Breeding Periodicity in Western Australian Birds: With an Account of Unseasonal Nestings in 1953 and 1955

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I. INTRODUCTION

The brilliant pioneer work of Rowan (1926) led to an era of photo-stimulation of captive birds, and to the emergence of a widespread belief that day-length fluctuations constitute the critical external factor governing reproduction time in temperate and even equatorial regions (see Wolfson, 1952, 1953). It has been shown, however, that such a hypothesis is fallacious in the case of at least some Arctic species (Marshall, 1952), and in Australian desert forms (Keast and Marshall, 1954). Further, in one equatorial species, gross laboratory photo-stimulation will cause testis modification even though such a stimulus cannot be operative in nature (Marshall and Disney, 1956).

Many authors have considered alternative factors which might initiate breeding cycles in various parts of the world, where the light hypothesis appeared unsatisfactory. Baker (1938, p. 171) emphasized the importance of rain as one such regulating factor. He pointed out that its significance was well known to many naturalists, especially in tropical and subtropical countries, but that it had been generally overlooked by laboratory workers. Moreau (1950) has shown how closely breeding is linked with the rainy seasons, and not only in the semi-arid regions, in Africa. Lack (1950) has demonstrated the same fact for many Galapagos birds.

Serventy and Whittell (1948, p. 7), too, showed that although most south-western Australian birds nested in the spring, and hence might *appear* to be stimulated by increasing light, the situation could not be so simply explained. An appeal was made that field observers should take advantage of occasional sharp fluctuations in local weather to identify the true factors which might influence particular species.

Exceptionally heavy March rains, associated with a tropical cyclone, were followed by sexual activity among many species near Kalgoorlie (Serventy, 1946, p. 10). Further south, where rain did not penetrate, breeding did not occur. Many years earlier, Carter (1923, p. 224; 1924, p. 232), had reported that after heavy February thunderstorms several species of passerines nested in March in an area between

Kellerberrin and Gnowangerup. Nearly 70 years ago Carter was able to generalize, for the northern pastoral areas at any rate, that "many species of birds here lay whenever a good rain falls, no matter what time of year" (1889, p. 208).

The recent publication of a rich series of original data on nesting in various parts of Western Australia (Carnaby, 1954, p. 149; Robinson, 1955, p. 187; Sedgwick, 1955, p. 46), together with a field and laboratory investigation in connection with unseasonal nesting in the southern part of the State in 1953 and 1955, has enabled us to undertake the present review of breeding periodicity in Western Australia.

II. Unseasonal Breeding Activity

1. *Preliminary Remarks*

It is convenient first to describe in some detail the unseasonal breeding phenomena that were studied in 1953 and 1955. In southern Western Australia nesting is essentially a spring-time event, as is general in temperate climates. There are, however, many exceptions, particularly among marine and aquatic species (Serventy, 1952, p. 51; 1955, p. 18). Even with land birds, however, slight breeding activity may begin before the winter solstice. This is most pronounced with the Banded Plover (*Zonifer tricolor*), the Common Bronzewing (*Phaps chalcoptera*), and the New Holland Honeyeater (*Meliornis novae-hollandiae*). Usually, however, early winter attempts at nesting are abortive. Robinson (1955, p. 189) states that "Magpie-Larks and Yellow-tailed Thornbills have been known to start building in May at Coolup in the south-west, but did not continue and the nests remained unattended until August". S. R. White (1950, p. 142) has reported similar behaviour in the Tree-Martin (*Hylochelidon nigricans*) at Morawa. He noted "abortive breeding behaviour during March, April, May and June when rain has fallen in 1948, 1949 and 1950, but full-scale breeding [i.e. leading to egg-laying] does not commence until August".

Widespread, and occasionally successful, autumn reproduction may take place in years in which there occur abnormal southerly penetrations of the summer cyclones which bring rains more or less regularly to northern parts of the State. The usual pattern of these weather systems has been described by Gentilli (in Robinson, 1949, p. 313).

In 1953 such a weather system brought heavy rains to a portion of the wheat belt and resulted in local autumn breeding to a degree comparable to that described by Carter and Serventy (see above). In 1955 an abnormal weather system in February brought an unprecedented summer deluge and floods to the entire southern half of the State. The effect on the breeding of birds was correspondingly pronounced. For both seasons we were able to obtain field data and specimens.

2. *Material and Methods*

The present study is based on field observations on 22 species that in 1953 exhibited 'out of season' sexual behaviour, together with the laboratory examination of 71 specimens belonging to 25 species. For the 1955 season we had at our disposal field observations on 41 species and were able to make laboratory examinations on 27 specimens of 13 species.

The birds were dissected immediately after collection. The testes were measured in millimetres and fixed as follows—(1) Formal calcium, for the preservation and subsequent Sudan colouring of interstitial and post-nuptial tubule lipids; and (2) Bouin's fluid, for subsequent staining with iron haematoxylin for the determination of spermatogenetic stages. The diameter of the largest oocyte was measured.

3. *The 1953 Cyclone and its Effects*

(a) *Weather*: The cyclone swept Western Australia between March 22 and 26. Heavy rains fell south and west of a line from the mouth of the Fortescue River, in the north-west, nearly to Eucla, in the south-east. Only very meagre falls occurred in the south-west corner, south-west of Gingin, York, Wickepin, Lake Grace and Hopetoun. Generally speaking, only light rains fell south of the Great Eastern Railway (Perth to Kalgoorlie) but the northern agricultural areas had soaking rains (up to 6 inches). At Morawa (lat. 29°S., long. 116°E.), where most of the present data were obtained, the official registration was 169 points, but S. R. White informed us that a local gauge recorded 320 points. Neighbouring stations registered 490 points (Canna) and 361 points (Perenjori). The salt lakes at Morawa were flooded by waters coming down from the north-east along the salt Indaga River, and were flowing for the first time since 1926.

(b) *Observational*: Unless otherwise stated, the following observations apply to the Morawa area—

Banded Plover (*Zonifer tricolor*).—Many eggs in May and June.

Australian Dotterel (*Peltohyas australis*).—Pintharuka, nest with three eggs on April 27.

Avocet (*Recurvirostra novæ-hollandiæ*).—A nesting colony of nine pairs was studied at the salt lakes at Morawa. On April 26 two nesting scrapes each had an egg; on July 14 three pairs were still brooding four eggs each.

White-headed Stilt (*Himantopus leucocephalus*).—Six pairs had eggs (clutches varying from one to four) on May 14; 25 pairs in another colony had young in early July; two of these pairs were still brooding four eggs each on July 14.

White-faced Heron (*Notophoÿx novæ-hollandiæ*).—Nest with three almost-fledged young on June 27.

Black Swan (*Cygnus atratus*).—Pintharuka, a nest with three eggs on May 15; Mellenbye Station, egg-laying at same time; Morawa, nest with seven eggs on June 7.

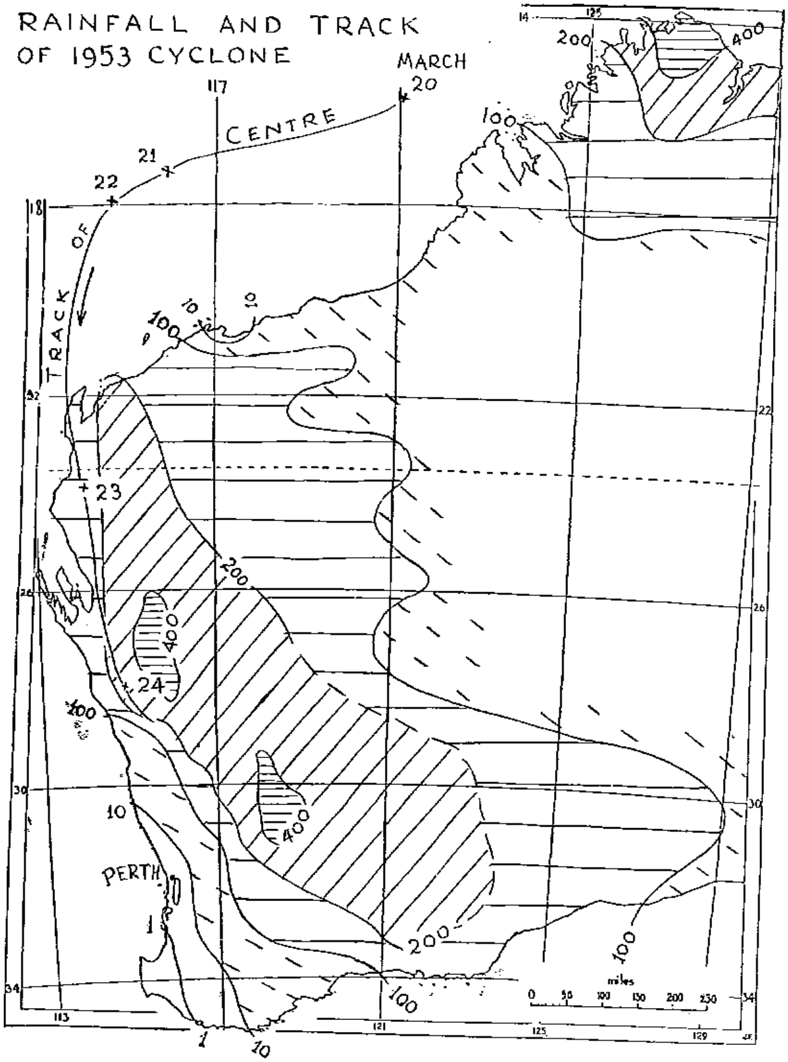

Fig. 1—The 1953 cyclone. The total rainfall is given in points.

Blue-winged Shoveler (*Anas rhynchotis*).—Nest with six eggs on June 20, and these had increased to a full clutch of twelve on June 27.

Grey Teal (*Anas gibberifrons*).—Nest with eight eggs on May 2; another with seven eggs on May 12.

Smoker Parrot (*Polytelis anthopeplus*).—Perenjori, young on May 15.

Welcome Swallow (*Hirundo neoxena*).—Wyening and New Norcia, attending nests mid-April; Morawa, bird seen carrying feathers on April 27. No egg-laying or other nesting behaviour subsequently reported.

Willie Wagtail (*Rhipidura leucophrys*).—Perenjori, nest with three eggs on May 1.

