



The four male plumages of the Superb Blue Wren, *Malurus cyaneus*. *Upper*: left immature, right sub-adult. *Lower*: left adult in breeding plumage, right adult in winter plumage. The immature plumage is the same for both sexes and very similar to that of the adult female.

Painting by Betty Temple Watts

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The Life History of the Superb Blue Wren *Malurus cyaneus*

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Summary

A completely colour-banded population of these small, sociable, multi-brooded passerines of the sub-family Malurinae was studied for more than four years at Gungahlin, Canberra, A.C.T. Their plumage, behaviour, song, breeding biology and population dynamics are discussed with particular reference to the persistence of the young-of-the-year within the family group throughout the winter, the consequent problems of dispersion and, ultimately, the frequent occurrence of more than one mature male in the breeding group. It is suggested that this apparent polyandry enables the species to be reproductively more successful within the limits of a variable climate.

I. INTRODUCTION

Different species have different requirements and react in different ways to a changed environment—the Superb Blue Wren, *Malurus cyaneus*, is one of the few species that actually seems to thrive in association with man. Besides the gardens, which surround houses and public places, the opening of the bush and the spread of exotic plants such as Sweetbriar, *Rosa rubiginosa* L., and Blackberry, *Rubus fruticosus* L., have all provided additional ecological niches suitable for *M. cyaneus*, and in consequence the Superb Blue Wren is widely known and frequently mentioned in the literature.

The Blue Wren is a multi-brooded, sedentary, and territorial small passerine of the sub-family Malurinae (Mayr and Amadon 1951). Throughout most of the year they may be seen foraging energetically in groups numbering from 6-12, or even more—in other words they are obviously a sociable species. The main object of the present study was to investigate these social units—their formation, the relationships within them, the constancy of membership, and their general utility; to achieve this it was first necessary to thoroughly “know” the species and to this end details of plumage, song, behaviour patterns, breeding biology, territory and population dynamics are presented before the social organization of the species is discussed.

The study of *Malurus cyaneus* was initiated in 1955 at “Gungahlin”, the headquarters of the Division of Wildlife Research, CSIRO, at Canberra. About the same time the Misses Bradley

PLATE 13



Aerial photographs of Gungahlin study area.

Upper to show cleared pastoral surrounds which isolate the population.
Lower to show the variety and nature of the vegetation.

Photo by C. Totterdell

started a similar study at Mosman, N.S.W. (Bradley and Bradley 1957). Later Pate and Courtice (unpubl.) banded Wrens in the grounds of Sydney University. Where possible I have amplified my own figures and checked my findings with theirs; I am most grateful for their co-operation.

II. METHODS

Gungahlin is an old homestead surrounded by a mature garden of lawns, trees, and shrubs. The drive, half a mile long, links the house with the main road and is flanked by hedges on both sides, beyond which are open paddocks. The study area comprised some 49 acres (see Plate 13), most of which was eminently suitable for Wrens, but which was conveniently isolated from similar habitat by surrounding grazing leases. The nearest other Wrens were over a mile away—a significant distance for a species with weak powers of flight.

The study was based on the capture and individual marking of the entire population, followed by regular fortnightly identification of all Wrens still present in the area; notes on plumage, behaviour, and territorial boundaries were made at the same time. Throughout the breeding season an attempt was made to find all Wren nests and band the offspring before they fledged. It was not always possible to locate the nests before the eggs were laid, but where this was done particular care was taken to obtain incubation and fledging data. Details of nest height, aspect, and location were recorded and intensive observations at selected nests were carried out.

Trapping. Nearly all the birds were caught in a box-type trap (30" cube) with four funnel entrances at ground level and a sleeved aperture at the centre top. When trapped Wrens saw humans approaching their invariable reaction was to fly upwards; a few small branches placed crosswise half way up the trap took advantage of this by providing perches and very few escaped via the funnels.

The trap was baited with bread crumbs fried in fat and scattered on the ground. The funnels were left out for several hours (frequently overnight) to allow the birds to become thoroughly familiar with the trap before it was set.

Most Wrens show no trap-shyness, although one female eluded all methods of recapture (including mist-nets) for five years. In no instance was any disturbance to general behaviour observed, resulting from handling or trapping—in fact birds frequently re-entered the trap minutes after release.

Banding. By the end of September 1956 all adult Wrens in the area had been trapped and each given a different colour-combination of two celluloid bands—on each leg. The bands were fused with acetone. Besides celluloid bands, the marked birds carried a

numbered aluminium band supplied by the Australian Bird-Banding Scheme, which was placed on the left leg of females and the right leg of males, thus extending the available colour-combinations quite safely.

Although the banding of nestlings is generally regarded as wasteful of colour-combinations due to high mortality, it was essential to have the young pedigreed if social relationships were to be solved. This difficulty was overcome by using striped and bi-coloured bands, common in aviary studies but generally avoided for field work because of identification difficulties. Twenty contrasting patterns were selected and each used to distinguish a particular brood; a plain-coloured band denoting the year of birth ('56 red, '57 blue, '58 yellow etc.) and a numbered aluminium band on the left leg completed a nestling's quota. By alternating the positions of these three bands (see Fig. 1) four individual combinations were possible (the clutch size never exceeded that figure). When

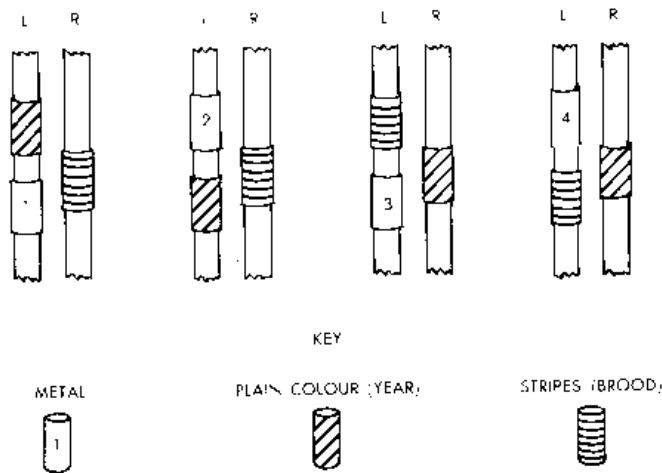


FIG. 1.—Four different combinations of three bands used to achieve individual marking of nestlings; by changing the metal band to the right leg a further four combinations are possible.

seven days old the legs of the young are firm enough to take bands. Size 1 fits satisfactorily, even though the nestlings' legs at that age are fatter than those of adults. If the young are left until more than nine days old they are likely to "explode" from the nest on handling—a useful defence mechanism for the species, as they scatter rapidly and then freeze motionless in the ground litter, where they are extremely hard to locate; a predator might find one or two, but some would survive. This performance is further complicated by the distraction display of the parents (Rowley 1962).

Those nestlings which survived until the following July were trapped and given adult colour combinations.

Identification. Wrens are not shy of humans, so that recognition of colour bands was usually done at close quarters. Occasionally the bands could be read by the naked eye, but generally binoculars were used (Hensoldt Wetzlar, Dialyt 8 x 30).

Of the seven plain-coloured bands used, red, black, and white lasted indefinitely, but blue, green, yellow, and orange tended to fade to a uniform dirty grey after more than 18 months' wear.

III. RESULTS

1. General

(a) *Plumage*

Mack (1934) has described the plumage of *M. cyaneus* in detail and only those aspects important for the field identification of age or sex are given here. Both male and female birds weigh 10g. (± 0.5 g.) and their tails average 60 mm, which is approximately half their total length.

Four distinct plumages (see Plate 12) can be separated in the field with the aid of binoculars:

Female. The mature breeding female is a brown bird whose tail shows greenish-blue lights. The bill and the skin surrounding the eyes are orange brown, while the legs are pinkish brown.

Juvenile. At fledging the colouring of the bill and the skin round the eye is poorly developed and pale, while the tail is a mere stub (c. 10 mm.) adapted to the confined space of the small domed nest. During the cryptic stage the tail grows rapidly and the colours of the soft parts deepen so that when the young are next seen, feeding independently, they are almost identical with the mature female, except that they lack the bluish-green lights in the latter's tail feathers. By this time wear and tear on the tail feathers of the adult female, who will be attending her second or third brood, further distinguishes her from her offspring, with their new rectrices.

For a period of from four to six months male and female juveniles are indistinguishable in the field or hand.

Sub-adult male. In the late autumn or winter (usually April-May) male juveniles grow their characteristic royal blue tail feathers, but it is not for several weeks, or even months, that the colours of the soft parts change, usually not until they moult into their first nuptial plumage. Late hatched individuals (e.g. 1012 and probably 602) may not gain their blue tails until August (see Fig. 2).

Off-season male. Males over one year usually assume an off-season or winter plumage following the autumn post-nuptial moult. As will be shown later the duration of this plumage varies with social responsibilities, age, and climate. Basically the plumage is similar to that of the female (body-feathers), but the new tail

remains blue; the black bill, and pale soft parts distinguish this category from sub-adult males.

Male nuptial plumage. This consists of black and blue and is very striking. This vividness enables the early appearance of bright feathers to be easily seen among the brown of the off-season plumage—conversely the first brown/grey feathers amidst this bright array appear dishevelled and clearly mark the start of the moult.

(b) Moults

In the autumn, all Wrens in the study area, except juveniles, underwent a complete moult, the onset of which was determined by the end of the breeding season, coincident with the start of dry summer conditions, and varied from December to February in different years. The autumn post-nuptial moult began about six weeks after the laying of the last egg, and since pairs nested at different times the onset of the moult was not uniform within the population.

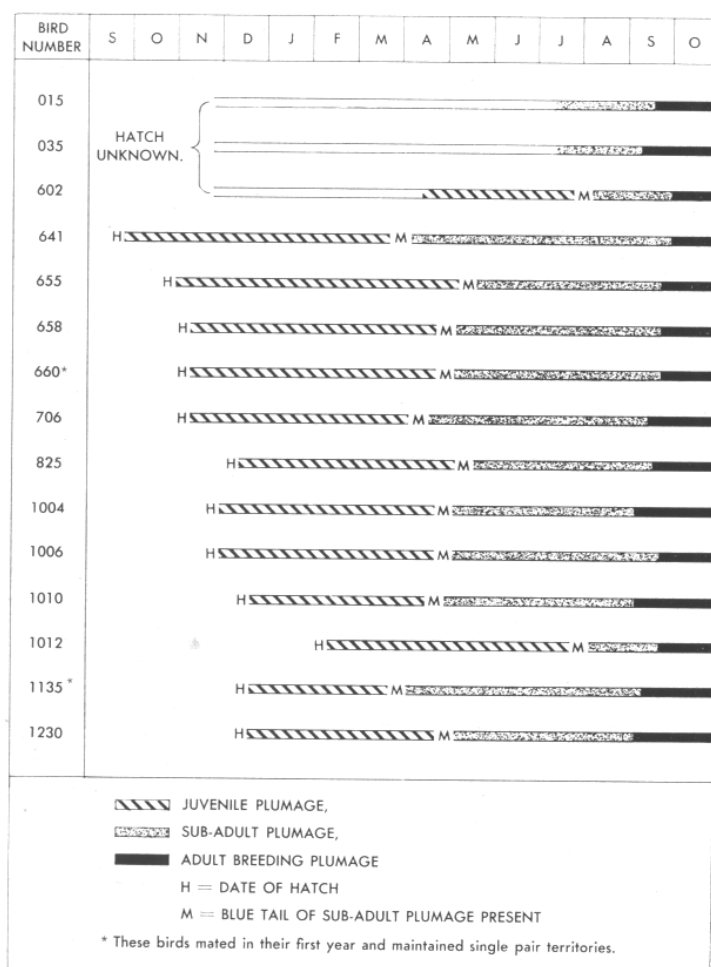


FIG. 2—Male plumage changes in *Malurus cyaneus* during the first year of life; Canberra A.C.T.

