TERRITORIALISM AND CO-OPERATIVE BREEDING OF THE EASTERN YELLOW ROBIN Eopsaltria australis

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I studied the Eastern Yellow Robin *Eopsaltria australis* from 1975 to 1986 near Moruya, N.S.W. The birds were distributed in territories of 1 to 2 hectares. A fire in 1980 did not at once reduce breeding numbers; they declined next season. Established pairs held territories while breeding. In the non-breeding season they lived in the same areas but were not seen to defend territories. Some first year birds also bred, almost always without success; having attempted to breed, these pairs then dispersed. Others attended the nests of their parents or near neighbours. These attendants were first-year males. First-year females were unobtrusive and were not known to act as attendants. Mildly threatening disputes within territories early in the breeding season were probably directed towards evicting unwanted immature birds by established pairs. Attendants were attached to only about one fifth of the annual breeding attempts.

INTRODUCTION

From 1975 to 1983 I studied the life history of the Eastern Yellow Robin Eopsaltria australis, with special attention to its breeding, near Moruya, N.S.W. (35° 52'S., 150° 03'E.). I chose the area simply because it was where I lived so that I could observe all day and even at night and could check nests at a moment's notice. The area had no special advantages for the birds, as far as I could judge, but perhaps represented an average habitat in the district. An account of the breeding activities has already been given (Marchant 1986); references to the small amount of previous work on this species may be found there. This paper presents further information on occupation of territories, behaviour and co-operative breeding.

From 1975 to mid 1979 rainfall was average (1 000 mm) or above. Drought started in 1979 and lasted till March 1983. Plot A and a small part of Plot B were burnt out in 1980.

METHODS

My two areas of study, each of about 10 hectares, lay on opposite sides of a north-south ridge, 80 to 100 m above sea level (Plot A to the west), along which ran a dirt road. The plots were only 50 m apart and neither covered the interfluve. I rarely saw robins in this gap and judged that territorial pairs on either side of the road seldom came in contact with each other; yet the birds on either side could not be considered as two distinct populations because colour-banded birds moved between the two areas. A description of the habitats has been given by Marchant (1979). Here it need be said only that Plot A was in disturbed regenerating woodland of mixed eucalypts with thickets of Kunzea and Melaleuca spp; Plot B lay in a stand of Spotted Gums Eucalyptus maculata and Grey Ironbarks E. paniculata with scattered undergrowth.

I studied the robins in Plot A throughout the entire period, trying to find all nests of all pairs each season. I did the same in Plot B from 1976

to 1979 inclusive. Thereafter, because the area had been damaged by logging and to some extent by fire, I worked in it less systematically. Both plots were gridded at 50 m. In 1975 I began to colour-band the birds (metal bands supplied by the CSIRO Australian Bird Banding Scheme; colour-bands partly by the Scheme and partly by myself). I soon had most robins in both plots individually marked. I did not maintain this effort after 1979 so that latterly the number of unbanded birds increased.

Usually I opened no more than six 10 m nets at a time because, unaided, I could not tend more nets satisfactorily. Most net sites were along my gridded paths. At first I opened the nets regularly from about dawn to 10:30 or 11:00 hours and after no more than 3 days at a site moved them gradually and systematically from one end of my plots to the other. I later discovered that the robins were attracted to my activities, when clearing paths or chopping wood. I put this to use in Plot B in 1977 by setting two or three nets round fallen trunks; up to ten birds might assemble as I chopped wood and were consistently caught. Thus, after about 6 weeks of operation in each plot, I had caught most of the population. When birds were breeding, however, by watching the nests I detected which adults were unbanded and then caught them at their nests, siting one to three nets across likely approach routes. I usually caught the female within minutes of opening the nets and males or attendants within the first 30 minutes. At no nest did this cause the birds to desert, though I took care not to catch birds at the nest during or soon after laying. For netting at the nest, 6 m nets were much more convenient than the 10 m ones, although the smaller size is no longer available. Pulli were banded only when 6 to 8 days old and never later because they then tended not to settle back and stay in the nest. After breeding was over, I relied on catching survivors for colour-banding by my method of systematic netting throughout the plots; this must have been successful because I rarely saw or caught a bird bearing only a metal band after March of any