Western Shrike-Thrush (*Colluricincla rufiventris*).—Coonana (east of Kalgoorlie), song heard frequently in late April; Morawa, singing males conspicuous in May.

Magpie-Lark (*Grallina cyanoleuca*).—Perenjori, nest-building on May 1; Morawa, a fresh egg found below a nest on May 20.

White-fronted Chat (*Epthianura albifrons*).—Kalgoorlie, during May, about six nests with eggs and young.

Redthroat (*Pyrrholaemus brunneus*).—Coonana, a week-old chick on April 25.

Blue-and-white Wren (*Malurus leuconotus*).—Morawa, on April 26 males in full colour calling strongly and giving territorial song, with chases.

Black-capped Sittella (*Neositta pileata*).—Coonana, bird seen carrying food on April 17.

Rufous Tree-creeper (*Climacteris rufa*).—Coonana, birds carrying food on July 1; early August, many young birds.

Red-tipped Diamond-bird (*Pardalotus substriatus*).—Kalgoorlie, two nests with eggs in May.

Yellow-fronted Honeyeater (*Meliphaga plumula*).— Kalgoorlie, a fledged chick in May.

Yellow-throated Miner (*Myzantha flavigula*).—Perenjori, bird incubating on May 1.

Australian Pipit (*Anthus novae-seelandiae*).—Coonana, nest with three eggs on April 18, hatched on April 24; another with two eggs on June 23, and two nests with young on August 15. Kalgoorlie, two almost-fledged young in nest in May.

(c) *Spring Reproduction*: At both centres the normal spring nesting took place. Thus in the Morawa district eggs of the following species were found during the period August to October: Black Swan (birds incubating on August 17 and 20), Little Eagle (*Hieraaëtus morphnoides*), Kestrel (*Falco cenchroides*), Crested Bell-bird (*Oreoica gutturalis*), Magpie-Lark (*Grallina cyanoleuca*, young seen on August 17), Black-faced Cuckoo-Shrike (*Coracina novæ-hollandiæ*), Whiteface (*Aphelocephala leucopsis*), Rufous Song-Lark (*Cinclorhamphus mathewsi*), Spiny-cheeked Honeyeater (*Acanthagenys rufogularis*), Australian Pipit, Little Crow (*Corvus bennetti*), Grey Butcher-bird (*Cracticus torquatus*), Black-throated Butcher-bird (*C. nigrogularis*), and the Western Magpie (*Gymnorhina dorsalis*).

At Coonana the following species were observed nesting in the spring: Banded Plover, Black-fronted Dotterel (*Charadrius melanops*), Collared Sparrow-Hawk (*Accipiter cirrocephalus*), Galah (*Kakatoë roseicapilla*), Red-backed Kingfisher (*Halcyon pyrrhopygia*), Narrow-billed Bronze-Cuckoo (*Chalcites basalis*), Red-capped Robin (*Petroica goodenovii*), Hooded Robin (*Melanodryas cucullata*), White-fronted Chat (*Epthianura albifrons*), Crimson Chat (*E. tricolor*). Yellow-tailed Thornbill (*Acanthiza chrysorrhoa*), Brown Song-Lark (*Cinclorhamphus cruralis*), Red-tipped Pardalote, White-fronted Honeyeater (*Gliciphila albifrons*), Spiny-cheeked Honeyeater, and Western Magpie.

(d) *Histological*: When a seasonally-breeding bird sheds its spermatozoa the exhausted testis interstitium regenerates and at the same time the seminiferous tubules undergo a profound metamorphosis, resulting in the production of massive quantities of fatty substances that are easily identified by a variety of histochemical methods. Thus, the presence of large quantities of such post-nuptial lipids in the seminiferous tubules are an infallible indication of a previous spermatogenesis in all orders of birds so far investigated (Marshall, 1949b, 1955b). These tubule fats gradually disappear, the rate varying between species. In birds and one fish (Lofts and Marshall, 1957), but not in amphibians and reptiles (Marshall and Woolf, 1957) so far studied, the tubule lipids disappear at or before the onset of the next season's spermatogenesis.

However, after a certain period the rate of tubule clearance is greatly expedited under the influence of whatever external factors initiate the onset of breeding. So the persistence of post-nuptial tubule lipids is an indication that any given bird has not yet been stimulated to begin its next sexual cycle. If spermatocytes, or later stages of the germ cells, are found in the tubules it is possible to assert that a definite stimulus has taken place.

Because the clearance of the tubules seems to be part of the semi-autonomous internal rhythm of reproduction in at least some temperate zone species of birds (Marshall, 1954; Robinson, 1956) we are unable to draw conclusions concerning individuals whose tubules had lost their post-nuptial lipids yet did not exhibit the pronounced signs of spermatogenesis that are normal a few months later in spring.

The material discussed below, which is confined to males, is, therefore, placed in several categories. All specimens were collected in areas where rain had fallen and where its influence might be suspected. Except where otherwise mentioned the skulls were 'pneumatised' (Harrison, 1949). The dimensions of the left testis (or of the usually smaller right testis, when the left was too damaged to measure) are given below, following the date of collection.

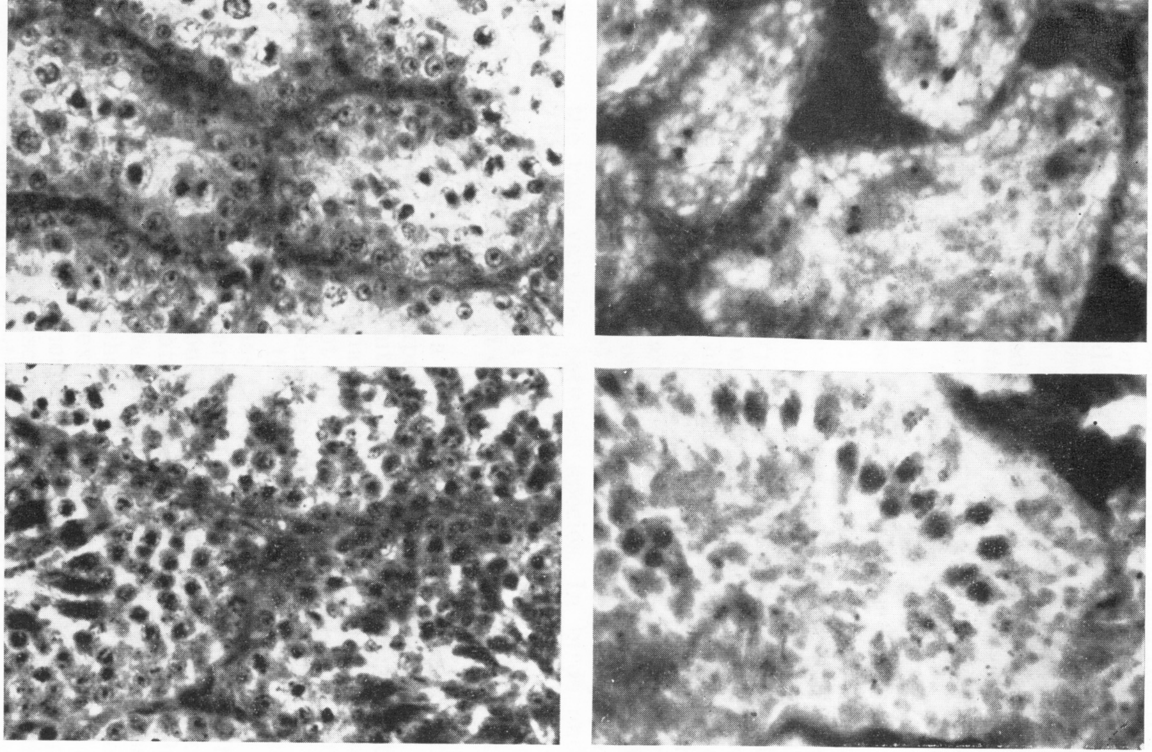

PLATE A. Histology of the testis.

Fig. 1 (left, top). Twenty-eight Parrot (Morawa, May 14, 1953), appreciably influenced by rainfall. Tubules enlarged, with many primary spermatocytes and a few secondary spermatocytes. Bouin fixation, haematoxylin staining. (x 340).

Fig. 2 (right, top). The same, with formal-calcium fixation and Sudan colouring, revealing the aggregation of heavily lipoidal Leydig cells. (x 340).

Fig. 3. (left, bottom). Magpie-Lark (Morawa, May 12, 1953), much influenced by rainfall. Bunched spermatozoa, with a few already free in lumina. Bouin fixation, haematoxylin staining. (x 340).

Fig. 4 (right, bottom). The same, with formal-calcium fixation and Sudan colouring, revealing the aggregation of heavily lipoidal Leydig cells. (x 340).

A. *Specimens influenced by the unseasonal precipitation or its effects*—

Long-billed Corella (*Kakatoë tenuirostris*). Morawa, April 15. 6.5 x 3.5 mm.; mitotic spermatogonia in every tubule; plumage fresh.

Galah (*K. roseicapilla*). Morawa, April 15. 5.0 x 1.5 mm.; mitotic spermatogonia in a few tubules, some of which retained the faintest traces of post-nuptial lipids; interstitium heavily lipoidal; moult almost completed.

Port Lincoln Parrot (*Barnardius zonarius*). Morawa, April 15. 4.5 x 2.3 mm.; many primary spermatocytes and odd secondary spermatocytes; interstitium aggregated, becoming lipoidal; body moult almost completed. Morawa, May 13. 4.0 x 1.5 mm.; many secondary spermatocytes and a few spermatids; interstitium massively lipoidal; moult almost completed. Morawa, May 14. 5.5 x 3.3 mm.; tubules cleared of lipids, some enlarged, with primary spermatocytes and a few secondary spermatocytes; interstitium aggregated and heavily lipoidal (plate A, figs. 1 and 2); in moult.

Rufous Whistler (*Pachycephala rufiventris*). Morawa, May 14. 3.5 x 2.4 mm.; primary spermatocytes in division; in fresh adult plumage.

Western Shrike-Thrush (*Colluricincla rufiventris*). Morawa, April 14. 3.8 x 2.0 mm.; most tubules cleared of lipids, occasional spermatogonia in mitosis; interstitium aggregated and lipoidal; plumage fresh.