Males have a second or pre-nuptial moult, the onset of which was found to vary according to age and social status; both moults in the male take about a fortnight to complete. Males assuming nuptial plumage for the first time (see Fig. 2) did so by mid-September, but never earlier than the beginning of that month even when they were mated and holding territory on their own (660 and 1135). Birds coming into their second breeding season moulted according to their social position (see Fig. 3); cocks maintaining a territory (the dominant where more than two males were present in the group) moulted during July (003, 035, 660, 706, 1135) whereas subordinate (supernumerary) males remained

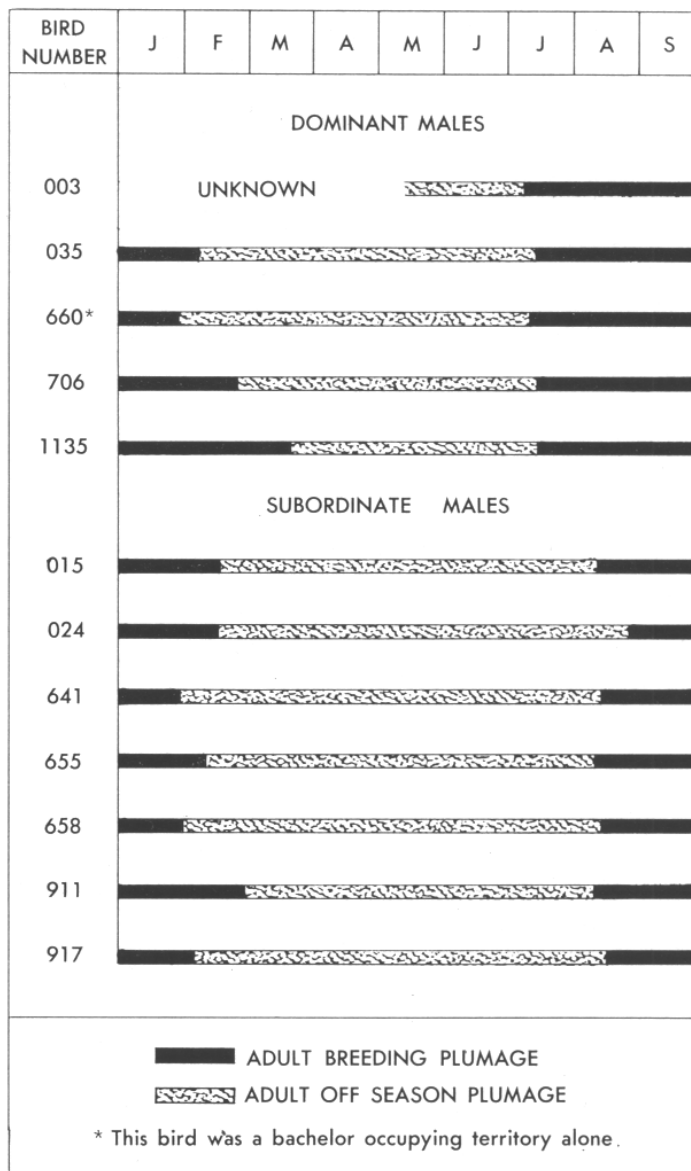
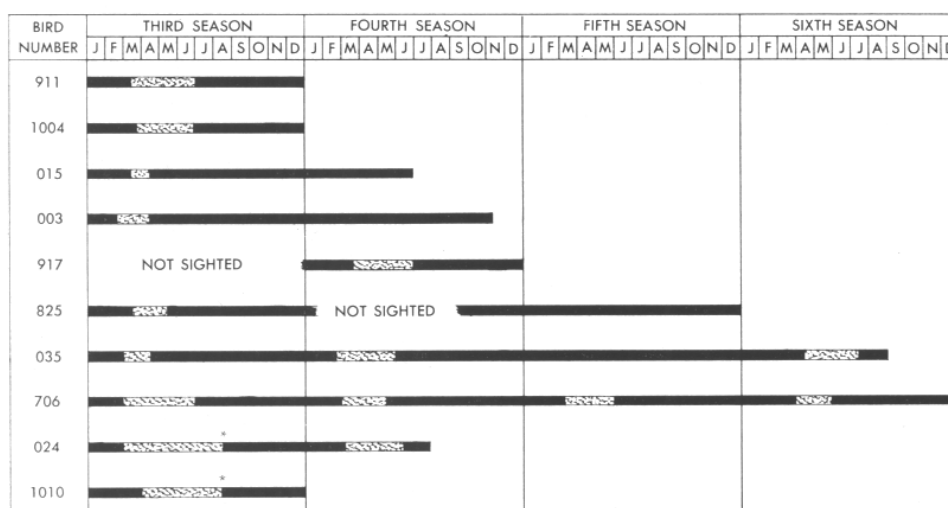


FIG. 3—Male plumage changes in *Malurus cyaneus* during the second year of life; Canberra A.C.T.

in off-season plumage for another month (015, 024, 641, 655, 658, 911, 917). The presence of a mate to establish this "dominant" early moult is not essential; 660 was maintaining a bachelor territory, alone.

Figure 4 shows that sometimes a male may enter its third breeding season still in a subordinate rôle; this occurred twice (024, 1010) and the cocks in question assumed nuptial plumage in August, whereas eight other birds of a similar age, but maintaining a dominant rôle, moulted in April, May or June.

Seven birds of known age reached their fourth breeding season and of these, four (024, 035, 706, 917) definitely moulted into off-season plumage and remained in it for a month or more. Two birds (003 and 015) moulted straight from one breeding plumage to the next with no sign of the off-season grey-brown feathers whatsoever. Male 825 was not viewed at the critical time during his fourth winter.



*Both these birds were still subordinate to older males (003 and 706 respectively) in their third year.

FIG. 4—Male plumage changes in *Malurus cyaneus* more than two years old; Canberra A.C.T.

In the fifth winter there is again considerable individual variation; 706 moulted into off-season plumage while 035 and 825 remained in breeding plumage right through; all three were dominant cocks. Two birds (035, 706) reached a sixth winter and both reverted to off-season plumage in the autumn.

(c) Territory

Territory has been simply defined as "a defended area" (Hinde 1956) and, depending on the species, it may fulfil part or all of the requirements of the occupants. With *M. cyaneus* individuals may remain within the same territorial bounds from the day they hatch until they die and this area must therefore supply: adequate foraging throughout the year; sufficient cover to provide nest sites,

roosts, song-perches and shelter from both predators and bad weather. Wrens have relatively weak powers of flight but long legs and spend most of their time on the ground or in shrubs, progressing in a series of hops as they gather food; usually they forage as a group and it is quite possible that this is to their mutual advantage—insects disturbed by one bird falling victim to another; I have called this the “hop-search”. It will at once be apparent that open spaces are best suited to this kind of hunting, yet because of their weak flight they seldom venture far from cover to which they fly at the first sign of danger. Suitable territory, therefore, needs to be an admixture of open spaces and shrubby cover to fulfil the needs of this species; the suitability of mown lawns and closely grazed sheep pastures, interspersed with ornamental shrubs on the one hand and various bushy “weeds” on the other, probably explains the successful adaptation of this species to the changing environment after settlement.

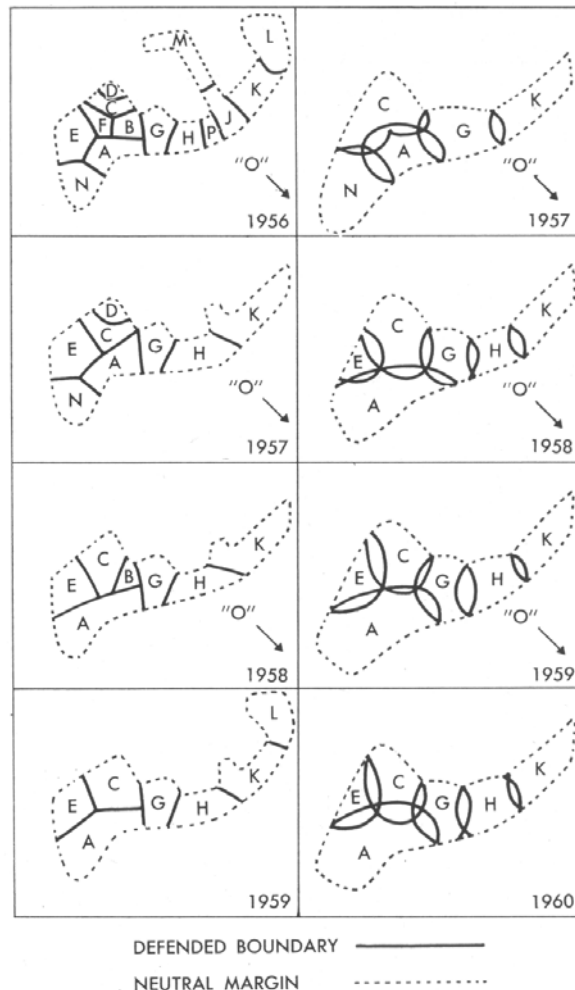


FIG. 5—Wren territorial boundaries, summer (left-hand column) and winter, over four years at Gungahlin, Canberra A.C.T.

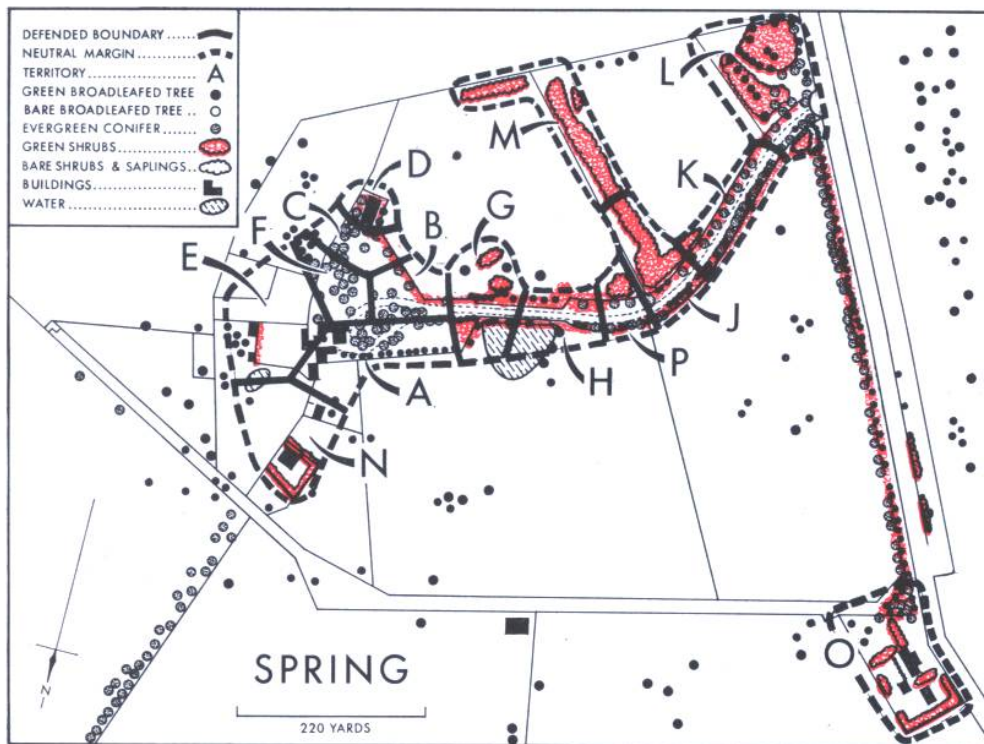


FIG. 6—Wren territories during spring 1956, when the population was at a maximum; Canberra A.C.T.

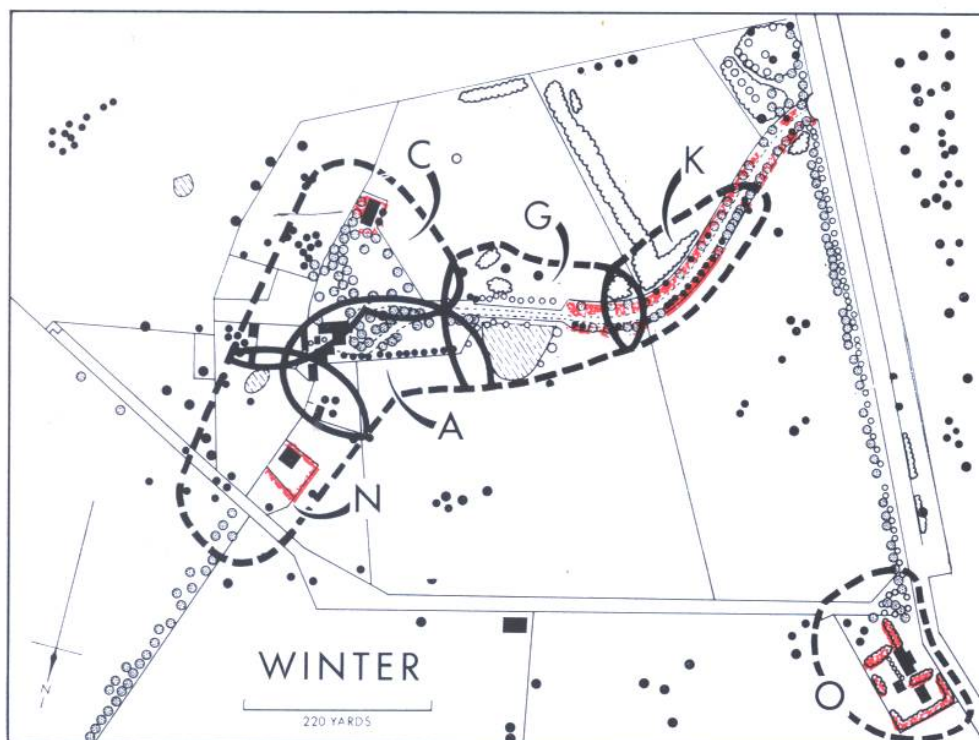


FIG. 7—Wren territories during winter 1957, showing how the reduced population was dispersed; Canberra A.C.T.

When the study started, in 1956, the Wren population at Gungahlin was at a very high density, probably due to the previous wet summer and mild winter, resulting in good breeding success and a high survival rate. This level was not maintained throughout the study; the 15 territories of the first year reduced to an average of eight in the following four years, an aspect discussed more fully later under "population dynamics".

Figure 5 shows that once the population stabilised (at about eight territories) the territorial boundaries changed very little over the years; other workers who have studied birds which maintain territory all the year round (Erickson 1939, Southern and Morley 1950, and Dixon 1956) have found a similar constancy. This is because it is rare for calamity to strike both members of a pair simultaneously and loss of a mate does not necessarily mean desertion of the territory; replacement of breeding casualties is remarkably quick in most field populations and, at least with Wrens, the newcomer, male or female, simply steps into the vacancy and learns the boundaries that are already established.