I used all combinations of two of the seven colour-fast bands (red, white, dark blue, yellow, light green, orange and black) on one leg and a metal band on the other leg. Then I went to a three colour combination on the one leg. On the whole there was no difficulty in identifying

the birds up to 30 m distance at least, with x8 binoculars, though dark blue/black was a bad combination under any lighting conditions; it is best avoided with this species. It would really have been better to use the same three colour combination on both legs (though this would prevent the use of a metal band) because, when the robins perched sideways on trunks, one leg was obscured and recognition was delayed if that leg carried the colour bands.

Being out in the bush all day and every day, once the breeding season began, I found many nests by seeing the female engaged in nest building, sometimes led to her by the males or attendants when they were engaged in courtship feeding. If this failed and I suspected an undiscovered nest, I searched systematically until I found it; I was usually successful within an hour or so and indeed it was sometimes harder to find the birds than the nest. With second broods (including second nesting attempts) I often had to search the territory for a day or so before finding the robins; once they were located, I found the nest quickly. Naturally, nests in the scrub layer or understorey were much more easily found than those in trees above 10 m high. In all, however, judging from the one or two nests found after they had been used, I think that I found well over 90% of all nests in both plots in years of thorough searching.

To get details of attendance at nests, of parental care and of the role of the sexes (see Marchant 1986), I watched from any convenient place at about 10 to 15 m from the nest, generally without concealment but sometimes behind a rude screen of hessian to insure that my movements did not disturb the birds. For the most part they seemed indifferent to my presence but naturally there were individual variations; one or two females that I knew for four seasons remained shy throughout.

RESULTS

Voice

Though the three types of call given by the robins are generally known, it is necessary to give my interpretation of them because they are related to particular aspects of behaviour discussed below and because I have noticed that their significance is not always understood. In general, the robins are not noisy. Their three sorts of call are:

- 1. A loud emphatic 'chop-chop' (Pizzey 1980; or 'churp-churp', North 1912; 'chit-chit', Macdonald 1973; 'chuck-chuck', Slater 1974), uttered in a long series with an interval of 1 or 2 seconds between each double note or occasionally only one to three 'chop-chops' at a time. I identified the primary males (recognised by colour-bands and behaviour during courtship feeding) of 10 pairs with this call and did not trace it to any known female. It was only heard during the breeding season from late July to December (e.g. first records in 1975, 1977 and 1979 on 4 August, 8 August and 27 July respectively), usually from 30 minutes before first light till about 30 minutes after sunrise and again before sunset till almost dark. The number of calling males, particularly at dawn, gave a good indication of the number of breeding pairs in an area. I heard it rarely during the middle of the day and it was not much used by males with active nests. When a nest was lost or when a male was bereaved, as happened once with an identified pair, there was a recrudescence of this call. Evidently it was used to advertise territory and perhaps to attract a mate, by the male alone.
- 2. A series of even plaintive monotonous piping calls given at various speeds and volume in short bursts or in long persistent spells. This was less rapid, strident, urgent or emphatic than the calls of the White-throated Treecreeper Climacteris leucophaea, with which it is sometimes confused. I noted this call from both sexes in various circumstances: when apparently unalarmed and foraging normally; when predators were near; softly when in the hand and from the female on the nest; and during boundary disputes. It was probably used with subtle differences of speed and intensity as a contact, warning or distress note.
- **3.** A grating scold, 'k-k-kair' (Pizzey 1980), given when I was near a nest with young almost ready to leave or near recently fledged young; when birds were mobbing a predator (e.g. Lace Monitor *Varanus varius*); and during boundary disputes. Evidently it was used for alarm, warning and threat. Calls of these last two sorts were sometimes used in the same circumstances of warning or threat.