Crested Bell-bird (*Oreoica gutturalis*). Morawa, April 15. 5.4 x 3.3 mm.; a few tubules entirely unmodified, with traces of post-nuptial lipids remaining in varying degree, others large with secondary spermatocytes and spermatids; interstitium aggregated and massively lipoidal (plate B, fig. 3); moult almost completed.

Magpie-Lark (*Grallina cyanoleuca*). Morawa, April 15. 7.7 x 4.4 mm.; spermatids and first sperms; interstitium aggregated and massively lipoidal; in moult. Morawa, May 12. 10.0 x 5.4 mm.; bunched spermatozoa in every tubule, a few free in lumina; interstitium aggregated and heavily lipoidal (plate A, figs. 3 and 4); plumage fresh. Morawa, May 12. 2.2 x 1.5 mm. (right testis); primary spermatocytes in mitosis; interstitium aggregated and massively lipoidal (*Emu*, vol. 56, plate 21, fig. 2).

Weebill (*Smicrornis brevirostris*). North-west of Dandaragan, April 16. 2.7 x 2.7 mm.; tubules asymmetrically developed, the biggest with bunched sperms, others of relatively small diameter though cleared of lipids; aggregated interstitium; plumage fresh.

Whiteface (*Aphelocephala leucopsis*). Morawa, April 15. 2.4 x 1.8 mm.; tubules cleared of lipids, with a few primary spermatocytes; interstitium aggregated and heavily lipoidal; plumage fresh.

Western Thornbill (*Acanthiza inornata*). Bolgart, April 13. 0.9 x 0.9 mm.; odd tubules showed occasional spermatogonia in mitosis; formal-calcium material was not available, but cavities in the tubules suggested the retention of some post-nuptial lipids and orange-coloured testes indicated a heavily lipoidal interstitium (Serventy and Marshall, 1956); plumage fresh.

Brown Thornbill (*A. pusilla whitlocki*). Morawa, May 13. 2.5 x 2.1 mm.; secondary spermatocytes; interstitium mature and aggregated; plumage fresh.

Chestnut-tailed Thornbill (*A. uropygialis*). Morawa, May 13. 1.5 x 1.5 mm.; tubules cleared of lipid and numerous spermatogonia in mitosis; interstitium aggregated and mature; plumage fresh.

Singing Honeyeater (*Meliphaga virescens*). Morawa, April 15. 7.3 x 3.7 mm.; tubules of varying size, some containing only spermatogonia, but many with bunched spermatozoa; interstitium largely depleted of its lipids; plumage fresh.

White-eared Honeyeater (*M. leucotis*). Buntine, April 14. 2.6 x 1.8 mm.; tubules almost cleared of lipids, some with primary spermatocytes; interstitium aggregated and lipoidal; plumage fresh.

Yellow-throated Miner (*Myzantha flavigula*). Morawa, April 15. 3.9 x 1.9 mm.; tubules cleared of lipids with primary spermatocytes; interstitium aggregated and heavily lipoidal; moult almost completed. Morawa, May 14. 3.9 x 2.0 mm.; most tubules cleared, some with secondary spermatocytes; interstitium heavily lipoidal; in moult. Morawa, May 14. 2.6 x 1.4 mm.; tubules still with faint traces of lipids; some tubules slightly wider but no mitotic activity in the spermatogonia; interstitium aggregated and heavily lipoidal and on one side of testis Leydig cells partly depleted of lipids; the slightly wider tubules and the aggregation of some interstitial cells suggest there had been a slight influence; moult almost completed.

Western Magpie (*Gymnorhina dorsalis*). Morawa, April 15. 6.3 x 4.6 mm. (right testis); most tubules cleared of post-nuptial lipids, but some remain heavily lipoidal, many cleared tubules show spermatogonia in mitosis; interstitium asymmetrically developed, in some places non-lipoidal and in others beginning to be besprinkled with lipid droplets; moult almost completed; this specimen was an inter-sex and is described in detail elsewhere (Marshall and Serventy, 1956a). Northampton, April 29. 5.9 x 3.8 mm.; tubules entirely cleared of lipids, with a few spermatogonia in mitosis; interstitium inactive; plumage fresh.

B. *Specimens doubtfully influenced*—

Red-capped Robin (*Petroica goodenovii*). Morawa, May 12. 2.2 x 1.5 mm. (right testis); tubules cleared of lipid, but

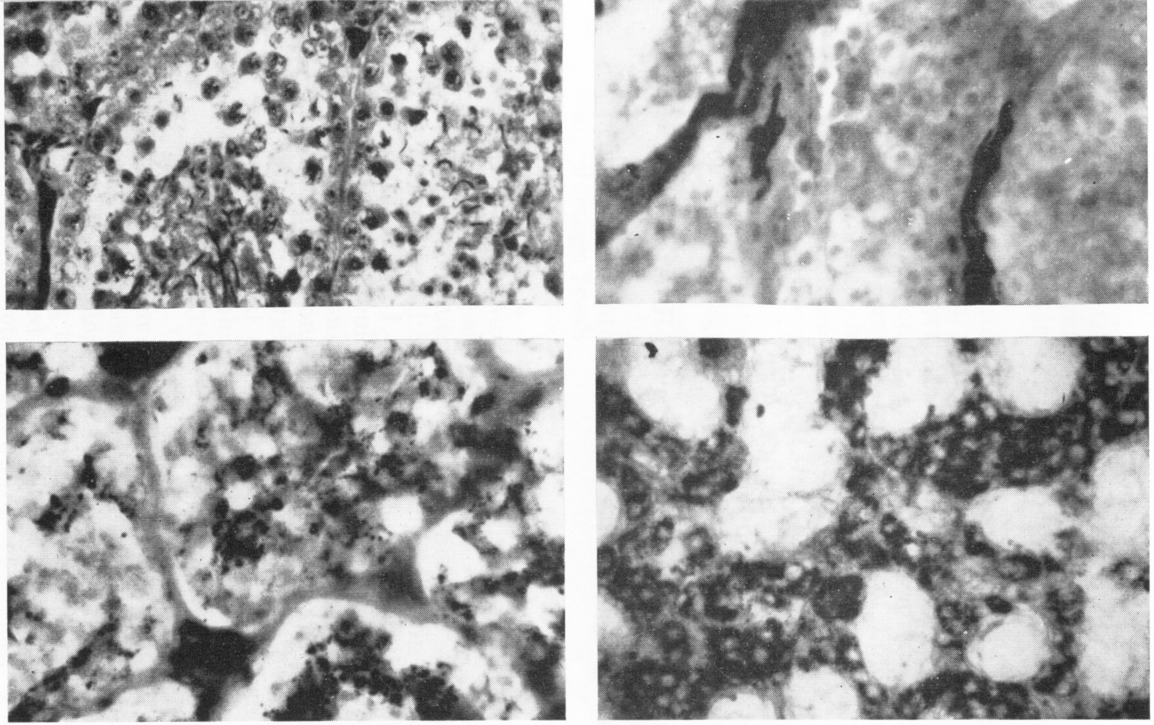

PLATE B. Histology of the testis.

Fig. 1 (left, top). Hoary-headed Grebe (Lake Grace, June 6, 1955), considerably influenced by rainfall. Small numbers of spermatozoa are present. Bouin fixation, haematoxylin staining. (x 340).

Fig. 2 (right, top). The same, with formal-calcium fixation and Sudan colouring. Aggregated, lipoidal interstitium in process of lipid depletion. (x 340).

Fig. 3 (left, bottom). Crested Bell-bird (Morawa, April 15, 1953), partly influenced by rainfall. Tubules in picture are sprinkled with post-nuptial lipids, while others (not shown) showed modification up to spermatid stage. The interstitium is aggregated and massively lipoidal. Formal-calcium fixation, Sudan staining (x 340). Fig. 4 (right, bottom). Yellow-tailed Thornbill (Morawa, April 15, 1955), doubtfully influenced by rainfall. Tubules cleared of lipids and surrounded by great masses of heavily lipoidal Leydig cells. Formal-calcium fixation, Sudan colouring. (x 340).

Bouin-fixed material was not available to show whether the spermatogonia were active; interstitium very heavily lipoidal and so the bird might have been influenced; plumage fresh.

Yellow-tailed Thornbill (*Acanthiza chrysorrhoa*). Morawa, April 15. 0.8 x 0.8 mm.; tubules cleared of lipids; great masses of interstitium surrounding almost every tubule and all heavily lipoidal (plate B, fig. 4); Bouin-fixed material not available; plumage fresh.

Chestnut-tailed Thornbill (*A. uropygialis*). Buntine, April 14. 1.1 mm.; tubules cleared of lipids, but spermatogonia inactive; interstitium heavily lipoidal; plumage fresh.

Brown Honeyeater (*Gliciphila indistincta*). Dandaragan, April 16. 1.4 x 0.6 mm.; tubules cleared; interstitium becoming mature; moult almost completed.

Western Spinebill (*Acanthorhynchus superciliosus*). Dandaragan, April 16. Two specimens (1.0 x 1.0 and 1.0 x 0.5 mm.) showed the tubules cleared, with the interstitium aggregated and heavily lipoidal; in one the plumage was fresh, in the other the moult was almost finished.

Yellow-throated Miner (*Myzantha flavigula*). Morawa, April 15. Two specimens (2.5 x 1.0 and 3.9 x 1.9 mm.) had tubules cleared of lipids but no mitotic activity; interstitium was aggregated and heavily lipoidal; in one bird the moult was almost, and in the other fully, completed.

C. *Specimens not influenced*—

Rufous Whistler (*Pachycephala rufiventris*). Dandaragan, April 17. 1.7 x 1.1 mm.; lingering trace of post-nuptial metamorphosis in tubules, but mostly cleared of lipids; interstitium juvenile and still practically non-lipoidal; adult plumage, fresh.

Weebill (*Smicrornis brevirostris*). Merkanooka, May 11. 1.3 x 1.3 mm.; tubules lipoidal, interstitium aggregated and heavily lipoidal; plumage fresh.

Black-faced Wood-Swallow (*Artamus cinereus*). Coorow, April 16. 2.5 x 1.4 mm.; some tubules cleared, but many retained appreciable quantities of lipids; interstitium aggregated and heavily lipoidal in some parts of the testis and less so in others; moult almost completed.