Unfortunately an assessment of food was beyond the scope of this study, but for a resident, insectivorous bird (see App. II) decreasing temperature and, consequently, insect activity, must mean less food available and it is therefore reasonable to suppose that territorial resources would be strained at this time. At Gungahlin, particularly during the winter of 1957, when the population was densest, some territories were modified presumably in response to food shortage; four alternative modifications were identified:

i. The family group continues to respect (though less rigidly) the same boundaries as previously but may concentrate their foraging over different areas within the territory as the vegetation changes under the influence of severe winter conditions. Limited trespass is common and frequently passes undetected if the "owners" are foraging elsewhere—this is shown in Figure 7.

ii. Where all the boundaries of a territory are not shared with other groups the unrestricted boundary or "neutral margin" (Southern and Morley *loc. cit.*) may be extended. As shown in Figures 6 and 7 this was the general case and group feeding during the late autumn and winter spread quite extensively into the pastures, which by then had "hayed" off and were closely grazed, providing only sparse ground cover. During the growing season these areas are too dense to permit Wrens to forage by hop-search.

iii. Two or more breeding groups may merge and spend the winter as one unit. These off-season groupings behave as any other group with reference to boundaries and intruders, even though they may consist of several adults and their offspring; the relationships are possibly simplified by there rarely being more than one male in full plumage for most of this time. With the onset of spring

these "super-groups" break up into a number of separate and mutually aggressive breeding groups (see Figures 6 and 7, groups C, D, and F of spring 1956 became group C winter 1957 and groups C and D again the following spring).

iv. A group may abandon its territory and follow a nomadic existence until the next breeding season. Once such a break is made, large areas unsuitable for breeding become adequate foraging grounds—in fact "typical wren habitat" is avoided by nomads, or passed through rapidly and inconspicuously. At Gungahlin, the groups that spent the winter away from the study area were those which occupied territory where the vegetation consisted chiefly of deciduous exotic species, providing virtually no shelter for either birds themselves or their insect food. That such territories were obviously sub-optimal was clear when these groups occupied better localities on their return, as these became available through death or other causes (e.g. Figs. 5, 6, and 7, Group M of spring 1956 left for the winter of 1957 but returned in the spring to take up H territory). Two strange groups entered the study area during the winter and established themselves; it therefore seems likely that if these nomadic groups encounter potentially better habitats in the course of their wanderings they settle there.

(d) Song

The Wren has a loud and characteristic song starting with a few short notes and, as the interval between these decreases, building up to a terminal trill of surprising volume for such a small bird (see Fig. 8); each phrase may last up to four seconds. The frequency of singing varies throughout the year and is at a maximum in early spring and minimal during the post-nuptial moult. There is also considerable diurnal variation in song-intensity, starting with a general chorus at dawn lasting for 30-45 mins. around sunrise, which is followed by a quiet period during which

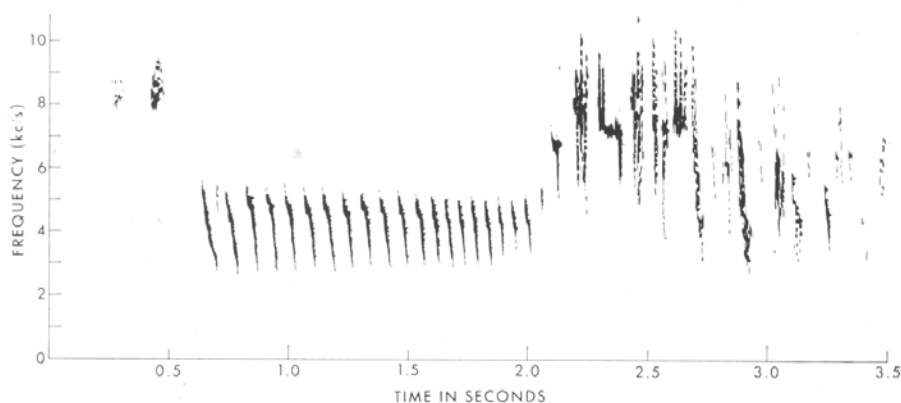


FIG. 8—Sonograph of *Malurus cyaneus* song; adult male No. 001, Lake George, N.S.W.

the first feed of the day is sought. For the rest of the day foraging and singing are interspersed until evening when a second, subsidiary, peak is reached just before going to roost. During hot weather in particular there is usually a song-lull around midday coincident with a general cessation of activity at this time. I once heard a male give his full song close to midnight at full moon (but this is extremely rare).

This song appears to serve two functions, firstly, as a "challenge-and-answer" it is uttered by males on territory and responded to by neighbouring males—this is particularly evident with the dawn chorus and probably reaches a peak of perfection at this time. Although this use of the song may recur throughout the day it is then more commonly heard as a duet between a mated pair and may be of a somewhat abbreviated form—in fact the females seldom, if ever, reach the level of male competence in this field. Young Wrens may be seen quietly calling in an experimental way as early as four weeks after leaving the nest; it is not known when they perfect their efforts but certainly by winter the "duet" referred to above, has been taken up by all the family party.

Song in *M. cyaneus* therefore serves at least three functions, namely, the advertisement and defence of territory, the maintenance of the pair bond, and the cohesion of the family group.

Besides the major song *M. cyaneus* uses a number of calls each of which has a specific purpose or at least is used only in certain circumstances. In order of increasing loudness these are:

Brooding purr. While incubating or brooding the female often emits a very soft and almost continuous call that I find hard to describe better than as a "purr". This call is usually given after the female has been on the nest for some time and, whereas it has every appearance of being a "contentment" utterance, it is quite possible that it denotes that the female is ready to leave the nest to forage. It evokes no response from either mate or other group members, and can only be heard by an observer very close to the nest.

Threat call. During experiments with models (Rowley 1963), the initial challenging song battle was followed by a stationary threat posture during which a low churring call was uttered. Only males were heard to give this and then only during these experiments. When this, as well as the song "battle", had failed, actual physical attack usually followed.

Feeding-young call. This is a louder version of the brooding purr but is given by any member of the group who is near the nest and carrying food for the young. It is usually answered by the chicks if they are more than six days old. It is really a brief reel of song, with no introductory notes. The begging call of the dependent young appears identical to this call.

Flock "pipping" call. This is the Bradleys' terminology which I have adopted as it conveys the essential brevity of the utterance. It is obviously a contact call and is constantly in use by all members of the group as they forage, often out of sight of each other, and presumably serves to cohere the "flock". It is interesting to note that a completely unrelated species, the Red-browed Finch, *Aegintha temporalis*, has an almost identical flocking call which it, too, utters as it forages; this species sometimes feeds through Wren territory and I have twice seen Wrens appear to respond to the flocking call of these Finches, resulting in temporarily mixed feeding flocks.

Alarm call. This is given by any and usually all members of the group when an intruder is located in the territory. It sounds like a staccato version of the flock pipping call uttered at a much greater frequency, and has the effect of gathering the group rapidly to the scene of disturbance when it may be followed or accompanied by either aggressive or distraction displays (Rowley 1962).

(c) Behaviour patterns

Although *M. cyaneus* is not a shy species it is nevertheless a difficult one to study in the field from a behaviour viewpoint because so much of its life is spent in cover. Even if some aspect of behaviour is observed in the open it is very rare for the full sequence to be completed within view. Reasons such as these have led ornithologists to study behaviour under aviary conditions; the following notes are based on field observations and are included not with any sense of finality but because without some discussion of them the paper would be incomplete.

Agonistic. Wrens usually resolve aggressive encounters by song-battles; sometimes a chase may be necessary to evict a persistent trespasser and this generally takes the form of a "supplanting attack"—the pursuer lands in the precise spot vacated by the pursued. If both song and chase fail, the threat posture with or without the threat call may be used. This is a stationary posture directed at the intruder; the body feathers are part-erected, the wings are held slightly out from the sides and both the head and tail are lowered. The churring call is sometimes omitted as the display is often only fragmentary and brief before either chase or combat follows. However, it is used in its entirety in mobbing other species, as occurred when ten Wrens mobbed a Golden Bronze-Cuckoo, *Chalcites plagosus*, and when a female drove off an inquisitive Sparrow, *Passer domesticus*.

The ultimate in agonistic behaviour is reached in physical combat (Bradleys *loc. cit.*). Such fights were only seen in Canberra under the extreme duress of the model experiments, and then only after the model had failed to respond to both song-challenge and threat-posture. That the Sydney Wrens showed a much greater

agonistic intensity probably reflects the higher Wren population density and smaller territories.

Appeasement. The Bradleys have described a form of display and named it "blue-and-black" (*loc. cit.* p. 322); they have observed this pattern from birds on the ground, perched and in flight. In my experience this display is only given by a male who is trespassing in another's territory and is most clearly seen as the bird retreats, vanquished after a song-battle. The flight path is usually direct; the Wren appears to take the shortest route "home" and ignores convenient cover to the side. This often involves a flight that is unusually long for the species. The erectile black feathers of the back are raised throughout and this may account for the appearance of "impeded flight", which is given. Viewed from the rear, which is the aspect presented to the victor, the bird resembles a ball of black fluff, no other colours being visible; the performer is silent though the victor may sing loudly.

The conspicuousness of the display, the slowness of the flight and the fact that convenient cover is ignored suggest that this is not a simple escape reaction and that there is a strong appeasement tendency in the pattern.

Table 1 shows that the display is commonest early in the breeding season—this corresponds with a peak of male trespass and also accounts for the mistaken impression created when people observe this display from unbanded birds and conclude that they are witnessing courtship. This pattern has never been observed from females.

TABLE 1
Monthly incidence of four behaviour patterns in
Malurus cyaneus

Pattern	Numbers of Records	Month											
		J	A	S	O	N	D	J	F	M	A	M	Ju
Aggression	50	2	7	12	11	4	1	2	2	2	1	4	2
Allopreening	32	2	2	10	5	2	—	3	4	3	1	—	—
Appeasement	14	3	2	5	1	—	1	1	—	1	—	—	—
Petal-carrying	7	—	1	1	1	—	—	1	—	1	1	1	—

Distraction Display. When the intruder takes the form of a potential predator the aggressive display may be replaced by distraction display; this occurs particularly when a nest containing young birds is threatened, and commonly takes the form of a "rodent-run", directed away from the predator and the nest. The performing bird fluffs up its feathers, holds its wings slightly out from the body, lowers its tail, and scuttles along the ground at a run as opposed to its more usual hop. This is an unusual pattern of behaviour for a passerine and has been fully described and illustrated elsewhere (Rowley 1962).

Another display that seems to belong here has only been seen twice and because of its effectiveness details are rather scanty. As will be seen later in the paper, most Wren nests are below four feet in height, but at Gungahlin a number of nests were built at three and four times this height and when searching for them on two occasions the brooding female plummeted to the ground and scuttled off into cover. In both cases the nests were directly above the spot where the female had hit the ground; this, together with the complete silence of the performance, although I was within two feet of the falling bird, and the loudness of the thump with which the ground was struck, suggests that the action was a deliberate and unimpeded drop—I have named this pattern “the falling stone” display. As the recovery from the crash is instantaneous there can be no question of the display being cataleptic in origin. Armstrong (1947) quotes Jourdain (1936-7) as describing a similar type of display with hawks, eagles, and falcons; Van Someren (1944) records a similar performance from several African tree-nesters, and Took (1941) has observed it with a female Nuthatch, *Sitta europaea*. The last two authors described the falling stone display as being immediately followed by another distraction display pattern, Van Someren—injury feigning, and Took—rodent-run type; with *M. cyaneus* it was followed by a brief rodent-run display into thick cover, where the performance ended, and was not repeated as is customary when the latter display is given on its own.

Allopreening normally occurs during the warmer part of the day and is often preceded by a spell of idle sunbathing. The birds are generally sitting on a horizontal branch or fence wire when one of their number begins to probe its plumage. This behaviour seems to be very infectious and soon the whole group will either be preening themselves or their neighbours. The bird receiving attention remains motionless, perhaps lowering its head to present the more inaccessible parts of the nape. Throughout the performance excitement mounts rapidly from the passive sun-bathing to a climax when the birds are constantly changing position by sideways shuffles, or by a lateral leap-frog hop. As the intensity increases so the duration of each preening session shortens from about half-a-minute until it becomes little more than a token peck before positions are changed. Wrens thus engaged usually crouch low with their abdomens touching the supporting perch and their legs obscured from view.

Although the entire group may engage in allopreening simultaneously it is much more common to see only two birds thus engaged. Table 1 shows that there is a marked peak of occurrence in spring and it is not surprising that several sessions have terminated in copulation. However, allopreening cannot be regarded solely as courtship procedure as it occurs throughout the year, is

both intra- as well as inter-sexual, and involves both immature and mature individuals; furthermore it by no means invariably precedes copulation.

Courtship behaviour in Wrens tends to be both unspectacular and brief, which reflects the "contact" nature of the species (Crook 1961), and the consequent absence of any need for elaborate displays to reduce the individual distance to a level where coition can be achieved (Marler 1956). This may seem very much at variance with previous published accounts of the species in which obviously agonistic and appeasement elements of behaviour have been broadly classed as "courtship".

As mentioned above, allopreening sometimes culminates in copulation; this may be regarded as the simplest form of courtship. Sometimes it takes the form of a quite extensive follow-my-leader chase, frequently surprisingly high up in mature trees, where the whole process is easily followed. Most often courtship, and presumably consummation, take place in dense cover and only portions of the performance are visible, although the excited vocal commentary is clearly audible. This is emphasised by the fact that in the five years of the study copulation was only observed, with certainty, six times and unconsummated courtship only a further thirteen times.

