dancing grounds, significant differences in histological changes were found between the more dominant of the centrally located males, and the less dominant of the peripheral males. In particular, the testes of the central males achieved both a more rapid and a higher degree of spermatogenesis than did those of the peripheral males. In addition, the testes of the central males contained higher levels of cholesterol than did those of the males located at the periphery. Androgen is responsible for the final differentiation in spermatogenesis as well as influencing the

development of both morphological and behavioural secondary sex characters (Witschi, 1935; Sturkie, 1954; Barrington, 1963), hence it is likely that the increased secretion of androgen in the testes of the more dominant of the central males may be causally related to the higher levels of spermatogenesis found in the same birds.

The greater spermatogenesis and higher cholesterol levels of the more dominant central birds suggest that they are best suited both to occupy the most dominant status within the reproductive hierarchy and to perform the majority of the matings. The present results thus suggest a close and important functional relationship between gonad condition, social organization within large dancing grounds and the degree of reproductive potential actually realized by the males.

SUMMARY AND CONCLUSIONS

The testis cycle of Sharp-tailed Grouse on a 20-square-mile study area at Hodgson, Manitoba, was examined during the spring breeding periods of 1967 and 1968. The following hypotheses were examined: (i) that in Sharp-tailed Grouse, like the Blue and Sage Grouse, testis development and dominance status may be greater in adults than juvenile males. (ii) that reduced social facilitation on small dancing grounds may result in reduced testis development. (iii) that more dominant males located in the central portions of the dancing grounds, where most matings occur, have a greater testis development than the less dominant peripheral males that rarely mate.

Four males were collected each week, one high-dominance male from a central and one low-dominance male from a peripheral position on a large dancing ground containing 11 or more males and one collected randomly from each of two different small dancing grounds containing 10 or fewer males. Body weight, testis volume, state of spermatogenesis, maximum internal seminiferous tubule diameter, interstitial cell cholesterol levels, testis vascularity, and incidence of interstitial mitochondria were measured.

The total number of males on the dancing grounds in the study area increased from 179 in 1967 to 215 in 1968. In 1968, at least three small dancing grounds were relocated and one disappeared. Such changes in locations of large dancing grounds were not observed, which suggested that the small dancing grounds tended to be less stable than large dancing grounds.

Data obtained from 25 males collected in 1967 and 39 in 1968 indicated that significant differences in the proportion of adults and juveniles did not exist between large and small dancing grounds, or between the central and peripheral males collected from the large dancing grounds. These observations suggested that social organization on these Sharp-tailed Grouse dancing grounds was not based upon a differential positioning of adult and juvenile males.

Results from the 64 testes analyzed during the present study indicated that during the breeding period, spermatogenesis in Sharp-tailed Grouse was similar to that for the Sage and Blue Grouse. As in the Blue Grouse, cholesterol levels for Sharp-tailed Grouse testes were greatest at the beginning of the display period and declined thereafter. At the beginning of the breeding season, the testes of Sharp-tailed Grouse, as

in the Fulmar, were highly vascularized. Subsequently, when lumen diameters increased and testes regression commenced, mitochondria incidence reached maximum levels.

Testis volume, degree of spermatogenesis, cholesterol levels, incidence of mitochondria and vascularity did not differ significantly between adults and juveniles. Evidence reviewed from other studies indicated that in the Sage and Blue Grouse, testis development of adults was greater than in juveniles. The observations of the present study suggested therefore, that the Sharp-tailed Grouse males matured more rapidly than either the Sage or Blue Grouse.

Adverse and prolonged winter conditions in 1967, in contrast to 1968, resulted in a delay in the testis cycle of approximately four weeks compared to 1968. These observations suggested that as for other species that breed in temperate regions, testis physiology of male Sharp-tailed Grouse may have been affected by weather conditions.

Analyses of 39 testes signified that hormone levels did not differ significantly between males from large and small dancing grounds. Similarily, analyses of 64 testes indicated that the degree of spermatogenesis did not differ between males from large and small dancing grounds. These data thus did not provide any evidence for the hypothesis that social

stimulation, and hence gonad development, may have been sub-optimal on small as compared to large dancing grounds. However, on large dancing grounds, high-dominance central males had greater levels of cholesterol and also achieved an earlier and greater rate of spermatogenesis than low-dominance peripheral males on the same large dancing grounds. These observations were taken as support for the conclusion that dominant males located near the center of the dancing ground, where most matings occur, were best suited, physiologically, both to maintain a relatively high dominance status within the reproductive hierarchy and to carry on the majority of the matings.

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APPENDIX I

Sample of data sheet used to record information from the Sharp-tailed Grouse collected from dancing grounds.

SPRING DATA SHEET

NUMBER:

PLACE: Hodgson, Manitoba.

DATE:

DANCING GROUND NUMBER:

BODY WEIGHT: g

TESTES VOLUME: RT. ; LT. ; ml

POSITION ON DANCING GROUND:

AGE: ADULT or JUVENILE

CENTRAL RECTRICE LENGTH: mm

9th PRIMARY LENGTH: mm

9th PRIMARY DIAMETER: mm

CENTRAL RECTRICE DIAMETER: mm

FEATHER SHAPE: ADULT or JUVENILE

DIFFERENTIAL WEAR PATTERN: ADULT or JUVENILE

TESTES COLOR: RT. ; LT. .

SEX:

OTHER INFORMATION:

APPENDIX II

Processing procedure sequence of solutions and time schedule used in blocking Sharp-tailed Grouse testes tissues fixed in Bouin's.

SOLUTION	TIME
70% alcohol	indefinite
85% alcohol	3 hours
95% alcohol	3 hours
95% alcohol	3 hours
100% alcohol	3 hours
100% alcohol	3 hours
100% + xylene	½ hour
xylene I	¼ hour
xylene II	¼ hour
xylene + paraplast	½ hour
paraplast I	1 hour
paraplast II	1 hour

After being infiltrated with paraplast the tissue was placed in an embedding pan which had been greased with a glycerine and alcohol solution. Paraplast was poured into the pan and a film allowed to form before the tissue was placed in the middle of the pan. A tissue - tek was placed on top and paraplast added to form a positive miniscus. Once the paraplast commenced to crystalize it was immersed in cold water. After about 10-15 minutes the embedding pan was removed, leaving a blocked piece of tissue ready to be sectioned.

APPENDIX III

Modification of Masson's trichrome technique (Culling, 1963).

In the present study the following modifications were employed. Since the fixative used did not contain mercury, a solution of iodine-sodium thiosulphate was not used to wash the sections.

The counterstaining was limited to a maximum of 15 seconds in both light green and ponceau 2R rather than the outlined 5 minutes which resulted in heavy overstaining.