Singing Honeyeater (*Meliphaga virescens*). Dandaragan, April 17. 1.5 x 0.7 mm.; tubules without lipids; interstitium becoming lipoidal; moult almost completed; skull incompletely pneumatised, probably indicating this specimen to be a bird of the year.

Black-throated Butcher-bird (*Cracticus nigrogularis*). Morawa, April 15. 2.8 x 1.8 mm.; no lipid anywhere except for faint traces coming up in the interstitium; in immature plumage and in body moult.

Western Magpie (*Gymnorhina dorsalis*). Morawa, April 14. 7.0 x 4.0 mm.; most tubules cleared but some still heavily lipoidal; interstitium with some tracts heavily lipoidal, others lacking lipid; fresh sub-adult plumage. Three Springs, April 16. 7.6 x 3.8 mm.; tubules completely cleared, with immature spermatogonia; interstitium heavily lipoidal in some parts; fresh adult plumage. New Norcia, April 17. 4.0 x 2.5 mm.; most tubules cleared, but particles of lipids remained; some interstitial tracts heavily lipoidal and aggregated, others lacked lipids; fresh adult plumage.

4. *The Rains of February 1955 and their Effects*

(a) *Weather*: "One of the most extensive rain-bearing systems on record was that of February 9 to 18, 1955. Several of the features usually associated with tropical cyclones were not present, e.g. the lowest pressure recorded was about 998 millibars, there were no general strong winds blowing more or less spirally towards a centre, and the pattern of heavy precipitation was not oriented in the customary north-west/south-east trend in the extra-tropical parts of the State. Precipitation from February 14 to 18 was very widespread, but on two days at least it extended very remarkably along a broad west/east front.

"A tentative interpretation of the pattern assumes that a remarkably extensive invasion of equatorial monsoonal air took place during this period. This is supported by the recording of extensive streams of north-westerly winds at high altitude. These streams were forced to rise above the relatively cool air of an anticyclone located unusually far to the south of the continent. The anticyclone was not an intense one, but it had a great west/east extent, and so presented a broad obstacle to the advance of the north-westerly streams. The cold front at the surface extended from west to east more or less at the latitude of Kalgoorlie or little farther north from February 14 to 18, and probably accounted for all the rain recorded in the area.

"From the biological point of view, the already remarkable effect of such heavy rains out of season was enhanced from the very beginning by the scattered precipitation recorded between February 9 and 11; on this last day rain was recorded from south of Perth to well east of Kalgoorlie, over the very area which was to be literally flooded a few days later.

"Broadly speaking, the whole rain-bearing system affected the entire western portion of the State inland to Wiluna, Leonora, Menzies and almost as far as Zanthus near the edge of the Nullarbor Plain. The rain fallen amounted to 5 to 7 inches in places, and many south-western rivers, including the Swan, the Murray and the Blackwood, were in flood. Hot and remarkably humid weather followed the rains."

The foregoing four paragraphs from J. Gentilli, *in litt.*

(b) *Observational*: Because of the remarkable penetration into the south-west of these unseasonal rains, an endeavour was made to obtain a greater coverage of any breeding phenomena which might be associated with it—

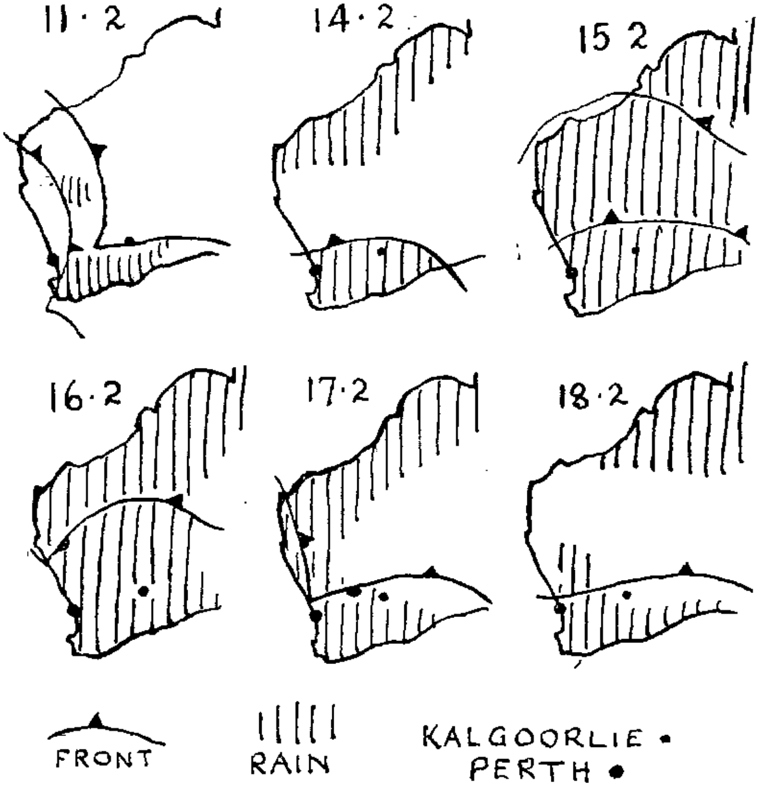

Fig. 2—Weather maps, February 1955.

Common Bronzewing (*Phaps chalcoptera*).—Narrogin, fledgelings on April 10; Corrigin, fledgelings on June 18.

Dusky Moorhen (*Gallinula tenebrosa*).—Perth, young on May 8.

Coot (*Fulica atra*).—Moora, nest with six eggs early April, another with five eggs mid-April.

Little Grebe (*Podiceps novæ-hollandiæ*).—Perth, chicks on April 8.

Little Black Cormorant (*Phalacrocorax sulcirostris*).—Perth area, attempted copulation noted May 13.

Banded Plover (*Zonifer tricolor*).—A certain amount of autumn nesting may take place by this species in normal years, but in 1955 autumn nesting occurred on a most impressive scale. Some 40 nests were recorded. Earliest eggs observed on February 23 (Seabrook, near Northam), and last on June 4 (Doodlakine). Other localities were—Ardath, Bolgart, Corrigin, Dumbleyung, Katanning, Moora, Narrogin, Nyabing, Rottnest Island, Tammin, Trayning, Waddi Forest, and Yorkrakine.

Red-capped Dotterel (*Charadrius alexandrinus*).—Kellerberrin, six records of eggs or young between April 10 and May 24; Pingrup, eggs on July 5.

Black-fronted Dotterel (*Charadrius melanops*).—Moora, nesting late February.

Australian Dotterel (*Peltohyas australis*).—Kellerberrin, three nests with eggs between March 10 and 14; Coorow, three nests with eggs between mid-April and late May; Dowerin, eggs May 6; Yorkrakine, eggs and young May 15.

Avocet (*Recurvirostra novæ-hollandiæ*).—Pingrup, nesting colony with eggs on July 5; a few 2 or 3 day old chicks also present.

White-faced Heron (*Notophoÿx novæ-hollandiæ*).—Hamilton Hill (Fremantle district), nest-building in May; Williams, feeding young on April 17.

Black Swan (*Cygnus atratus*).—Newdegate, a pair with six cygnets June 5.

Mountain Duck (*Tadorna tadornoides*).—Lake Grace, young on July 5.

Black Duck (*Anas superciliosa*).—Katanning, ducklings on April 15; Moora, ducklings in May.

Grey Teal (*Anas gibberifrons*).—This indefatigable wanderer (Downes, 1955) is well-known as an opportunist breeder whenever it discovers newly-filled inland lakes and clay pans. Ten days after the February rains a shelled egg was found in the oviduct of a bird at Lake Dumbleyung (R. Aitken). Altogether 20 nesting reports were received: Moora, many ducklings seen; Perth, two families of small ducklings, six and eight birds, on May 13; Wagin, six ducklings on April 30; Lake Dumbleyung, eleven separate clutches seen by one observer from last week in April onwards.

Maned Goose (*Chenonetta jubata*).—Katanning, eggs on March 16 and ducklings on April 20; Kojonup, ducklings in mid-April; Broomehill, small ducklings on April 30; Nyabing, nesting.

Blue-billed Duck (*Oxyura australis*).—Perth, female with two small ducklings on May 8.

Galah (*Kakatoë roseicapilla*).—Moora, in possession of nesting holes May 5.

Smoker Parrot (*Polytelis anthopeplus*).—Katanning, nesting in early May.

Welcome Swallow (*Hirundo neoxena*).—Coolup, attention shown to old nests just after the rains, but without reconstruction; Rottnest Island, entering nests March 7; Moora, nest-building early May; Dumbleyung, building May 21; Wickepin, building May 23. No actual breeding was reported anywhere.

Willie Wagtail (*Rhipidura leucophrys*).—Doodlakine, young on May 25.

Brown Flycatcher (*Micrœca leucophæa*).—Nyabing, nesting on April 16.

Scarlet Robin (*Petroica multicolor*).—Narrogin, young on May 18.

Magpie-Lark (*Grallina cyanoleuca*).—This was the third most frequent autumn-breeder, many young being successfully fledged in the wheat belt. However, nesting attempts were frequently abortive, particularly towards the south-west corner. Altogether 14 separate records were obtained—Bibra Lake (near Fremantle), young on May 20 and on June 1; Coolup, some birds began renovating nests immediately after the February rain but did not persist, and one pair abandoned a nest they had built; Dale, young left nest on April 21; Hamilton Hill (near Fremantle), young on June 9; Dumbleyung, young on May 15 and 20; Kellerberrin, young on April 24; Kojonup, nesting; Nyabing, two pairs gathering mud on April 24; Seabrook, young; Williams, 2 young left nest on April 13, at a second nest on April 17 the male completed construction of the brim, but failed to brood, at a third nest on April 17 there were fledged young.

At Williams, on September 11, there was observed a young bird which could not yet fly freely. This was "apparently one of a spring brood of the pair which bred in April, i.e. reared in the same territory which has been occupied continuously. Adults later observed feeding two young until September 25. The (presumed) same birds were constructing a nest on October 11, but this was, apparently, not used" (E. H. Sedgwick, *in litt.*).

White-browed Babbler (*Pomatostomus superciliosus*).—Narrogin, eggs on May 4; Yorkrakine, eggs on May 15.

White-fronted Chat (*Epthianura albifrons*).—Kellerberrin, three nests with eggs or young on April 17.

Weebill (*Smicrornis brevirostris*).—Narrogin, deserted nest with two eggs on April 18, nesting on April 21.