Petal-carrying has been reported in the literature several times and discussed thoroughly by Hindwood (1948, 1951). It appears that *M. cyaneus* males have a marked preference for yellow blossoms and in the course of this study only yellow items were seen to be carried—yellow petals on six occasions and a yellow leaf once; the former were twice identified as Catsear, *Hypochaeris radicata*; the leaf was from an autumn-coloured elm, *Ulmus* sp. Table 1 shows that each of the seven occurrences happened in different months. Once the male appeared to present the petal to his mate but neither then nor at any other time did the "display" evoke any noticeable response from another member of the species, nor was it accompanied by any display or noise from the bird carrying the petal.

This display, which is not restricted to yellow coloured petals (see Hindwood *loc. cit.*), occurs in other members of the genus too: *M. splendens* (Loaring 1948) and *M. melanocephalus* (Jack 1949). Most of the observations refer to periods of some minutes but none of the descriptions, nor my own records, point to any clear tendency behind this behaviour, although the literature broadly groups it as "courtship". The irregularity and rarity of its occurrence and the conspicuous lack of response from other group members make it unlikely that it now serves any courtship function—courtship in birds is usually of a stereotyped and characteristic pattern within the species. The biological goal of courtship

is copulation and for multibrood species this must occur frequently; if petal-carrying were a part of the normal display it could hardly be missed and would be seen very much more often than it is.

Roosting. Following the evening chorus of song, described above, the whole group of wrens moves towards its customary roosting site, usually in a dense bush or tree, and, to the accompaniment of a lot of soft calling, they take up their positions for the night side by side on a horizontal branch. Warham (1957) has described this process for *M. splendens* and his paper includes a flash-light photograph of six birds roosting close together, which illustrates the posture very clearly.

This behaviour is in striking contrast to the "true wrens" (Troglodytidae) of the Americas, Europe, and Asia, many of which roost communally at night, but which customarily use a roosting nest which may be built for the purpose, a relic of the breeding season, or that of another species adapted for the purpose (Armstrong 1955; Skutch 1954; Anderson & Anderson 1957).

2. Breeding Biology

(a) *Breeding season*

At Lakemba, N.S.W., Gilbert (1938) has recorded *Malurus cyaneus* nesting in every month of the year except May; however, no eggs laid before August or after February were found in Canberra during the course of the present study (see Fig. 9).

Table 2 shows the dates when the earliest and last eggs were laid during six seasons. Figure 10 shows the monthly rainfall as recorded at the CSIRO Dickson Experimental Station, less than two miles from Gungahlin, during this period; 1956, 1958 and 1959 were normal "good years" by farming standards with ample spring

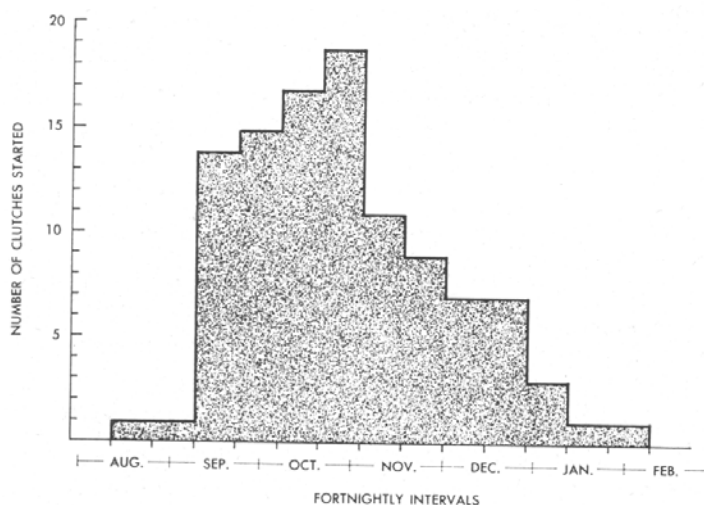


FIG. 9—Distribution of egg-laying by *Malurus cyaneus* at Canberra A.C.T.

TABLE 2
Duration of breeding season of *Malurus cyaneus* at Canberra

Year	First Egg laid	Last Egg laid
1956	6.ix.56	3.i.57
1957*	19.x.57	10.i.58
1958	12.ix.58	4.i.59
1959	18.ix.59	2.i.60
1960	17.x.60	24.i.61
1961	14.viii.61	4.ii.62

* Drought year—no eggs at all laid in November or December.

growth haying off in December and January as the temperatures rose; egg-laying began in September and was virtually completed by the end of December. The year 1957 was very dry and the Southern Tablelands of N.S.W. which, climatically, includes Canberra, were proclaimed "drought areas"; the first Wren clutch was not laid until October and none was laid in November or December, but heavy

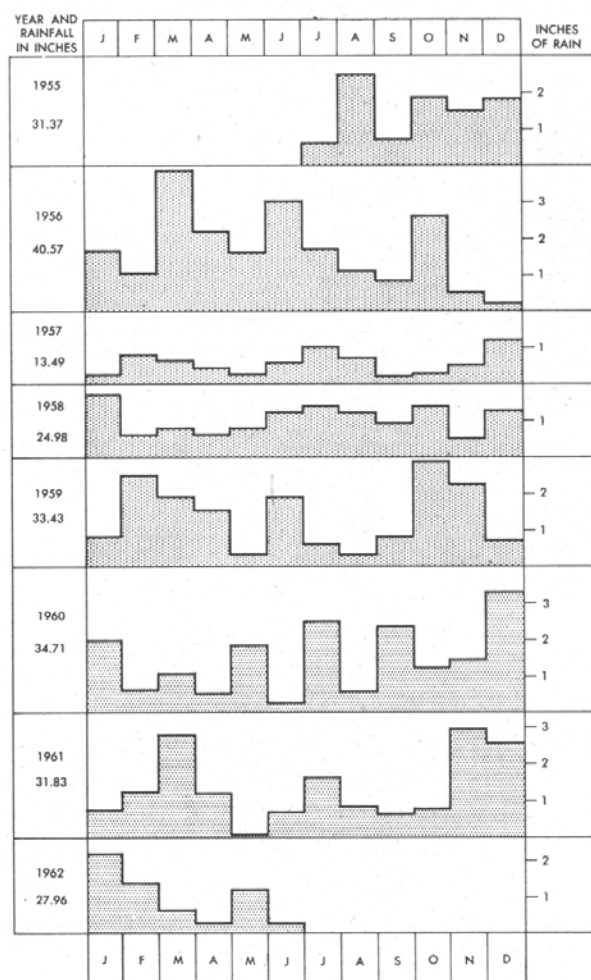


FIG. 10—Monthly rainfall recorded at CSIRO Dickson Experimental Station, 2 miles from the study area.

rains after Christmas and early in the New Year stimulated two females to build again and to lay. In 1960 nest building began early in September, as usual, but a fortnight of cold weather delayed the laying of the first egg until October. In both 1960 and 1961, December rainfall was well above average ($> 4''$ av. = $2''$) and the Wrens continued to lay for a month longer than in the three "average" years. A very early and mild spring in 1961 also stimulated the earliest clutches recorded in Canberra (August) and together with the wet summer permitted a six-month breeding season.

Whether photoperiodicity is important in determining the breeding season of *M. cyaneus* or not, the above evidence suggests that temperature and rainfall either directly or via the food supply play an important part. This would account for the almost year-round breeding of the species at Lakemba, with its milder temperatures and summer rainfall.



FIG. 11—Early stage of nest-building, *Malurus cyaneus*; note framework of egg sacs and rootlets built into the base of a grass tussock, *Phalaris tuberosa*.

Photo by Ederic Slater

(b) Nest-building

Nest-building is usually done entirely by the female and is completed in 3-4 days. An initial framework of spider's web and egg sacs is fastened on the site (Fig. 11) and into this coarse grass (e.g. *Phalaris*, *Bromus* spp.) and fine roots or twigs are woven, followed by finer grasses (e.g. *Briza* sp.); finally the nest is lined with softer materials such as wool, feathers, animal hair or string,

depending on what is locally available. It is usually domed and has an entrance two-thirds of the way up one side, which may have a slight "porch" over it; two out of more than 100 nests examined lacked the domed roof and were open cup nests.

The nest site is usually in dense cover, but so situated that direct approach and exit by the bird are possible—in other words it is usually on the fringe of the supporting shrub, tree, or grass clump. Gungahlin provides a very wide choice of cover for Wrens (see Table 3) and in consequence height, substrate, and aspect vary considerably, not only between birds but between successive nests of the same pair or female.

TABLE 3
Location of *M. cyaneus* nests—Gungahlin 1956-60

Substrate chosen for nest	Number per Height Group						Total
	< 12"	12"	24"	36"	48"	> 6 ft.	
		24"	36"	48"	72"		
1. Pencil pine, <i>Cupressus sempervirens</i>	—	—	—	—	—	15	15
2. Privet, <i>Ligustrum vulgare</i>	1	—	2	2	2	1	8
3. Elm, <i>Ulmus</i> sp.	3	2	2	1	—	—	8
4. Annual grasses/herbs	8	—	—	—	—	—	8
5. Pampas-grass, <i>Cortaderia</i> sp.	—	—	4	3	—	—	7
6. Rose, or Bramble, <i>Rosaceae</i>	—	1	4	2	—	—	7
7. Hawthorn, <i>Crataegus acerifolia</i>	—	—	7	—	—	—	7
8. Garden rubbish	3	2	—	—	—	—	5
9. Juniper, <i>Juniper chinensis</i>	—	—	—	1	2	1	4
10. Laurestinus, <i>Viburnum tinus</i>	—	—	1	1	1	—	3
11. Perennial grasses	1	1	1	—	—	—	3
12. Firethorn, <i>Pyracantha angustifolia</i>	—	1	1	—	—	—	2
13. Jasmine, <i>Jasminum primulinum</i>	2	—	—	—	—	—	2
14. <i>Veronica</i> sp.	1	—	—	—	—	—	1
15. Laurel, <i>Laurus</i> sp.	1	—	—	—	—	—	1
Totals per height group	20	7	22	10	5	17	81

Height was largely determined by the nature of the shrub, tree, or plant built in. The selection of a particular substrate was influenced by the season and possibly other factors. Early in spring (September) little growth has taken place and perennial grass tussocks and piles of garden trimmings are suitable sites; later, as the flush of growth accelerates, such sites become hard of access and the general level of nests rises. The 15 high nests were nearly all in pencil pines (see Table 3) and over 10 ft. high—the record being 21 ft. These trees provide a vast choice of sites, which are very hard to find, but the Wrens encounter considerable opposition from Goldfinches, *Carduelis carduelis*, and Sparrows in such situations, both of which compete for sites and may rob the much smaller Wrens of nest material.

The aspect of 76 nests at Gungahlin is plotted in Figure 12, which shows little constancy in this regard. That one third of the nests faced north or north-west, from which direction most of the rough weather in Canberra comes, might suggest that in a covered nest adequate light is more important than protection from the elements, but nearly one-third of all nests were so placed (facing south-east to south-west) that they would receive no direct sunlight at all.

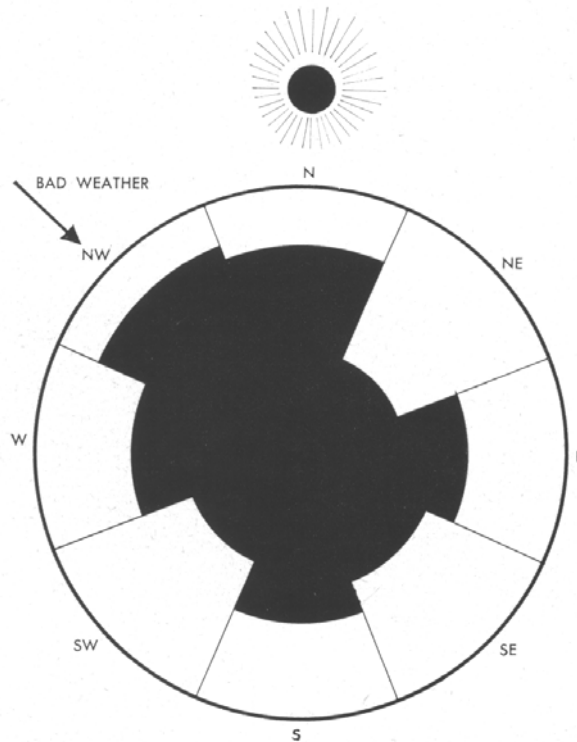


FIG. 12—The aspect of 76 *Malurus cyaneus* nests built at Gungahlin, A.C.T.

Individual females showed little constancy in nest selection. Female 037 throws some light on the subject. She bred for five successive seasons and mated with five different cock birds. Table 4 shows the great variation in height, aspect, and substrate of her 13 nests. The point of interest, however, is the consistency shown, at least as regards substrate, while mated to a particular cock, e.g. to 003 and 024 in 1958 and to 706 in 1960. Some of the changes in mate involved change of territory too, and therefore, of necessity, a change in substrate availability. In 1958 her mate died half-way through the season and the subsidiary male (024) took over; the territory remained the same throughout, but the height, substrate, and aspect of her nests altered markedly. This suggests that although cocks were never seen to participate in nest-building they may influence site-selection. De Warren (1926) describes a cock-bird building two nests. The first was refused by the female but she

accepted and used the second. Since the literature contains no other references to such male behaviour it must be regarded as abnormal, but nevertheless the record serves to illustrate the male's capacity in this regard.