Territories

Distribution of territories in Plot A for the seasons 1976 to 1981 is shown in Figure 1 and in

Plot B for the seasons 1976 to 1979 in Figure 2. Figures 3 and 4 chart the occupants of the territories respectively, showing their relationships and histories as far as I knew them. For some individuals or pairs I could extend the record back to 1975 or forward to 1985. As can be seen in Figures 3 and 4, Males D and R and Female 1 lived in their territories for at least 7 to 9 years, all having been banded as older than 1 year in 1975 or 1976, with Male R surviving into 1984 or longer. The longest lived birds of known age were Male G (still breeding in 1985, aged 10 years) and Male B' (surviving into 1984, aged 8 years).

The sizes of territories that fell entirely or almost entirely within my plots varied from about 0.8 to 2.0 hectares, averaging slightly larger (1.4 ha, n=20) in Plot A than in Plot B (1.2 ha, n=15). Birds were not commonly seen on the drier, less vegetated interfluves between and outside the plots, though I did not try to quantify this. The impression gained was that they either did not inhabit these areas or that territories there were larger than in my plots.

In Plot A the population (8-11 birds) remained fairly stable from 1976 to 1980. Where the territory did not lie wholly within the plot, I assessed it by counting one bird only per pair. Numbers declined to three pairs in 1981 and did not recover to the time of writing. In Plot B I did not fully assess the population after 1979 but till then it remained similar (12-15 birds) for the first three years, rising to 21 in 1979, apparently because then there were more attendants. During the whole period the density of the population varied annually from 0.6 to 1.2 birds per hectare in Plot A and from 1.0 to 1.7 birds in Plot B.

The fire on 11 August 1980 took place just when the robins were starting to nest. All individuals that I knew to be alive before the fire survived. It apparently did not interfere with nesting because Female 6 began to build a nest about 16 August; Female 11, in the last week of August; and Females 1 and 10, in the first week of September. Outside my plots I even found a nest with eggs that was being incubated while the fire passed below without damaging it. It was not till the 1981 season that the population in Plot A declined (Figure 1).

Once established, a primary pair occupied roughly the same area for several years. If one of the pair died or disappeared, the other remained

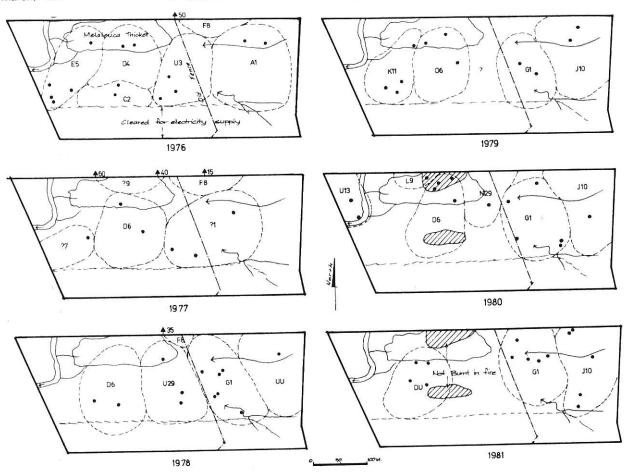


Figure 1. Territories of Eastern Yellow Robins in Plot A, Moruya, N.S.W., 1976 to 1981.

Pairs identified by capital letters for males, numbers for females (A 1). U=unbanded. ?=not identified or uncertain. Boundaries of territories dotted. Arrowheads outside frames point to nests with distance (number) in metres. Solid circles=
nests.

and mated with a third bird (e.g. Pair A1/G1/GU in Plot A for 11 years; Figures 1 and 3). Other examples were Male D and his mates, Pair J10 (Plot A), Male R and his mates, Pair B'15/U and Male E' (Plot B). The primary pair, helped by attendants, defended its territory during the breeding season. At other times I recorded only once, activity that suggested a boundary dispute but, when I chopped wood in Plot B in winter 1977, males that were occupying an area certainly chased visitors.