Yellow-tailed Thornbill (*Acanthiza chrysorrhoa*).—Bolgart, young on April 8; Dumbleyung, building on May 25; Gorge Rock, building on April 14; Katanning, nesting April; Kellerberrin, nest on May 14 abandoned later without laying; Narrogin, nest on April 18 abandoned later without laying; eggs on May 25 later abandoned, June 2 building.

Redthroat (*Pyrrholaemus brunneus*).—Moora, singing males on May 5.

Reed-Warbler (*Acrocephalus australis*).—Perth, singing heard on April 6, continued until early May.

Spinebill (*Acanthorhynchus superciliosus*).—Dumbleyung, eggs on May 25, abandoned later.

Singing Honeyeater (*Meliphaga virescens*).—Narrogin, courtship behaviour on April 10; Moora, bird brooding on May 5.

New Holland Honeyeater (*Meliornis novæ-hollandiæ*).—Bibra Lake (near Fremantle), building on June 4 and another deserted nest contained a dead chick and egg; Narrogin, deserted nest with two eggs on April 21; Katanning, nesting in April.

White-cheeked Honeyeater (*Meliornis niger*).—Narrogin, fledgelings on April 10, and a second freshly-built nest was subsequently deserted.

Yellow-throated Miner (*Myzantha flavigula*).—Trayning, successful nesting (? date).

Red Wattle-bird (*Anthochæra carunculata*).—Nyabing, building on April 21.

Little Wattle-bird (*Anthochæra chrysoptera*).—Bibra Lake (near Fremantle), two fresh empty nests on June 4.

Australian Pipit (*Anthus novæ-seelandiæ*).—Bolgart, young on March 23; Kellerberrin, eight nests with eggs between March 7 and April 25 and young on May 3; Nyabing, young on April 22.

Grey Butcher-bird (*Cracticus torquatus*).—Dumbleyung, three in mid-May.

Western Magpie (*Gymnorhina dorsalis*).—No autumn breeding was proved but some behaviour characteristic of the nesting season came under notice. Attacks on people were reported at Claremont in early March and Perth on May 28.

(c) *Spring and Summer Reproduction*: The regular spring-nesting in the south-west and the wheat belt was, after good winter rains, an unusually successful one. Water-birds, including Little Pied Cormorants, Coots, Black Ducks and Grey Teal, continued to breed until after mid-summer. Duck shooters had the unusual experience of finding fully-developed eggs in birds in January (1956). Land birds also nested freely, including the Banded Plover and other species which had nested during autumn. The earliest report of a spring-nesting Banded Plover was from Bullsbrook (four eggs on August 29).

(d) *Histological*: The material discussed below differs from the 1953 gonads, which were obtained in two series, three and seven weeks respectively after the precipitation, whereas the 1955 material was mostly, though not all, collected some sixteen weeks after the rains. Therefore, in the 1955 series a number of individuals might be expected to have proceeded so far in their development that the gonad cycle would have passed beyond the peak of gametogenesis, showing greater or less post-nuptial rehabilitation. Thus considerable care had to be taken in the interpretation of those gonads showing post-nuptial lipid metamorphosis, in order to ascertain whether such changes were the sequel to the previous normal spring breeding period, or due to the current unusual autumn one.

A. *Specimens influenced by the unseasonal precipitation or its effects*—

Hoary-headed Grebe (*Podiceps poliocephalus*). Lake Grace, June 6. Left testis, 10.5 x 6.0 mm., and small numbers of spermatozoa in many tubules; interstitium large and prominent, with slightly depleted lipids (plate B, figs. 1 and 2); in full breeding plumage.

White-headed Stilt (*Himantopus leucocephalus*). Lake Grace, June 6. Three males collected out of one flock had been influenced in various degrees—(a) 6.8 x 5.0 mm.; tubules cleared of lipids, some with bunched spermatozoa; interstitium heavily lipoidal in places, faintly so in others; (b) 7.0 x 4.0 mm.; most tubules cleared of post-nuptial lipids with many primary spermatogonia in mitosis; interstitium aggregated, with many tracts highly lipoidal; (c) 8.5 x 4.3 mm.; a partial spermatogenesis had taken place and premature metamorphosis of the advanced germinal products was going on with some steatogenesis; the tunica albuginea was crinkled and distorted as a result of sharp over-all reduction in testis size; the aggregated interstitium was still massively lipoidal, indicating that the bird had not bred.

Black Duck (*Anas superciliosus*). Coolup, April 3. 5.5 x 2.5 mm.; tubules cleared of lipids, with spermatogonia in mitosis; interstitium well developed, lipoidal in some places, juvenile in others; in body moult.

Brown Hawk (*Falco berigora*). Lake King, June 4. 4.0 x 2.0 mm.; interstitium showed a curious unevenness of the Leydig cells, some parts had become heavily lipoidal whereas in others they remained immature; faint mottlings of post-nuptial lipids remained in some tubules and the unseasonal influence was seen in the expansion of a few peripheral tubules with the development of odd primary spermatocytes but the activity had halted.

Smoker Parrot (*Polytelis anthopeplus*). Lake Grace, June 6. Two specimens, 4.5 x 2.6 and 4.0 x 2.7 mm., had a few spermatogonia in mitosis; interstitium massively lipoidal and aggregated.

Willie Wagtail (*Rhipidura leucophrys*). Dumbleyung, June 4. 3.0 x 1.7 mm.; interstitium becoming aggregated but fairly lipoidal; tubules remained substantially to fairly lipoidal (*Emu*, vol. 56, plate 21, fig. 1). This bird had almost certainly reached the height of spermatogenesis, had perhaps reproduced, and was now undergoing post-nuptial metamorphosis.

Magpie-Lark (*Grallina cyanoleuca*). Moulyinning, June 6. 7.3 x 4.0 mm.; many primary spermatocytes in mitosis; interstitium aggregated and becoming lipoidal.

Red Wattle-bird (*Anthochæra carunculata*). Lake Grace, June 4. 2.7 x 1.5 mm.; primary spermatocytes in mitosis; interstitium becoming aggregated and heavily lipoidal in some tracts, remaining relatively juvenile in others.

Grey Butcher-bird (*Cracticus torquatus*). Perth, June 10. Odd spermatogonia in mitosis; interstitium aggregated and partially lipoidal.

Western Magpie (*Gymnorhina dorsalis*). Lake Grace, June 6. 5.4 x 3.0 mm.; tubules cleared of lipids, odd spermatogonia in mitosis; interstitium aggregated and heavily lipoidal in some parts yet relatively juvenile in others. Moulyinning, June 6. Right testis, 5.4 x 4.0 mm.; a proliferation of spermatogonia occurred in some tubules whilst others remained unmodified and contained small quantities of post-nuptial lipids; interstitium relatively lipoidal in one section and in others remained in juvenile condition. Moulyinning, June. 6.1 x 3.0 mm.; abundant mitotic activity in spermatogonia in most tubules, though a few still retained traces of post-nuptial lipids; interstitium becoming aggregated and lipoidal, though in some parts it remained in the juvenile condition. Perth, June 11. 6.0 x 3.5 mm.; traces of post-nuptial lipids remained in the tubules, but some spermatogonia were in mitotis; interstitium still in juvenile phase and only faintly lipoidal. Coolup, June 12. 5.1 x 2.9 mm.; primary spermatocytes in mitosis; interstitium meagrely lipoidal except in one or two aggregations where it was heavily so.

B. *Specimens doubtfully influenced*—

Western Shrike-Thrush (*Colluricincla rufiventris*). Lake King, June 5. 4.3 x 2.0 mm.; tubules cleared of lipids, but remained small and undifferentiated; owing to the lack of Bouin-fixed material it was not possible to ascertain whether there was any activity among the spermatogonia; interstitium aggregated and exceedingly lipoidal.

C. *Specimens not influenced*—

Grey Butcher-bird (*Cracticus torquatus*). Juvenile, Coolup, April 11. No lipids in tubules or juvenile interstitium; skull incompletely pneumatised. Adults, Coolup, June 13. 4.0 x 2.2 mm.; most tubules cleared of lipids; and the new interstitium contained only the faintest traces of lipids.

Western Magpie (*Gymnorhina dorsalis*). Coolup, May 25. Tubules heavily lipoidal; juvenile non-lipoidal interstitium. Moulyinning, June 6. 5.4 x 2.4 mm.; tubules laden with post-nuptial lipids and contained inactive spermatogonia; interstitium still juvenile but cytoplasmic lipids had appeared in places. Perth, June 11. 5.0 x 3.0 mm.; tubules cleared of post-nuptial lipids but spermatogonia were inactive; interstitium juvenile but becoming lipoidal in places. Perth, June 11. Abundant post-nuptial lipids remained in tubules; interstitium becoming lipoidal in parts but remaining juvenile in others.

5. *Discussion of Histological Results—1953 and 1955*

Although the 1953 material was collected at the same time of the year as the Ayers' Rock material discussed by Keast and Marshall (1954, p. 495), there was a striking difference in tubule condition. In most of the Ayers' Rock specimens the tubules still retained varying amounts of post-nuptial lipids. In the great majority of the present birds these were lost. The Ayers' Rock region was drought-stricken and no breeding could have taken place since the previous spring—the common, perhaps regular, nesting period for that region (H. L. White, 1924). As these Central Australian birds were collected six or more months after the latest probable breeding period, and therefore should have passed out of the refractory state, it would seem that the immature conditions of their Leydig cells and the lingering tubule lipids were due to an absence of environmental breeding stimuli. The effect of an external stimulus in hastening tubule clearance several months after reproduction has been experimentally shown in the equatorial African finch, *Quelea quelea* (Marshall and Disney, 1956).

The portion of our 1953 material collected, in almost every instance, only three weeks after the cessation of the cyclone, showed a complete clearance of lipids from the seminiferous tubules. Therefore it would appear that the external factor operating in this case had accelerated tubule clearance, even if it was insufficiently strong to affect the gonad further.

Of the 36 adult male specimens collected at random in 1953, 23 (64 per cent) exhibited some degree of germinal activity as the result of unseasonal stimulation. Of these seven (19 per cent) had produced spermatids or spermatozoa. Eight additional specimens (22 per cent) were doubtful and might have been stimulated. Only five (14 per cent) showed no effects.