Although to human eyes Gungahlin appears to offer an enormous range of nest sites for Wrens, some must appear more suitable than others to the birds. A possible example of this occurred with a nest built in a juniper bush. All nests were labelled with small metal tags in 1956 and when, two years later, a tagged nest was found it was ignored as a relic. As no other was found, however, this "relic" was inspected and found to be a completely new nest, containing fresh eggs. The second nest was constructed by a pair that had been in no way connected with the birds that first chose the site.

TABLE 4

The position of 13 nests built by female 037 over five seasons

Year	Mate	Height	Aspect	Substrate*
1956	023	30", 42"	NW, N	12, 7
1957	024	Ground level	NW	4
1958	003	18", 32"	NW, E	6, 6
	024	60", 96"	SW, SW	9, 9
1959	825	9", 18"	W, SW	15, 8
	706	?	?	1
1960	706	84", 144", 120"	NE, S, SW	1, 1, 1

* Numbers refer to vegetation listed in Table 3.

Two instances have been recorded of Blue Wrens using the nests of other species; Favaloro (1932) describes the usurping of a White-browed Scrub-Wren's nest, *Sericornis frontalis*, and McGarvie (1957) observed Wrens using a freshly built Goldfinch nest to which they added a roof and lined the cavity with feathers.

The location of Wren's nests is therefore largely determined by the substrate available and, although he does not normally build, the cock may influence the selection.

(c) *Egg-laying*

From five days to a month may elapse after the nest is completed before the first egg is laid. This interval is influenced by weather (1960, cold spell in September mentioned above) and the stages of the breeding cycle; with the season's first nests bad weather may postpone egg-laying for up to a month after the nest is completed. With rebuilds following failure, the delay is minimal as there are no dependent young to be tended.

The eggs are laid between dawn and 0900 hrs, usually on successive days. Some hens laying four-egg clutches lay the fourth

egg on the fifth morning. The shells of the eggs are very thin and fragile and are coloured pinkish-white, spotted with reddish-brown markings, especially towards the blunt end. The average dimensions of 41 eggs from Canberra were 16.09×12.14 mm, the largest measuring 18.2×13.4 mm and the smallest 15.1×11.1 mm. Clutch size varied from 3 to 4 in the ratio 2: 1, the mean for 67 nests being 3.37 eggs. There is a tendency for larger clutches to occur later in the season, and some females lay more four-egg clutches than others (see Table 5). Table 6 shows that a known-age female (689) laid four-egg clutches only in her second season; female 037 is presumed to have been in her first season in 1956, and

TABLE 5

Showing variation in clutch size as season progresses; Canberra 1956-61

Clutch Size*	Fortnightly Periods									Total
	9.ix- 22.ix	23.ix- 6.x	7.x- 20.x	21.x- 3.xi	4.xi- 17.xi	18.xi- 1.xii	2.xii- 15.xii	16.xii- 29.xii	30.xii- 12.i	
3 egg	8	9	10	9	2	1	1	1	1	42
4 egg	2	2	4	3	3	4	5	1	1	25

* Only those nests where at least two visits confirmed that the clutch was complete are included.

TABLE 6

Successive clutch sizes of individual females at Gungahlin

Female No.	Numbers of Eggs laid per Clutch				
	1956	1957*	1958	1959	1960
037	3, 3	3	3, 4, 4, ?	3, 3, ?	3, 3
030	Failed to lay	4, 4, 3*	3, 4	4, 4	
689	Hatched	3	3, 4, 4	?, ← dead →	

* 1957 was a drought year and nesting was poor. 030 successfully renested after the drought broke in January, but with only a 3-egg clutch.

laid four-egg clutches only in her third year, reverting to three-egg clutches in her fourth and fifth, so that ovulation in the female may reach a peak and then decline in some birds, but not in all (cf. 030).

(d) Parasitism

White (1914) recorded *M. cyaneus* acting as foster-parents to the following: Pallid Cuckoo, *Cuculus pallidus*, Fan-tailed Cuckoo, *Cacomantis pyrrhophanus*, Square-tailed Cuckoo, *Cacomantis variolosus*, Horsfield Bronze-Cuckoo, *Chalcites basalis*, and Gol-

den Bronze-Cuckoo, *Chalcites plagosus*. Hill (1906) recorded parasitism by the Black-eared Cuckoo, *Misocalius osculans*. Around Canberra *Chalcites plagosus* most frequently parasitizes Wrens' nests.

The Blue Wren is not readily "fooled" by cuckoos, and it is quite common to find the "alien" egg buried in the nest lining and a complete Wren clutch laid on top—the lining between providing sufficient insulation to prevent the cuckoo's egg being incubated. An extreme example of this is recorded by Parsons (1918), who describes a Wren's nest with no less than three *C. basalis* eggs at different levels. On top and separate from these was a normal clutch of three *M. cyaneus* eggs—by this time the egg cavity was half full of feathers.

Apparently this covering behaviour happens when the cuckoo lays before the Wren—in only one case (McGillp 1929) have Wrens' eggs been found buried also. When the cuckoo lays into a partly or wholly completed Wren clutch, even if it removes one of the rightful eggs (Ross 1919), the Wrens may react by deserting.

During the past five years some 116 nests have been observed (including 35 outside the study area). Buried cuckoo eggs were located on two occasions—both nests were deserted, and twice Golden Bronze-Cuckoos were fledged. This gives a parasitism rate of 3.4%.

Mellor (1917) has described the hatching of a parasitized clutch; Barrett (1905, 1906) described the ejection of young Wrens from the nest by a young *C. basalis*, and photographed the process.

(e) *Incubation*

Brooding starts with the laying of the last egg in the clutch, though occasionally the female may roost in the nest before that. The eggs usually hatch within a few hours of each other 13-15 days later. Only the female sits, the male "keeping guard" in the neighbourhood and periodically calling the female off the nest to feed, when he accompanies her. Rarely the male feeds the female at the nest, but this is unusual. Later in the cycle the male may pass food to the brooding female, who, in turn, passes the food on to the nestlings below or eats it herself. Warham (1958) describes such a case and erroneously calls it "courtship" feeding.

Air temperature appears to affect the duration of incubation. From the limited Canberra data available, six first nests took 14 days each to hatch, whereas three later clutches required only 13 days. From Sydney, with its milder climate, Pate and Courtice have recorded incubation periods of 13 days (11 times), 14 days (7 times), and 15 days (once). Dove (1910) in Tasmania recorded 15 and 14-day incubation periods; Cutcher (1944) recorded 14 and 12-day, Hindwood (1951) a 13-day, and the Bradleys (1958)

PLATE 14



Both male and female *Malurus cyaneus* attend the nestlings.

Photos by Roy Cooper

two of 14-day and one of 13-day incubation period. The Bradleys (personal communication) also recorded one incubation period of 18 days ending in a successful complete hatch, which is quite exceptional, as is Mrs Cutcher's 12-day one.

(f) *Nestling development*

The freshly-hatched young are blind, naked, pink-coloured, and silent. By the second day the colour has turned bluish as the feather tracts develop, and a weak call can be heard. On the fifth day the eyes begin to open, and thereafter the gaping response is elicited only by the parents and not, as previously, by any casual stimulus that vibrates the nest. Feathering develops rapidly and the nestlings are completely covered by the ninth day.

Premature departure of nestlings that have been over-disturbed in the nest complicates measurement of the duration of the nestling stage; one cannot be sure of the degree of disturbance that accompanied published records. Dove, Cutcher, Hindwood, and the Bradleys (*loc. cit.*) give 10 and 11, 10-11, 11½, 2 × 13 and 12-day periods respectively; my own observations, where I banded the nestlings early and was sure that fledging was natural, gave 12 days three times, 13 days twice, and 14 days once. The nestling period is therefore from 10-14 days depending on such factors as weather, reflected in the parents' behaviour, and the availability of food, the number of nestlings in the brood and disturbance, human and otherwise.

(g) *Care of nestlings*

All members of the family group which have reached independence feed the nestlings; from my records the youngest juvenile seen helping at the nest was 58 days old. Six periods of intensive observation at three different nests showed so much variation between individual pairs, members of pairs, various-aged nestlings, the numbers of nestlings, and effects of different weather conditions, that this time-consuming aspect of the study could not be continued. Table 7 illustrates that variation: at the first nest the male never made more than a quarter of the feeding visits; at the next nest, at the same stage, the male made at least two-fifths of the visits; at the third nest, where a supernumerary male also attended, the combined male efforts outnumbered the female efforts. It is probably a significant feature of this individual variation that the first pair reared only two out of three nestlings hatched, whereas the second and third reared three and four (the complete clutch) respectively.

Observations on the first nest showed the rate of feeding increasing rapidly as the nestlings grew—from 12·6 feeds per hour at six days (3 nestlings) to 22·4 feeds per hour at 12 days (two nestlings).

TABLE 7
Feeding of nestlings by *M. cyaneus*—Gungahlin, 1956

Date	Nestlings		Duration of Observation		Number of Feeds made				Rate	
	No. present	Age in Days	Time	Mins.	♀	♂	(♂)*	Total	Feeds /Hr.	
27.x.56	†	3	5	1522-1700	098	17	1	--	18	11.0
28.x.56		3	6	1023-1440	257	41	13	--	54	12.6
3.xi.56		2	12	1027-1442	255	70	25	--	95	22.4
3.xi.56	†	3	5	1034-1433	239	24	22	--	46	11.5
4.xi.56		3	6	0952-1101	069	18	11	--	29	25.2
9.xii.56		4	9	1005-1405	240	16	10	14	40	10.0

* Supernumerary male.

† Braces link observations made at the same nest.

On 3.xi.56 two observers maintained separate watches.

The effect of weather is shown in the records of the second nest, since November 3 was cold with hail showers and the young nestlings were brooded by the female for much of the time at the expense of her foraging; the next day, which was warmer and sunny, saw the feeding rate rise from 11.5 to 25.2 feeds per hour. The unseasonable weather on November 3 did not affect the feeding rate at the first nest, as the young were well feathered and presumably capable of independent temperature regulation.

The third nest is not typical, since the observations were made very close to the nest from a hide erected for cinematography, and the adults would have been wary of feeding their young. Nevertheless it does show the distribution of labour between group members and the great value of the supernumerary, assuming that the shyness affected all individuals equally.

The Bradleys (*loc. cit.*) give rates of 18.5 feeds/hr by a female assisted by three males and 24 feeds/hr by a single pair; Rowlands (1960) gives 29 feeds/hr by three birds. Although these figures were obtained from relatively short periods of observation on different days, they serve to emphasize the extreme variability in attentive behaviour between different individuals.

Not only will the female brood young nestlings by day during adverse weather, but she frequently broods them by night right up to fledging.

(h) *Fledging*

Fledging takes place when the young are fully feathered except for their tails, which are only 10 mm long. The margins of their bills are still distinctively light-coloured, which, in the nest, probably helps the parents to feed the nestlings in poor light. All the offspring usually fledge on the same day around noon and this is

followed by a cryptic stage lasting about a week, during which the young keep closely to the cover of shrubs and are fed there by the parents. While cryptic their tails are still undeveloped and flight, though possible, is erratic and slow. After this they venture in the open and are capable of flying to cover rapidly.

Altogether the fledglings are, at least in part, dependent on the parents for food over about four to five weeks. The Bradleys (*loc. cit.*) record young still being fed 20, 26, and 32 days after leaving the nest (the figures refer to different broods)—I have several records of similar periods; the longest dependency shown was 40 days. The longer periods are probably unimportant so far as the fledglings' survival is concerned and appear to be frequently prompted by the sight of parents carrying food to a subsequent brood; they are more in the nature of fortuitous ambush by the young than intentional attendance by parents. After this they remain in the group with similar standing to that of supernumerary males, and help feed and care for later-fledged offspring of the group.

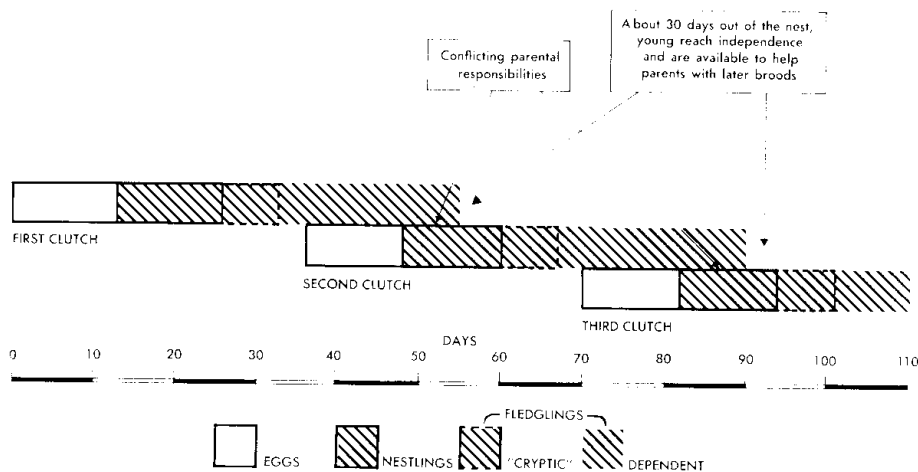


FIG. 13—The overlap of parental responsibility due to successive nestings of a multi-brooded species—*Malurus cyaneus*.