Territorial behaviour

The robins were often surprisingly inconspicuous for a species that is generally confiding and quite prominent. In non-breeding periods of 1976 to 1981 I recorded Female 1 some 22 times but saw her mate 49 times. In 1977 when I chopped wood in Plot B for a total of about 90 hours, I recorded known males attending me for a total of about 42 hours and known females for a total of about 12 hours; these birds had bred in 1976 or bred later in 1977. Thus, females seemed less obtrusive than males and may differ from them in feeding habits.

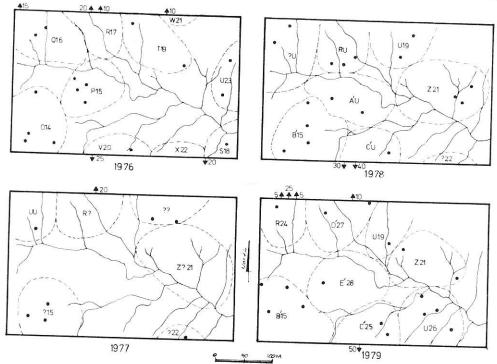


Figure 2. Territories of Eastern Yellow Robins in Plot B, Moruya, N.S.W., 1976 to 1979. Conventions as in Figure 1.

Boundary disputes, in which both members of a pair and sometimes attendants took part, were neither common nor spectacular. I noticed them only during the breeding period. The birds chased one another with agitated piping and scolding (calls 2 and 3 above) from perch to perch so rapidly that the roles of individuals were hard to follow. The chased bird usually gave way before the chaser arrived so that I noted no physical contacts during these encounters. The chaser then landed on or near the abandoned perch and slowly cocked its tail several times in an exaggerated manner, sometimes piping at the same time. Before an attack, the aggressor usually pointed itself at its opponent, crouched and sleeked its plumage. These attacks could be launched from a distance of 30 to 40 m, when the attacker glided towards its opponent on stiff outstretched wings in a parachute-like flight. I noted these disputes always between the ground and top of the understorey, never on the ground, but vigorous chases also took place in the treetops where I could get no details of the participants.

Before or early in the breeding season, I noticed robins on the ground or on low perches near the ground well inside a territory interacting differently. The aggressor gaped widely, fluffed out its feathers, sidled up to the aggressed bird on its perch and even nudged it aside. The aggressed bird meekly moved away. Reactions were confused and, because the birds fluffed their plumage and crouched, I could rarely identify them. However, I saw immature or young birds (Males Y and B') reacting thus to one another, perhaps in a tussle for dominance within a territory. I also saw a primary male (C') land beside an unmarked bird, peck it and shove it off its perch so that it hung down inert for some moments before flying away. During May I once recorded two of three unmarked birds engaged in an even more violent dispute: one bird flew at the other so that they clashed in the air and fluttered to the ground, struggling.

Outside the breeding season I saw no behaviour that seemed directed at maintaining the pair-

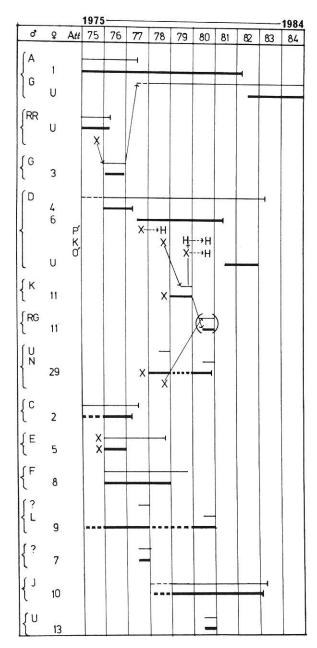


Figure 3. Occupants of breeding territories of Eastern Yellow Robins in Plot A, Moruya, N.S.W., 1975 to 1983.