The material collected in 1955 was obtained four months after the cyclone, and hence after most of the consequential breeding had taken place (see p. 109). However, of 23 adult male birds examined, only one had bred (or had reached full spermatogenesis and then undergone post-nuptial metamorphosis). Altogether, 17 birds (74 per cent) had been stimulated to some degree. Only five (22 per cent) remained uninfluenced. These figures are somewhat biased in favour of the uninfluenced section for the material contained a relatively large number of specimens of the Western Magpie, a species which is apparently never more than slightly affected by unseasonal rains (Robinson, 1956). In the present instance stimulated Magpies developed prematurely only to the primary spermatocyte stage.

A great proportion of birds had testes influenced by the unseasonal rain in both years even though only small numbers were able to breed.

III. The External Stimuli to Breeding in Western Australia

1. *Rain*

Although the majority of birds taken in both abnormal autumn periods showed gonad stimulation, varying from more hastened tubule clearance of the post-nuptial lipids to the production of spermatozoa, only a minority attained complete spermatogenesis. When the histological and field data are combined, it is seen that though autumn nesting may occur on an impressive scale (as in 1955) the external stimuli then were really less generally effective than those responsible for spring reproduction.

In fig. 3 are plotted the localities from which breeding data were forthcoming in the autumn of 1955. The solid dots represent actual nesting occurrences. The open circles indicate abortive nesting attempts or where gonad specimens showed only partial response. The south-west corner showed virtually no 'out of season' breeding.

There can be no doubt that the external factor which resulted in this sexual activity (partial gonad stimulation or successful breeding) was the unusually heavy, though isolated, precipitation (or its effects) that accompanied the cyclones.

We believe it is probable that rainfall is also the dominant external factor controlling spring breeding. It seems scarcely conceivable that individuals of the same subspecies living in the south-west corner (see map, fig. 3) should have evolved a susceptibility to some other wholly different factor, such as light, whilst others living only 50 miles away in the wheat belt had developed a response to the stimulus of rain. Thus, Magpie-Larks in the south-west corner did not breed after the abnormal rains of February, 1955. At Coolup some birds showed a perfunctory attention to the nest and even went so far as to attempt its renovation. In the frontiers of the south-west 'inner' corner (e.g. Perth and Williams) some individuals of this species bred. Others did not. Further inland in the wheat belt many Magpie-Larks bred. Even there, however, there were instances of arrested gonad development.

We believe the reasons to be as follows. The cyclonic rains of both years fell in one isolated period. They were followed by fine dry weather, although in 1955 the February precipitation was supplemented by additional unusually-heavy rains in April. The winter precipitation usually begins in May, continues until the spring months, and ends gradu-

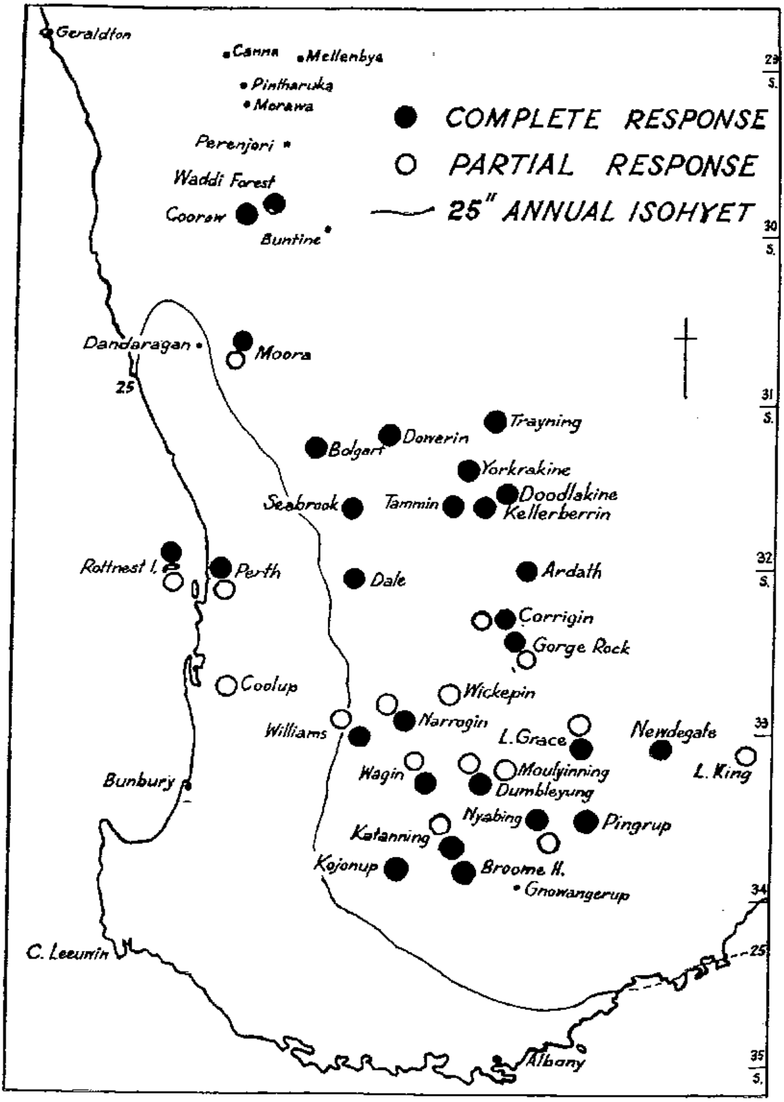

Fig. 3—Breeding activity following February rains, 1955. For explanation see p. 116.

G. M. Storr, del.

ally in September and October. This winter rain is regular in the south-western corner, but diminishes sharply in quantity as one goes north-east. Such rainfall is basic to the productivity of the entire country. From the time of the first showers a marked rejuvenating effect on the vegetation and all animal life is observed.

The winter in southern Western Australia is not a dormant period but is, for many organisms, a time of active growth. Failure of winter rains retards both natural populations and agriculture. South-west of say the 30 inches mean annual isohyet, failure hardly ever occurs. But in the lighter rainfall areas droughts are frequent and may seriously reduce avian reproduction during the following spring.

Bird populations living under these graduated rainfall conditions may respond essentially to *the amount of change in the environment caused by precipitation.* No genetic difference between the birds in the various regions is implied. Nevertheless, birds in the relatively well-watered Coolup area (mean annual rainfall 40 inches) may, for example, require a different threshold of rainfall effects than members of the same species living, say at Lake Grace (mean annual rainfall 15 inches) or at Morawa (mean annual rainfall 14 inches). The more profound the local environmental response to rain (involving the sudden appearance of fresh vegetation and insect or other food) the more rapid, and probably complete, the reflex response in the local avifauna. Thus, precipitation from a single cyclonic downpour seems to produce insufficient changes fully to influence Coolup individuals, whereas in the drier Morawa area there is a rapid, even dramatic, response. In this connection the observations of S. R. White (1952, p. 104) are significant—"One of the distinctive features of the nesting season (at Morawa) is its short duration. During a brief period, following the first fall of sufficient rain, life flourishes, Blossom and insects are abundant and when optimum conditions prevail the bird population is astounding in its density and in the high tempo of its activity. Then with surprising suddenness all declines. Only during the months of July and August may a 'water-surplus' be expected. With abundant feed supplies available over such a limited span it is necessary that birds initiate and conclude their breeding cycles in synchronization with optimum conditions".

Yet Morawa is not a desert. Although comparatively dry, it is part of the south-west agricultural area.

2. *Double Breeding Seasons and the Inhibition of Winter Nesting*

External *inhibitors* as well as stimuli are important in avian reproduction (Marshall, 1951, p. 253; 1954, p. 19; 1955a. p. 95). Everywhere south of the Kimberley Division, some inhibitory factor or factors retards or prevents reproduction during winter.

Thus in 1953 and 1955 there was no regular continuation of nesting from autumn *through the winter* to spring. In the Kalgoorlie and Coonana districts in 1953, for instance, Slater (*in litt.*) recorded the following numbers of nests found between April (when the effects of the March cyclone first became apparent) to August (after which observations were discontinued) : April, four nests; May, ten; June, one; July, one; August, seventeen. This bimodality of nesting frequency is even more pronounced in north-western Australia where both summer and winter rains may fall.

The records of Carnaby (1954) and Robinson (1955) demonstrate this fact and we have re-arranged their data in the form of graphs (fig. 4), which emphasize these authors' conclusion that two peaks of nesting occur in years of good rainfall. Egg-laying frequency declines sharply in April or May, remains at a low level during June and July, and rises again in August. The situation differs from that further south in that a small amount of nesting usually occurs throughout winter. The same species generally breed in both autumn and spring. Full details of the species concerned are given in tabular form by Carnaby and Robinson. Whether the same *individuals* nest in both seasons is still unknown. However, according to avicultural experience, individual Budgerygahs (*Melopsittacus undulatus*) and Zebra Finches (*Taeniopygia castanotis*) might be expected to breed during both seasons.

Such double nesting within twelve months does not recur regularly everywhere. Drought may eliminate the stimulus for one or other nesting period. Carnaby (1954, p. 152) has evidence that breeding is inhibited in some years by drought. In other years, when the rainfall is scattered (due to very local thunderstorms) reproduction is rigorously confined to these so-called 'thunderstorm patches'. Here the environment is providing for us the equivalent of experimental data in the efficacy of rain as a stimulus to breeding. Control areas, too, are closely adjacent.