(i) *Re-nesting*

Wrens are a multi-brooded species whose fecundity seems to be restricted only by the limitations of the season; most pairs nest at least twice and some rear three broods in the six-month "season". Immediately after the young fledge the female still helps to feed them, but within a week she is building again and she is soon fully occupied incubating the next clutch of eggs. The main responsibility for the fledged young therefore falls on the male and it is here that the supernumerary males serve a useful purpose. When the next clutch hatches it is quite possible for the earlier young to be still dependent on parental feeding (see Fig. 13); two alternatives appear to exist—either the female must feed the nestlings unassisted (which is possible, as it happened at one nest where the male

deserted during incubation), or the older fledglings will compete with the nestlings for male attention: not a very safe procedure near a nestful of vulnerable chicks. Where there is a supernumerary male in the group, however, he frequently takes sole charge of the fledglings, leaving the true parents unhindered to cope with the nestlings; the supernumerary usually keeps the fledglings well away from the nest.

In practice such an ideal nesting cycle as shown in Figure 13 rarely happens. It is rare for three clutches to be reared without any mishap, so that quite often more or less than this total of nests may be built and clutches laid. The maximum recorded at Gungahlin was in 1956, when one female built six nests and laid four complete clutches (16 eggs), none of which hatched. De Warren (*loc. cit.*) records a pair building five nests in a season; Littlejohns and Lawrence (1919) and Cutcher (*loc. cit.*) have recorded four nests, as I have twice at Canberra.

Parents seem unable to identify their own offspring in the early days after fledging, as was shown when two neighbouring nests hatched simultaneously and the cryptic young from both became completely and hopelessly mixed up. Territorial barriers disintegrated and all parents (plus a previously "bachelor" male from a third territory) fed the fledglings indiscriminately. After about a week one pair withdrew to their former territory and re-nested, leaving the other pair plus the bachelor to care for all six fledglings which they did successfully. Such a coincidence of timing rarely occurs and the formation of such a crèche was not seen again.

At Gungahlin no Wren ever used the same nest twice, although the Bradleys (*in litt.*) recorded such an occurrence once in Sydney, as also did Hyem (1936). The shell of the new nest is usually built from fresh materials, but frequently the lining is retrieved from the previous nest and used again.

(j) Predation

Evidence on this subject is rarely obtained for any bird so small as a Wren because few traces remain after the act. At the egg stage, shells which appeared to have been sucked, were sometimes found below the nest—probably the work of rodents; sometimes the nest was scarcely disarranged at all, suggesting a small culprit, but at others the whole structure was wrecked in the process of robbing and the predator had obviously had difficulty in gaining entrance. Warham (1958) described the taking of nestlings from a nest of *M. cyaneus* by a brown snake, *Demansia textilis*, and illustrates the incident (see also Chisholm 1928). Snakes of this species are quite common at Gungahlin in some seasons and although I have no evidence of predation by them, one was seen to be mobbed by Wrens on one occasion (Rowley 1962).

There is little doubt that the feral cat was by far the most significant predator on Wrens at Gungahlin. One winter a cat accounted for no less than five successive males in one group before it was shot.

During some experiments with a model Wren a Grey Shrike-Thrush, *Colluricincla harmonica*, was seen to attack the stuffed male. Tilt (1962) has reported a similar occurrence in the field. Campbell (1927) records a Kookaburra, *Dacelo gigas*, raiding a Wren's nest, and Legge (1901) found a Wren . . . "spitted on a large sweetbriar thorn in a hedge close to a grove of trees frequented by the Butcher bird". Both Kershaw (1932) and McKeown (1939) describe Wrens enmeshed in spider webs, but this is more likely an accident than deliberate predation.

(k) *Annual increment*

The breeding success over four years is shown in Table 8. Of the 240 eggs laid, for which full data are available, only two-thirds hatched. Most of the nestlings survived (81.5 %) but little more than half of these reached independence and the numbers were further halved in the ensuing six months.

TABLE 8
Showing breeding success over four seasons

Year	Eggs laid	Eggs hatched	Young fledged	Young independent	Young alive at 1: vii next
1956	117	64	52	28	10
1957	31	22	18	14	8
1958	45	42	38	16	6
1959	47	30	21	11	5
Total	240	158	129	69	29

Losses at the egg stage are relatively unimportant in a multi-brooded species such as *M. cyaneus*, because rebuilding quickly follows and little time is lost. However, it is interesting that in the first year, when the population density was greatest, these losses were very high, amounting to nearly half the eggs laid; this probably reflects the use of sub-optimal nesting habitat—a fact further emphasised in the following years, when there was less crowding and these areas were avoided.

The most vulnerable stage for young Wrens is the period immediately after leaving the nest when they are still dependent on the adults for food and before their powers of flight are properly developed. This is particularly so if their demands overlap with

those of the next brood. In 1957, a drought year, when few birds re-nested, the survival of young out of the nest was much higher.

The number of juveniles still in the population at July 1 each year, gives a measure of the replacements available for the coming breeding season (see Table 8).

3. Population Dynamics

(a) *Annual fluctuations*

As with most natural communities, the Wren population at Gungahlin varied in size over the years of the study. Table 9 shows that there was an initial decline in numbers and at first glance it is tempting to blame the methods of study but no evidence exists to show that banding contributed to mortality significantly, nor did the species show any tendency to desert after their nests had been found. The rapidly growing city of Canberra nearby may have adversely influenced the interchange of birds between local populations since the process of clearing land for the erection of new houses creates, at least temporarily, ecological deserts as far as Wrens are concerned.

TABLE 9

Population structure of *M. cyaneus* over five years at Gungahlin

Year	1956	1957	1958	1959	1960
Number of groups	15	9	8	7	8
„ „ breeding groups	15	7	6	7	8
„ „ bachelor groups	—	2	2	—	—
„ „ simple pairs	11	4	1	7	6
„ „ complex pairs*	4	3	5	—	2
„ „ adult birds	36	20	19	14	18

* Groups with more than one adult male.

The spring and summer of 1955-56 were very wet (see Fig. 10) and suitable for breeding; the winter which followed was relatively mild so that survival of young and the persistence of the groups were probably both exceptionally good. Whatever the cause of the decline that followed, a significant point appears to be a sudden shortage of females; the sex ratio fell from M20 : F16 in the first year, to M13 : F7 in the second, to M13 : F6 in the third and for the next two years it was 50 : 50. All this time first-year females were leaving the study area at the onset of breeding, although 'supernumerary' or 'bachelor' males were available locally for pairing. This suggests that in most years seven breeding groups was the capacity of the area, but that under certain favourable conditions this number may be doubled; observation suggests that under winter conditions of reduced cover and, possibly, lowered food availability this maximum (15 groups) breeding population

could not be maintained all the year round. This aspect has been discussed earlier under 'territory'.

(b) *Mortality*

Only one instance of sickness was observed during the course of the study and this bird (female 675) showed symptoms of pneumonia on post-mortem examination; this was unlikely to have been the cause of death which was probably an infection contracted during a period of weakness due to some other, unknown cause. All other known causes of death were due either to predation by cats or accidents: collision with car, twice; collision with window, once; leg caught in wire netting once, and trap misadventure once. The known cat predations all took place in one winter and affected only one territory (A/59*)—removal of the cat ended the killings so that it appears that a 'rogue' individual was responsible, one that became an expert killer of Wrens; it is interesting to note that the female of this group survived the five slaughtered males. This apparent mortality bias towards accident is understandable in a small, mainly terrestrial, species, surrounded by many potential predators (mammalian, avian, and reptilian), so that the weakened state induced by any sickness renders the individual a susceptible and rapidly accepted prey.

TABLE 10
Longevity of *M. cyaneus* at Gungahlin

No. of Birds which were at least One Year Old on:	No. of these Birds reaching				
	2 yrs.	3 yrs.	4 yrs.	5 yrs.	6 yrs.
1.iii.56 6	2	1	—	—	—
1.iii.57 17	11	6	4	3	1
1.iii.58 6	5	—	—	—	—
1.iii.59 5	4	4	4	—	—
1.iii.60 1	1	1	—	—	—
Total 35	23	12	8	3	1
Males 20	15	8	4	1	—
Females 15	8	4	4	2	1

(c) *Longevity*

Table 10 shows that once the hazards of immaturity, inexperience, and dispersal are overcome the expectation of life for an adult Wren is surprisingly long; three birds lived for at least five years. Lack (1954), considering a number of passerine species, suggests a life expectancy figure of between 1.9 and 0.9 years. Dixon for the Plain Titmouse, *Parus inornatus*, and Erickson for the Wren-Tit, *Chamaea fasciata*, both calculated much higher figures—both these species are resident territorial species, as is

* A/59 refers to the appendix—territory "A", during season '59.

M. cyaneus, for whom the respective calculations are that 66% of the adult breeding birds persist to breed the next year; from Lack's formula ($2 - m/2m$, where m represents the percentage (as a fraction) annual mortality) this gives an average expectation of further life of 2.5 years, a figure that agrees well with that for the other two species quoted above.

4. Social Organization

(a) *Dispersal of young*

As has been pointed out earlier Wrens are unusual in that the young of the year persist in the family group right through the winter and as a result a certain amount of reorganization is necessary before the next breeding season starts.

It has been shown from experiments with models (Rowley 1963) that during the winter only the dominant male bird is aggressive towards birds trespassing within the group territory. Dominant cocks also attain their full breeding plumage some months before the supernumeraries or first-year males, as mentioned above under "plumage". It is not surprising therefore to find that these males become sexually awake before any others in the group; unfortunately there is no histological evidence to support this theory, but it was frequently observed that early in August these older males indulged in an unusual amount of trespassing and were often seen to be paying attention to the females of other, established, groups. These sorties were terminated abruptly by the arrival of the resident cock—the intruder usually retired, giving the 'blue-and-black' display as he left. The impression given was that the resident females were unreceptive at this stage for no consummated matings were ever witnessed as early as this. The conclusions drawn from these observations were fully borne out when, on two occasions, a female maintaining territory on her own and advertising the fact loudly by song, not only attracted established males from other groups but, in both cases, managed to break the pair-bond and seduce the male from returning to its old group (M077, E/57 and M706, A/59).

Whether this early wandering of the males stimulates it or not, towards the end of August the females become mutually intolerant while the young males, still in eclipse plumage, cause no friction. In consequence the dispersal of young at this stage shows marked sexual differentiation and only twice during the study was more than one hen bird present by the time nest building had started. This differential dispersal is shown in Table 11 which shows that 70% of the young males present on the first of July each year (mid-winter) were still present in the parental group by mid-spring (1.x), whereas only 27% of the females of the same age group remained anywhere in the study area.

TABLE 11

Differential dispersal of young Wrens from Gungahlin over five years

Year	Number of Males		Number of Females	
	At 1.vii	At 1.x	At 1.vii	At 1.x
1957	4	4	6	3
1958	5	2	3	0
1959	4	1	2	1
1960	3	3	2	0
1961	4	4	2	0
Total	20	14	15	4

Dispersal outwards from a focus is difficult to trace since the area to be searched increases rapidly (as the squares of the radii) and soon becomes unmanageable, especially where, as at Gungahlin, a mile-wide buffer zone of unsuitable habitat meant that dispersing birds must travel at least this distance. However, two fortunate records show that dispersal may be quite widespread; in 1956 a female (017) was banded at Gungahlin and constituted one of the two occasions when more than one female attended at the same nest; she left, however, before the second nest was constructed and was not seen again until the next year when she was retrapped nesting five miles away. In 1958 two yearlings were seen to follow much the same route as the above female and a week later were established in a garden about two miles from Gungahlin. Only one of the four Gungahlin-hatched females who remained in the study area occupied a vacancy in a territory other than the parental one—F674 moved from N to O, a distance of about half a mile. The other three filled vacancies caused by the disappearance of the hen (675 and 689) or stayed as an extra (835).

During 1957 and 1958 there were two bachelor territories each maintained by a male bird on its own and yet five young females left the study area without settling with these unrelated and loudly advertising cock-birds. Of nine unbanded birds that entered the study area from outside during 1956-60, four of these were lone females while the others arrived as preformed groups (1M and 2F; 1M and 1F). This suggests that not only are young females more liable to disperse than males of the same age, but that once on the move they travel some distance rather than settle locally, even if vacancies are available.

Males, on the other hand, show very much less inclination to disperse and are frequently allowed to stay in the parental group and this appears to be the commonest way in which supernumerary associations (more than one male attending at a nest) arise. Dur-

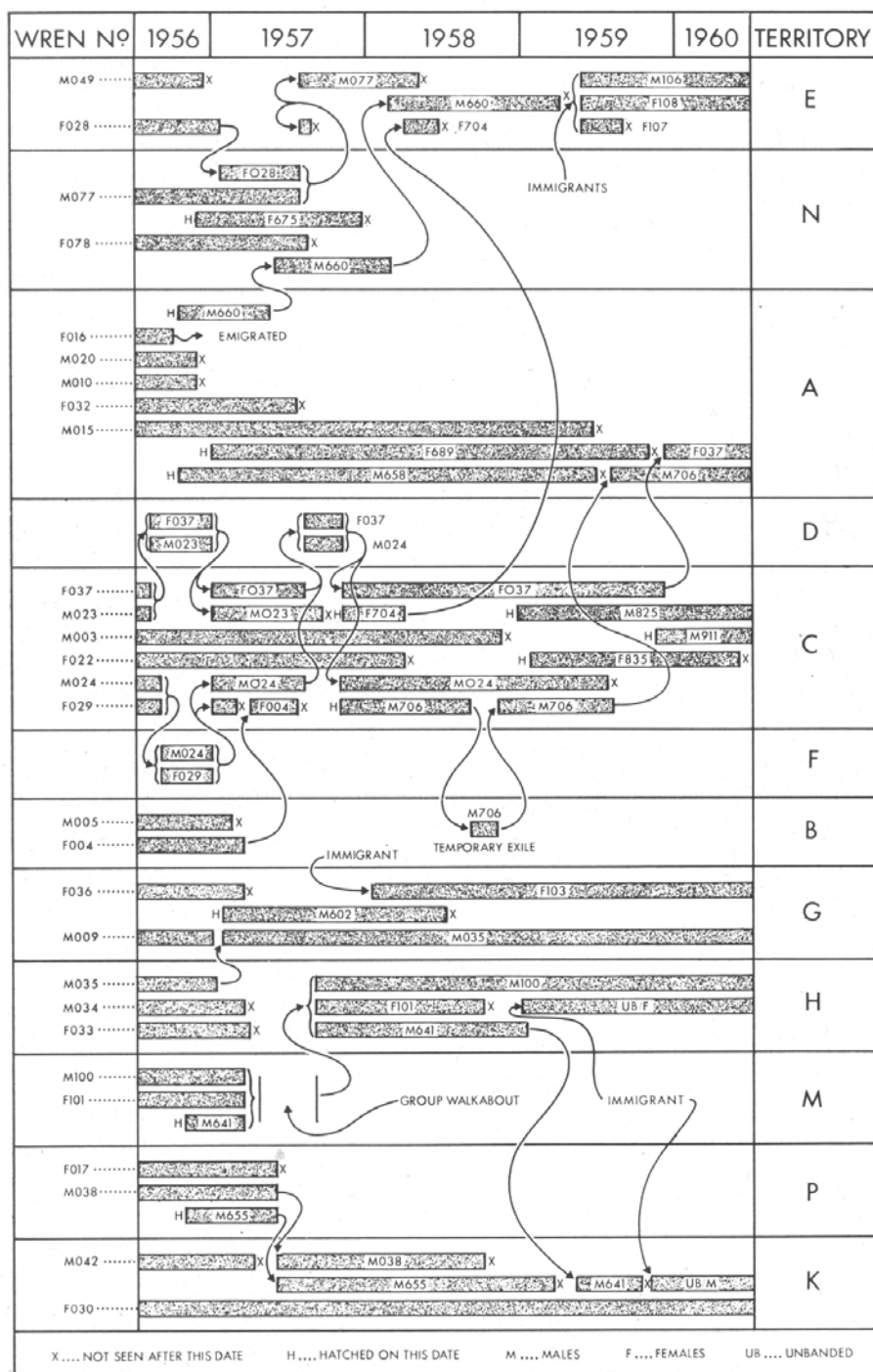


FIG. 14—*Malurus cyaneus*—group composition and changes as shown by individually colour-banded birds at Gungahlin, A.C.T., over four years.

ing the course of this study this happened nine separate times: 658 in A, 706, 825, 911 in C, 602 and 914 in G, 641 in M/H, 655 in I/K, 701 in O (see App. and Fig. 14). The only males known to have entered and established in the study area during this time came as preformed groups, as mentioned above, probably in the course of winter nomadic wanderings; the only male known to have left also moved as a preformed group. Finally, the fact that a number of males passed the breeding season in bachelor state in their territories rather than wander in search of a mate further emphasises the reluctance of males to disperse.

With a sedentary and sociable species such as *M. cyaneus* some interchange of group members must occur if inbreeding is not to become the rule; in fact three cases of inbred relationships were recorded: M015 mated with F689, his daughter, and M825 mated first with his mother (F037) and later with his sister F835. A measure of interchange is achieved because of the differential dispersal of the sexes as outlined above; in a population less isolated than that at Gungahlin it might well be expected that the exodus of young females in the spring would be equalled by a corresponding influx from other groups or populations.

(b) *Pair-bond*

Since the group social structure and the territorial limitations are maintained throughout the year, one might expect that the pair-bond would be a lasting feature. However, Figure 14 shows that it is rare for two birds to remain mated for as long as two years, and usually the cause of disruption is the death of one of the partners. This effect is emphasised by the sex-imbalance in the population already referred to, since this means that most males are at least two years old before they achieve a mate of their own (as opposed to supernumerary status), and she is then usually a young female. Mature hens, when widowed, are most likely to draw their new mate from supernumeraries nearby (see Fig. 14), i.e. from young males, so that pairs tend to be of unequal age.

Both males and females remain in the territory and attempt to attract new mates after one of a pair has died—this results in the territories persisting spatially intact, far longer than any one pair-bond, even throughout the five years covered by this study, in some cases (see Figure 5).

(c) *Surplus males*

As already pointed out Wrens frequently show a sex-imbalance within the population, in favour of the males. The surplus males, redundant to simple pair formation, are either tolerated within the family group or else hold 'bachelor' territories on their own, or even two males together (E/57 and 58; G/57; B/58). These bachelor establishments are obviously unproductive and their

value to the species is that they provide an established territory ready for completion the next season, they provide a ready source of replacements for casualties during the breeding season among the functional breeding pairs (G/56), and they may also, rarely, help in an avuncular fashion to rear the offspring of neighbouring groups (see E/57 with C's offspring).

Surplus mature males within the family group do, however, serve a reproductively useful function (see "re-nesting" above) and enable the true parents to concentrate on successive nestings unhindered by the clamour of dependent nestlings from earlier broods.

TABLE 12

A comparison of the productivity of supernumerary and simple groups of *M. cyaneus*

	Supernumerary Groups*	Simple Groups†
Number of nests 1956-8‡	32	32
Eggs laid	97	96
Eggs hatched	76	52
Nestlings fledged	69	39
Fledglings independent	34	24

* 12 breeding groups involved 37 adult birds.

† 16 breeding groups involving 32 adult birds.

‡ No data for 1959 are included as there were no supernumerary groups that year; their inclusion did not alter the overall findings but made the comparison less clear; the relevant figures are shown in Table 8.

Table 12 shows that from similar numbers of eggs laid, more eggs hatch and more nestlings fledge from groups with supernumerary males in attendance; in terms of efficiency per adult bird involved supernumerary groups produced, annually, 1.9 fledglings per adult, whereas the simple pairs produced only 1.2. This is a large difference and one that cannot be dismissed on the grounds that the supernumerary groups represented only the experienced breeders (see Fig. 14), since experienced simple pairs (pairs breeding for the second year) failed to produce any more fledglings than inexperienced pairs on average. The data suggest that the supernumerary contributes more to the population, acting as a nursemaid, than he would if he were breeding in a simple pair; this effect is most manifest at the egg and nestling stages and appears to be due to reduction of the demands made upon the female at this time.

IV. DISCUSSION

The clarification of the different age and sex plumages explains the paucity of "full-blue" male Wrens during the winter and the apparent "harems" herded by these few individuals. The differential timing of the male moult, depending on age and social status,

reflects the behavioural-hormonal determination of this event and probably reduces conflict within the group to a minimum. Whether the thyroid or the gonads are responsible for this variable response is not known, as the birds were not subjected to surgery in the interests of other aspects of the study, and opinions in this particular field are somewhat divided at present (Assenmacher 1958).

The breeding of animals is usually timed so that the period of greatest demand from the offspring coincides with a flush of food. With those territorial species which depend on a limited (defended) area for the maintenance of both the pair and the young, the balance between supply and demand may be extremely delicate and the sooner the offspring reach independence and leave the restricted area the better for all concerned. Where more than one brood is reared this becomes even more important and the young may be discharged from the territory less than a fortnight after fledging, e.g. *Erithacus rubecula* (Lack 1943) and *Passer domesticus* (Summers Smith 1963). These independent young, since they have no nesting requirements, can fulfil their nutritional and other needs in ecological niches which would be quite unsuitable to their parents' breeding activities; this achieves an economy of limited, specialized breeding environment.

Many species of birds, especially the migrants, only visit their breeding grounds for part of the year, spending the rest either in nomadic flocks (finches, tits, parrots, sea-birds, waterfowl and waders) or in remote winter quarters (swallows, warblers). In other words these species only occupy the nesting area at its optimum and therefore quite a small area may suffice. Animals which are locally resident all the year round place a much higher demand on their environment—namely that of supporting them at a period of least productivity, usually the winter, when both vegetative and insect activity are very much reduced. In many cases the shedding of the young from the family group before food becomes scarce sufficiently answers the problem, e.g. *Parus palustris* (Southern and Morley 1950), *Chamaea fasciata* (Erickson 1939), *Parus inornatus* (Dixon 1956). In other species loose aggregations of families may form which forage together over a combined area previously held as independent territories (*Aegithalos caudatus*, Lack and Lack 1957).

Crook (1961) has suggested that two sorts of flock occur depending on whether the animals concerned are 'contact' or 'distance' types. With distance species, as shown by Marler (1956) for the Chaffinch, *Fringilla coelebs*, the 'individual distance' is all important and any member of the species infringing it is either attacked or fled from. The distance varies with the season, obviously reaching a minimum at the time of copulation and nesting. As the young reach independence, so the conflict between parental res-

possibility and infringement of individual distance grows until the young cease to be regarded as part of the family and become intruders.

With contact types this individual distance does not arise within the species, as is evidenced by allopreening throughout the year and, in the extreme, by the clumping behaviour of woodswallows (Artamidae). Wrens are such a contact species and even in mid-winter on a warm day the whole family group may be seen perched side by side preening each other; at night they regularly roost close together. Therefore no behavioural mechanism exists which drives off Wren offspring when they are capable of looking after themselves and *M. cyaneus* provides an example of a resident contact species, maintaining territory all the year round, within which all the requirements of the entire family are met. The only other species known to do this, among the small passerines, are *Campylorhynchus brunneicapillus* (Anderson and Anderson 1957), *C. zonatus* and *Troglodytes aedon* (Skutch 1954).

The contact nature of the species and the fact that much of their lives is spent in dense cover, the open spaces only being sought for foraging, explain the paucity of behaviour patterns and their infrequent use—or, at least, observation. Some of these patterns such as petal-carrying and “blue-and-black” display suggest that in the past these may have played a more important part in the bird’s life, but are now infrequently, and even apparently, pointlessly performed. The advantages to be gained from the maintenance of family ties and social behaviour, such as that of the Wren, are varied. The young birds presumably benefit from the experience of older group members in such important matters as food-finding and avoidance of predators. Besides this the generally accepted advantages of flock behaviour apply to Wren groups, namely—increased vigilance against predators as the number of receptors (eyes and ears) increases, and the mutual advantage of close-feeding in that insects disturbed by one bird, but missed, may fall prey to another group member. Group or flock feeding also enables localised and temporary gluts of food, e.g. a hatch of insects, to be made full use of by several individuals, rather than benefiting only one or two birds who, often, could not cope with the quantity available, alone.

The breeding biology of the species shows high adaptability in the use of nest sites and a breeding season limited only by low temperatures and aridity. This in large measure explains the resilience of the species in contact with human developments together with their suitable temperament and enables them to take advantage of settlement, whilst other *Malurus* species disappear.

Copulation was seen too seldom to affirm or disprove actual polyandry, but the presence of more than one sexually mature male

in a breeding group was sufficiently common an occurrence to rate as normal behaviour. The results suggest that this unusual state of affairs arises from the differential dispersal of the sexes which, in turn, is due to mutual tolerance of old and young males but intolerance between females. In this species there is no question of the young males being sexually immature—siblings of subordinate males have bred successfully at nine months old and subordinate males have successfully assumed the dominant rôle at the loss of the dominant cock.

In regions with a climate as variable as that which characterises much of the range of *M. cyaneus* and in particular its drier extremities (e.g. Booligal, N.S.W., with 10" rainfall), a proportion of years will not be sufficiently suitable to furnish adequate replacements for the species. A multi-brooded species whose breeding is only restricted by climatic factors, such as rainfall and temperature, has a reproductive capacity capable of responding rapidly to particularly favourable circumstances. This not only enables the species to make the most of a good year, but enables rapid colonization following major ecological changes.

The ultimate reproductive limit is determined by the number of breeding cycles it is possible to complete within the prescribed climatic limitations. This depends on the frequency of the cycle, part of which (the incubation period) is inflexible, but part, the dependent fledgling stage, can be almost eliminated where supernumerary males adopt nursemaid duties.

In effect, then, the presence of supernumeraries in the family group shortens the frequency of the breeding cycle to the irreducible minimum occupied by the incubation and nestling stages and must therefore be regarded as a highly efficient adaptation to a widely varying climate, by a multi-brooded species.

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APPENDIX I

The full history of the groups occupying the study area during four years is given below: a few groups were observed for a fifth year. Since the territories were the most stable feature of the population the descriptions are given under the letters designating these and are referable to Figures 5 and 14 of this paper. The time period used is a year dating from July 1st: 'A56' refers to territory A from I.vii.56 to 30.vi.57.