In north-western Australia the winter environment appears to be favourable after rainfall, but some inhibiting factor operates to prevent *general* nesting. This inhibition is not there as stringent as in, for example, the south-west. We believe, with Robinson (1956, p. 321), that probably low temperatures prevent winter reproduction in the south-west. Because Rowan (1926) photo-stimulated the Canadian *Junco* at temperatures which fell as low as —46°c., there has been a tendency to depreciate the importance of temperature in breeding periodicity (Bullough, 1951, p. 39). Baker (1938, p. 171) and Marshall (1955a, p. 95), however, have drawn attention to the fallacy of such a view. Marshall (1949a) showed how the exceptionally hard winter of 1946-47 in England arrested the testis development of a number of local

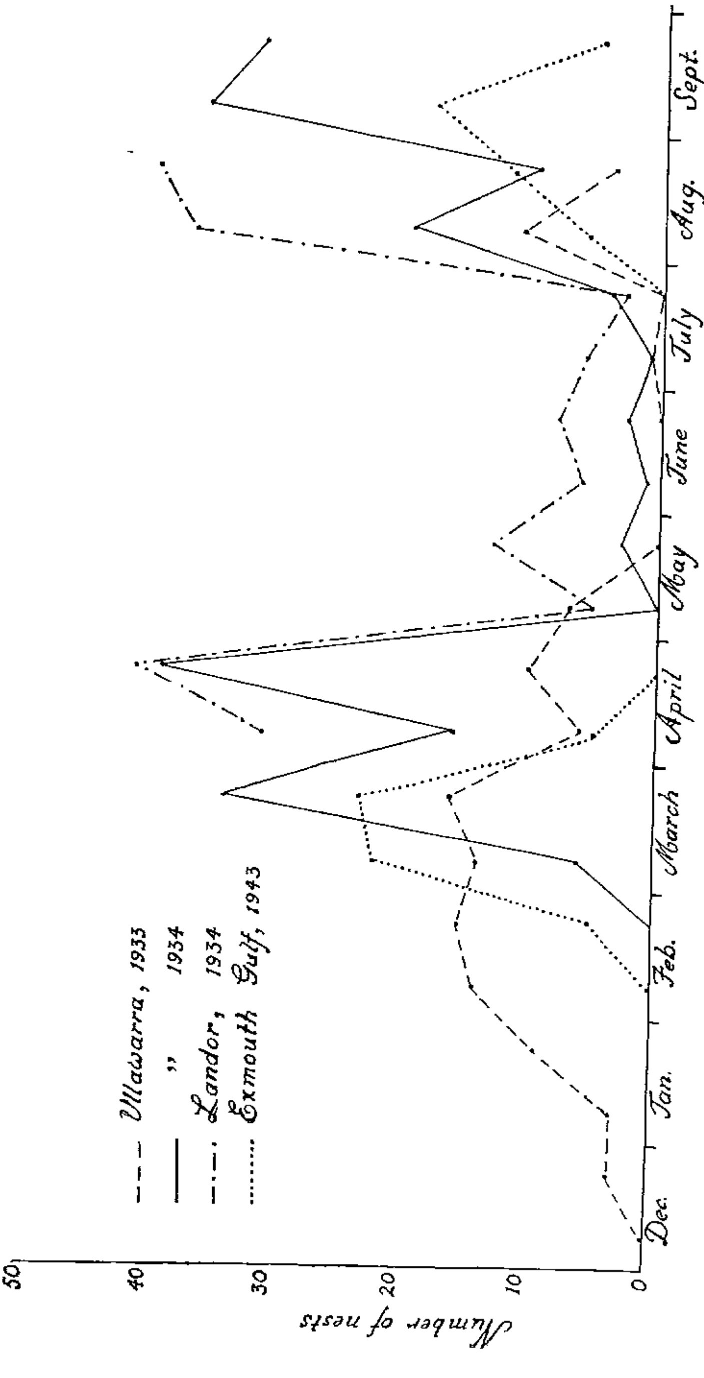

Fig. 4—Frequency of nests containing eggs, north-western Australia (data from Carnaby and Robinson).

passerines as compared with their cycle in a mild winter. Davis and Davis (1954), too, demonstrated how low winter temperature retarded spermatogenetic activity in the House Sparrow (*Passer domesticus*) in various parts of the United States. The degree of retardation varied with the cold. Conversely, Snow (1955) has reported how the unusually mild weather in England in November and December 1953 resulted in a considerable outburst of egg-laying in those months by several species of resident birds.

Though the winter days in north-western Australia are genial the night temperatures may drop to below freezing point. Thus writing of the winter climate on the east Murchison, not far south of the Tropic of Capricorn, Whitlock (1910, p. 187) stated that "the mornings are usually bitterly cold, the frost often severe . . . on 30th July . . . my rugs were white with hoar frost, a bucket of water had thick ice on it". In Central Australia, which would include the Ayers' Rock region, Whitlock (1924, p. 252) reported that in August ice three-quarters of an inch thick formed on water left in a washing bowl, and some days were marked by bitterly cold winds from the south-east. Such conditions are not conducive to reproductive success in nidicolous birds, the young of which are almost poikilothermous during the early stages in life.

In south-western Australia, too, and particularly in the forested south-west corner, heavy rainfall in the winter is combined with low temperatures, strong wind and reduced hours of sunshine. In the wheat belt, rainfall is less, and though the nights are cold there are longer and finer intervals in the daytime. Further inland the dismal winter climate improves, but the nights remain cold.

Fig. 5 shows the seasonal variation of temperature at Mundiwindi (lat. 23° 40′S., altitude 1,840 feet) in the north, and at Katanning (lat. 33° 40′ S., altitude 1,016 feet) in the south, illustrating the steep fall in winter. The graphs depict absolute maxima, mean maxima, mean minima and absolute minima for each month in degrees Fahrenheit.

Reproduction is correlated with the climatic gradient just referred to. If we may be permitted an analogy with the internal combustion engine, for purposes of illustration the situation could be set out as follows. The endocrine machinery controlling reproduction is started off by rainfall, or its effects, as the initial stimulus. But though the engine is running the car does not move whilst the foot is still pressing the clutch pedal, which action may be likened to the temperature and other factors inhibiting winter breeding. As the genial spring days return in the south-west the clutch pedal is lifted and the car moves forward. In the wheat belt the pedal is lifted somewhat earlier in the season. In the north-west the clutch is slipped to permit the vehicle to crawl along slowly in bottom gear until the spring, when it is allowed to leap ahead swiftly.

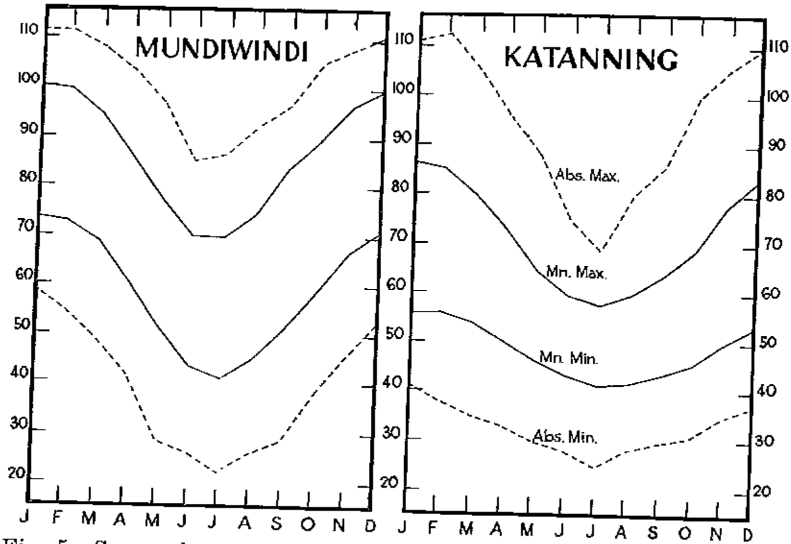

Fig. 5—Seasonal temperature fluctuations at Mundiwindi (left) and Katanning (right). For explanation see p. 121.

The breeding periodicity of birds in Western Australia may be diagrammatically represented in fig. 6. In the north-west the nesting season takes the form of a bi-modal curve. A low level of winter breeding continues between the two peaks. In unfavourable years, one or both peaks can be eliminated by the absence of rain and its effects. Autumn breeding is caused by monsoonal rains which in some years penetrate far south and affect the south-west. These may stimulate a certain amount of autumn breeding in the drier parts of the inland south-west, including the wheat belt, and even (as in 1955) the districts close to Perth. In the deep south-west, with its regular winter rains, we believe birds have developed a response only to the effects of prolonged precipitation. Inhibitory factors prevent winter breeding. Here the occasional, and brief, stimulation by cyclonic rain in the late summer and autumn is insufficient to produce breeding, though it may initiate some abortive sexual activity.

3. Light as a Possible External Factor

We believe that precipitation and its effects (as stimuli) and low temperature and associated factors (as inhibitors) are adequate to control reproduction in most Western Australian birds. Local climatic vagaries are important in the lives of almost all organisms and in Western Australia in particular. If such species were rigorously controlled by increasing light, they would miss the opportunity of breeding at favourable times when the light was decreasing. If, on the other hand, their cycles operated only during decreasing light, they would fail to take advantage of a favourable spring.

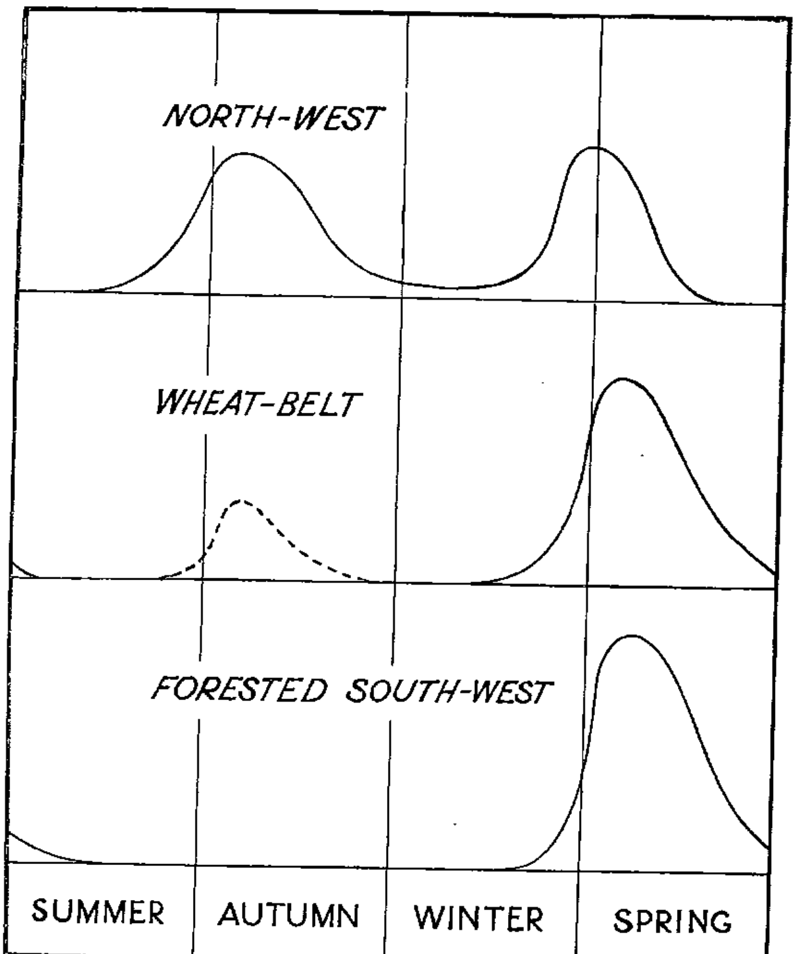

Fig. 6—Diagrammatic representation of breeding seasons in Western Australia.