A56.—The overwintering group consisted of seven birds, four males (014, 010, 020, 015) and three females (032, 016, 017). 010 was banded the previous winter and was the dominant cock, but the ages of the others were unknown. In August M014 disappeared and F017 moved to territory P and paired with M038. This left three males and two females. M010 and F032 were the effective pair but all the others assisted at the first nest once the young were hatched; despite this the young perished, soon after fledging. M010 and M020 disappeared while the second batch of nestlings were being fed; about the same time F016 left the area and was not seen until the next year when she was found breeding outside the CSIRO Insecticides Laboratory at Black Mountain, five miles away. Three young survived from this second nesting (658-660) and four from the third (689-692). These remained with their parents except for 660 who wandered to territory O for about two months of autumn and then joined up with group N and spent the winter with them—this is the only documented example of juvenile wandering soon after fledging. 659, 690-2 disappeared during the autumn and M015, F032 and 658, 689 overwintered together. F032 was last seen in July leaving M015 and F689 as the breeding pair (a father-daughter mating) and M658 as supernumerary male. 1957 was a drought year and only one nesting succeeded, all three young surviving through until ix.58 when one moved into Canberra and set up territory with a female from J—the others were not seen again. In 1958 three nestings were accomplished and three young from the 2nd overwintered with the adults. One cat accounted for all three young and both males of this group in July, before it was destroyed—this left F689 alone and in response to her vigorous advertising song she was soon joined by M706, the dominant male from C. Their first nest was destroyed (cause unknown) and F689 disappeared while incubating the second clutch; M706 was alone for a few weeks, but was then joined by F037, also from C, and together they reared a brood, two of which overwintered with them. In 1960 two nestings were completed and three young from the second overwintered with their parents. In 1961 one of these remained as a supernumerary male and the group entered the winter consisting of M706, F037, M1010 and three young of the year F037 was still alive in April 1962, after completing her fifth effective breeding season and surviving at least 2280 days (6½ yrs.), the longest of any bird in the study.

B56.—Seven birds overwintered in this group, M009, M005, M018 and

F004, F036, F019, F030, M018 and F019 were not seen after September, while F030 moved to K; M009 and F036 formed group G, leaving M005 and F004 as the breeding pair in B. This pair completed 6 nests during the season but never managed to hatch eggs. M005 disappeared in February 1957 and F004 joined group C for the winter but was not seen after June. In subsequent years this area became part of territories C and G except for a brief period when M706 was exiled in 1958 when he re-established the boundaries for a period of two months before he re-joined C.

C56.—Nine birds overwintered in C: M003, 021, 023, 024, and F022, 025, 026, 029, 037, 021, 025, 026 were not seen after September. M023 and F037 took up territory D, and M024 and F029 took up territory F, leaving M003 and F032 to breed in C. Of three nests started only one fledged young (3), one of which remained in the family group through the winter but was not seen in August (685). During the winter of 1957 groups C, D, F, and B merged identity and foraged over the combined area; M005 and F029 had disappeared leaving eight birds: M003, 023, 024; F022, 024, 027 and 653, 685. By spring these were reduced to the three males and only two females F022 and F037. In the previous year M023 and M024 had moulted in at about the same time (Aug.-Sept.) suggesting that they were, then, both still in their first year—in 1957, M024 moulted in at least two weeks ahead of M023 and gained F037 for a mate after some fierce battles; they re-established D. M023 was not seen after September. M003 and F022 only managed to nest once due to the adverse season, but fledged three young (704-6) who all survived into the winter: 704 joined bachelor M660 in E during April, while 706 persisted in C as a supernumerary male—705 perished when used as a decoy during trapping (the only casualty during the study). F022 failed to survive the winter and since groups C and D had merged again at this time, when spring came there was only one female between the three males (003, 024 and 706). M024 adopted supernumerary status while M706 was temporarily exiled to B. Four nests were built in C during 1958, the first was deserted after a cuckoo had laid in it, but the next three all fledged young, three of whom survived into the winter in the family group. M003 was not seen after the summer of 1958-1959, and M024 failed to survive the winter, so that spring 1959 found M706 as the dominant cock, M825 as supernumerary, and his sister F835 and F037 as hens. F689 managed to seduce M706 away from the territory early in August (A/59), and M825 mated with his mother, F037, with his sister in close attendance. While 037 was incubating, M825 and F835 kept close company, and when the young failed to hatch, F037 left the group and was not seen for a month when she turned up as a replacement of F689, who had disappeared. M825 and F835 (brother-sister mating) successfully reared three young, one of whom (911) persisted as a supernumerary during 1960-61.

D56.—As already indicated under C this small territory was only occupied during the breeding season in two years. The members spent the winter merged with group C and the area finally became absorbed into C. In the first year two young were fledged, one of which survived to join C during the autumn with its parents, but did not survive the winter. In the second year the hatching of young coincided with that of C and the two broods became hopelessly intermixed; the adults from C plus M660 from E cared for all the young while M024 and F037 withdrew to their old territory and re-nested, unsuccessfully.

E56. Two females (027 and 028) overwintered with M049, but F027 disappeared before nesting began. This pair nested twice and fledged young both times, but they failed to survive for long: M049 disappeared at the end of 1956 and the female and her offspring merged with A for the last of the summer when she then joined N for the winter. In July F028 resumed her old territory and advertised her solitude loudly until M077 left his old group (N) and joined her; however, she did not survive long and M077 spent the spring in solitary bachelor state in E, as his efforts to re-establish in N were repulsed. At the end of the summer (ii.57) M660, who had lost his mate, joined M077 and they both helped to care for the offspring of groups C and D, withdrawing in autumn with one of the young (704) in constant company. M077 was not seen after April, and 704 was not seen after June, by which time she was obviously a female. M660 spent the

season of 1958-59 as a bachelor in E but was not seen after the middle of April. In May 1959 an established group of three birds entered the study area from outside (M106, F107, F108), and by July were defending territory in E. F107 was repeatedly attacked by F108 during August and was not seen again; M106 and F108 nested successfully and took two young through the winter, a male who persisted as supernumerary, and a female who later became the hen of group C (1961).

F56.—This was another small territory comparable to D, but which was only occupied during the first year of the study (by M024 and F029); three unsuccessful nestings were made before the group merged with C for the winter, during which time F029 disappeared. The area was divided between C and E in subsequent years.

G56.—This territory was part of B during the winter of 1956 and was taken up by M009 and F036 in the following spring. Their first two nestings were destroyed before hatching, but the third clutch hatched successfully and young were fledged. It is particularly interesting that M009 disappeared early in January 1957, before the young had fledged, and his place was immediately taken by M035 who, until then, had been supernumerary to H. F036 was not seen after the autumn moult and M035 overwintered with one of his step-offspring, namely 602, who developed into a male. These two spent the season of 1957 in bachelor state until a strange female F103 joined them in January 1958; M602 did not survive the winter. For some reason M035 and F103 failed to produce any young during 1959 (cf. K/56) and overwintered alone, but in the ensuing season they were successful and fledged young, two of whom persisted into the winter, and one (M914) persisted as a supernumerary. In 1960-61 two broods were successfully fledged, one of which (M1010) persisted throughout the winter. M035 disappeared early in the spring of 1961; he was the longest lived male during the period of this study, having lived at least 2052 days (54 yrs.).

H56.—No information is available before the spring of 1956, when the birds were first banded and four birds were present, two males (034, 035) and two females (033, 031). F031 disappeared early in the spring, leaving a trio that finally reared young after failing at two earlier attempts. M035, the supernumerary, left to join G early in January 1957. This group went "walkabout" during the winter of 1957 and was not seen again. The pair that had nested in M during 1956 visited H in the course of their "walkabout" during the winter and finally settled there in August 1957 with one of their offspring, M641. This trio nested successfully for the next two seasons until F100 disappeared and M101 acquired a new mate. Whether this process involved rivalry with M641 is not known, but is quite likely since the latter disappeared for four months to reappear as the mate of F030 in K during the next season.

P56.—F017 from A and M038 nested successfully in this small territory, the first year, but thereafter became merged with H. This group merged with K during the winter of 1957 and is detailed further under that heading.

J56.—Another trio (M064, 066, F065) built three nests, of which only the last was successful. The whole group went "walkabout" during the winter and were not seen after April 1957.

K56.—F030 paired with M042, late in September, and although this pair maintained territory throughout the spring and summer no nest was ever found, and certainly no young were ever hatched. This is a similar state of affairs as occurred at G during 1958 where again no nest was found, although hours were spent searching. In both cases the area to be searched was quite small and was combed thoroughly, and observed for long periods; in ensuing years the nests of these females were found regularly. Careful checks during the winter, when the cover was more open, were also fruitless. In consequence it is quite likely that these were immature females who managed to attract a mate but who were physiologically unable to complete the breeding cycle.

M042 disappeared early in the winter and was replaced by M038 (P/56), whose female had also disappeared: he brought with him M655, a son, who remained as supernumerary for the next two breeding seasons during the last of which he became the dominant cock after M038 disappeared. M655 disappeared late in the summer of 1959 and was replaced by M641, who fathered an unsuccessful brood and disappeared before the end of 1959.

F030 survived until 17.ii.61 when she was shot because she had lost her colour bands and defied all attempts to retrap her, and in consequence could no longer be identified in the field. She was then at least 1874 days old (51 yrs.).

L56. Was occupied by a trio (M071, 073, F072) that nested three times and fledged young once during 1956. The entire family went "walk-about" in the winter and were not seen again. This territory became part of K during the ensuing years until late in 1959 when it was briefly occupied for the spring and early summer by a pair which disappeared after failing to rear nestlings.

M56.—A pair successfully raised two clutches here in 1956 but went "walkabout" during the winter and finally took up residence in H the next season (M101, F100, 641). In 1960 a fresh pair established themselves (the male was reared in H and fathered by M101) and successfully nested; they, too, abandoned the area during the winter.

N56.—After one failure a pair (M077, F078) nested successfully here and all three young overwintered with the parents, plus 660 from A and and 028 from E. As related under E, M077 was led away by F028 and after her disappearance 077 was not permitted to rejoin N by M660, who had taken over. F078 did not survive to breed that spring and her place was taken by F675, her daughter; one nesting failed to hatch and 675 died before another attempt could be made. M660 then joined M077 in bachelor state in E. This territory became part of A after this.

O56.—This group was not observed as fully as the others since it was more than half a mile from Gungahlin and in a private garden; however, it is included because one of the offspring from N56, F674, settled there and bred during 1957, and one of their offspring persisted as supernumerary in the parental group during the following season. After this the hedges surrounding the gardens were removed, which disrupted the Wrens.

APPENDIX II

ANALYSIS OF STOMACH CONTENTS OF 32 BLUE WRENS

Malurus cyaneus

Thirty-two birds (30 ♂♂ and 2 ♀♀) were taken during a distribution survey and therefore came from points as far afield as South Australia and Queensland and from widely different habitats (Rowley, in prep.). Further, the samples make no attempt to cover all seasons of the year—May-June — "winter" and January — "summer" (see Table 13).

Table 13 shows the different food classes represented in these Wren stomachs subdivided into two groups—winter and summer. Certain broad features are at once apparent and transcend the limited nature of the sample: firstly, irrespective of season, ants and shield bugs consistently make up a large part of wrens' diet. Certain species are taken only during winter (earwigs, cockroaches, beetle larvae and moth cocoons) probably reflecting aspects of insect ecology, though to some extent changed foraging habits on the part of the wrens may be important, i.e. more flies are taken during winter suggesting that a certain amount of "hawking" is done by the wrens. Conversely, species such as crickets and grasshoppers are only available in the warmer months.

The plant seeds present a problem; all except one (*Geranium* sp.) were seeds of a prostrate native herb, genus *Rhagodia*; one sample came from the A.C.T. and one from Lake Victoria, N.S.W. Of five specimens of other *Malurus* spp. taken (1 *M. leuconotus* and 4 *M. assimilis*), three of these contained seeds and all were from *Rhagodia* berries. The frequency of the occurrence of these particular seeds is beyond the realms of chance; in fact the ingestion of no less than 45 *Rhagodia* seeds by five different individuals makes it very unlikely that they were ingested in mistake for insects, and the fact that the fleshy pericarp had been effectively digested leaving only the hard seed suggests that *Rhagodia* spp. provide a minor source of food for *Malurus* spp.

[The insect remains were identified by Mr W. J. M. Vestjens of the Division of Wildlife Research, CSIRO, and the plant seeds by Mr Max Gray of the Division of Plant Industry, CSIRO.]

TABLE 13
Analysis of food from 32 *Malurus cyaneus* stomachs

Food Items Found in Stomachs	Winter		Summer	
	No.	% Occurrence*	No.	% Occurrence*
1. Centipedes			1	7
2. Spiders	1	6	6	27
3. Crickets			9	13
4. Grasshoppers			3	20
5. Earwigs	2	12		
6. Cockroaches	3	18		
7. Cicadas			1	7
8. Leaf-hoppers			2	13
9. Shield-bugs	22	47	71	67
10. Ant-lions (adult)			1	7
11. Moths (larvae)	4	24	2	13
12. Moths (cocoon)	2	12		
13. Moths (adult)	1	6	2	13
14. True Flies	24	53	6	27
15. Wasps	5	24	1	7
16. Ants	211	88	107	93
17. Shaler beetles			1	7
18. Dung beetles	1	6	1	7
19. Leaf beetles	4	18	14	13
20. Weevils	7	30	8	33
21. Undeterminable } adult	9	18	13	47
} larvae	7	24		
22. Plant seeds	7	6	13	7

* % occurrence gives the % of stomachs containing representatives of a particular food class; there were 47 stomachs in the winter sample and 15 in the summer one.