There are, however, certain species which breed at regular times, uninfluenced by the nature of the season. These may have retained a presumably ancient capacity for light stimulation. The most notable of such cases is the Emu (*Dromaius novæ-hollandiæ*). Serventy and Whittell (1948, p. 9) have listed several others, though some of these must, in the light of later knowledge, be eliminated. Possibly, also, many or most sea-birds are light-controlled (Serventy, 1952, p. 51). An outstanding instance of such a species, which apparently has no inhibiting or modifying factors to alter the nesting time in any way, is the Short-tailed Shearwater (*Puffinus tenuirostris*), breeding in south-eastern Australia (Marshall and Serventy, 1956b).

IV. Conclusions

1. Field and laboratory investigations of sexual phenomena in Western Australian birds during abnormally wet autumn periods in 1953 and 1955 reveal a widespread response to precipitation or its effects.

2. Both aquatic and terrestrial species were influenced, and individuals in both groups were affected in varying degree. In all, 39 species reproduced after unseasonal precipitation. A histological study of a random sample showed that at least 73 per cent of individuals showed some positive effect after unseasonal stimulation. Histological criteria for stimulation are described in the text.

3. A habitational gradient of effect occurs. Individuals in the south-west corner were little affected, those of the marginal belt (Perth, Dale, Williams, Kojonup) more so, and birds living in the wheat belt most of all. Gonad and weather data reveal that individuals tended to respond to the degree of beneficial change in the environment that followed precipitation. Thus, the breeding response at Morawa (mean annual rainfall of only 14 inches) was much greater than at Coolup (mean rainfall 40 inches).

4. The response to rainfall is seen as a physiological drought adaptation. Most xerophilous species that did not respond to rainfall stimuli would be eliminated by natural selection.

5. An analysis of the present data, including those of Carnaby and Robinson, emphasizes the importance of low temperatures as a breeding inhibitor. It is held that photoperiodicity is of relatively little importance as a regulator of the sexual cycles of most Western Australian birds, excluding sea-birds.

6. That spring-breeding occurs during a period of increasing day lengths is probably coincidental. The critical stimuli to reproduction are probably environmental conditions that arise after rainfall and with the relatively high temperatures that accompany the lengthening photo-period.

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VI. References

Baker, J. R., 1938. 'The Evolution of Nesting Seasons'. (In *Evolution: Essays on aspects of evolutionary biology*, pp. 161-177. Oxford University Press).

Bullough, W. S., 1951. *Vertebrate Sexual Cycles*. London, Methuen & Co.

Carnaby, I. C., 1954. 'Nesting Seasons of Western Australian Birds'. *West. Austral. Nat.*, vol. 4, pp. 149-156.

Carter, T., 1889. 'Notes from Western Australia'. *The Zoologist*, vol. 13, no. 151, pp. 267-268.

Carter, T., 1923. 'Supplementary Notes on Some Birds from Western Australia and from Dirk Hartog Island'. *The Ibis*, pp. 218-228.

Carter, T., 1924. 'Birds of the Broome Hill District'. *The Emu*, vol. 23, pp. 223-235; 306-318.

Davis, J., and B. S. Davis, 1954. 'The Annual Gonad and Thyroid Cycles of the English Sparrow in Southern California'. *The Condor*, vol. 56, pp. 328-345.

Downes, M. C., 1955. 'Recovery of Banded Ducks'. *The Emu*, vol. 55, pp. 313-314.

Harrison, J. G., 1949. 'Some Developmental Peculiarities in the Skulls of Birds and Bats'. *Bull. Brit. Orn. Club*, vol. 69, pp. 61-70.

Keast, J. A., and A. J. Marshall, 1954. 'The Influence of Drought and Rainfall on Reproduction in Australian Desert Birds'. *Proc. Zool. Soc. London*, vol. 124, pp. 493-499.

Lack, D., 1950. 'Breeding Seasons in the Galapagos'. *Ibis*, vol. 92, pp. 268-278.

Lofts, B., and A. J. Marshall, 1957. 'Cyclical Changes in the Distribution of Testis Lipids of a Teleost Fish, *Esox lucius*'. *Quart. Journ. Microsc. Sci.*, vol. 98, in press.

Marshall, A. J., 1949a. 'Weather Factors and Spermatogenesis in Birds'. *Proc. Zool. Soc. Lond.*, vol. 119, 1949, pp. 711-716.

Marshall, A. J., 1949b. 'On the Function of the Interstitium of the Testis: The sexual Cycle of a Wild Bird, *Fulmarus glacialis* (L.).' *Quart. Journ. Microsc. Sci.*, vol. 90, pp. 265-280.

Marshall, A. J., 1951. 'The Refractory Period of Testis Rhythm in Birds and its Possible Bearing on Breeding and Migration.' *Wilson Bull.*, vol. 63, pp. 238-261.

Marshall, A. J., 1952. 'Non-breeding among Arctic Birds'. *Ibis*, vol. 94, pp. 310-333.

Marshall, A. J., 1954. *Bower Birds*. Oxford University Press.

Marshall, A. J., 1955a. 'Breeding Seasons—Causes and Effects'. (In *Encyclopedia of British Birds*, pp. 93-95. London, Waverley Book Co.).

Marshall, A. J., 1955b. 'Reproduction in Birds: the Male' (Chapter in *Comparative Physiology of Reproduction*, Cambridge University Press).

Marshall, A. J., and H. J. de S. Disney, 1956. 'Photostimulation of an Equatorial Bird'. *Nature*, vol. 177, pp. 143-144.

Marshall, A. J., and D. L. Serventy, 1956a. 'A case of Intersexuality in *Gymnorhina dorsalis*'. *Emu*, vol. 56, pp. 207-210.

Marshall, A. J., and D. L. Serventy, 1956b. 'Breeding Periodicity in the Short-tailed Shearwater (*Puffinus tenuirostris* Temminck), in

Relation to Trans-equatorial Migration and its Environment'. *Proc. Zool. Soc. Lond.*, vol. 127, pp. 489-510.
Marshall, A. J., and F. M. Woolf, 1956. 'Seasonal Lipoid Changes in the Sexual Elements of a Male Snake, *Vipera berus*'. *Quart. Journ. Microsc. Sc.*, vol. 98, in press.
Moreau, R. E., 1950. 'The Breeding Seasons of African Birds—1. Land Birds'. *Ibis*, vol. 92, pp. 223-267.
Robinson, A. H., 1949. 'The Biological Significance of Bird Song in Australia'. *The Emu*, vol. 48, pp. 291-315.
Robinson, A. H., 1955. 'Nesting Seasons of Western Australian Birds —a Further Contribution'. *West. Austr. Nat.*, vol. 4, pp. 187-192.
Robinson, A. H., 1956. 'The Annual Reproductory Cycle of the Magpie, *Gymnorhina dorsalis* Campbell, in South-western Australia'. *The Emu*, vol. 56, pp. 233-338.
Rowan, W., 1926. 'On Photoperiodism, Reproductive Periodicity and the Annual Migrations of Birds and Certain Fishes'. *Proc. Boston Soc. Nat. Hist.*, vol. 38, pp. 147-189.
Sedgwick, E. H., 1955. 'Nesting Records—1946 and 1947'. *West. Austr. Nat.*, vol. 5, pp. 46-47.
Serventy, D. L., 1946. 'The Pituitary Gland and the breeding Cycle'. *West. Austr. Bird Notes*, no. 4, pp. 10-12.
Serventy, D. L., 1952. 'Bird Islands of the Sahul Shelf: with Remarks on the Nesting-Seasons of Australian Sea-birds'. *The Emu*, vol. 52, pp. 33-59.
Serventy, D. L., 1955. 'The Breeding Periods of the Black Cormorant'. *West. Austr. Nat.*, vol. 5, pp. 18-21.
Serventy, D. L., and A. J. Marshall, 1956. 'Factors Influencing Testis Coloration in Birds'. *Emu*, vol. 56, pp. 219-222.
Serventy, D. L., and H. M. Whittell, 1948. *A Handbook of the Birds of Western Australia*, Perth.
Snow, D. W., 1955. 'The Abnormal Breeding of Birds in the Winter of 1953-54'. *British Birds*, vol. 48, pp. 120-126.
White, H. L., 1924. 'Notes on Eggs Collected in Central Australia'. *The Emu*, vol. 23, pp. 243-247.
White, S. R., 1950. 'Breeding Behaviour in Tree Martins Stimulated by Weather Change'. *West. Austr. Nat.*, vol. 2, pp. 141-142.
White, S. R., 1952. 'Communal Nesting among White-winged Trillers and Other Birds'. *West. Austr. Nat.*, vol. 3, pp. 103-106.
Whitlock, F. L., 1910. 'On the East Murchison'. *The Emu*, vol. 9, pp. 181-219.
Whitlock, F. L., 1924. 'Journey to Central Australia in Search of the Night Parrot'. *The Emu*, vol. 23, pp. 248-281.
Wolfson, A., 1952. 'Day Length, Migration, and Breeding Cycles in Birds'. *Sci. Mon.*, vol. 74, pp. 191-200.
Wolfson, A., 1953. 'Gonadal and Fat Response . . . in the White-throated Sparrow'. *Condor*, vol. 55, pp. 187-192.

CORRECTION

For line 6 of the first paragraph under 'Discussion', on page 62, in the paper 'On the Rehabilitation of the Avian Testis Tunic' by A. J. Marshall and D. L. Serventy (*Emu*, vol. 57, pt. 1), there should be substituted the following— "tubule steatogenesis and interstitial regeneration (Mar-". This mistake occurred as a result of lifting out a wrong line after making an alteration and was beyond editorial vigilance.