Thin line for males; thick for females; broken when present but breeding not proved. Vertical bar at end of line for birds known to have died or disappeared. X=date of birth, H=in attendance at nests. Arrows indicate movements between pairs. Brackets for RG11=

breeding outside plot.

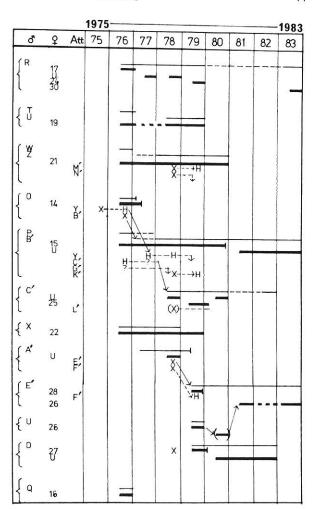


Figure 4. Occupants of breeding territories of Eastern Yellow Robins in Plot B, Moruya, N.S.W. 1976 to 1983. Conventions as in Figure 3, with additions:

vertical downward arrowhead=known departure from plot; ?=uncertain status. Brackets for Female 26 in 1980=breeding outside plot.

bond, for example allopreening. Indeed the members of a pair were rarely in close contact. When the breeding season approached in July and August, courtship feeding became common. It was then easy to distinguish the sexes, even if unmarked. The female usually spread and lifted her wings slightly, quivering them increasingly rapidly as the male approached and until he fed her. He delivered his offering quickly and rarely perched for more than a moment or two along

side the female before flying away. Some females did not always beg in this manner but others did so always, whether it was the primary male or an attendant that brought her food. In spite of many hours of watching at all times of the day, I witnessed only three brief attempts at copulation. None was proceeded by display or ceremony; all were carried out silently. The female crouched slightly with a tremor of her wings; the male mounted without preliminaries and flew away immediately after the act. For those primary pairs with attendants I could not be sure that they did not copulate with the female and indeed was not always sure which was the primary male; for example with the mate of Female 15 in 1977 (Figure 4).

In contrast, first year birds breeding together for the first time held ephemeral territories and apparently did not form permanent pair-bonds. The best examples were pairs K11 and E5 in Plot A (Figures 3). Pair U26 was almost certainly another. The two occurrences of divorce (K11 to RG11; U26 to E'26 were between first-year birds.

Attendants at nests

It was not easy to know whether a primary pair had attendants. To catch as many as five birds at one nest was not reliable evidence. The commotion and alarm calls of a trapped bird attracted neighbours. At one nest of Female 15 in 1976 I caught Male O of the neighbouring pair as well as Bird G' whose sex I never determined but which may have been female since it did not feed the young in the nest. At a nest of C'25 in 1979 I caught Bird L', also of undetermined sex. which did not attend the nest. The only way to decide the matter was by watching a nest regularly for long periods. This I could not do for all nests. At some I was frustrated from identifying one or both members of the primary pair by shyness of the birds and lack of time (sexes? in Figures 1 and 2). However, during the study I watched 54 annual breeding efforts (pair/ seasons), many by the same pair from year to year, for long enough to feel sure that only 11 pairs had attendants. In fact, I identified only eight individual attendants. One of them attended a primary pair for three seasons (Y); another (K) did so for two seasons. Male B' may have attended his parents for one season before breeding himself. Two attendants (K, C') proved to be males when breeding subsequently. The others must have been males also because female robins did not feed one another and because males supplied the female with almost all her food when she was incubating (Marchant 1986). All attendants were first-year birds when they started to help their parents (K, K', M', P', O') or the primary pair in their natal territories (Y) or a sibling and a female of unknown origin (F'). I did not know where attendant C' had been hatched.

In 1979, K', while attending his parents (B'15), approached Female 28 on her nest or followed her to it three times. He did not bring food but came very close to the nest and flew away after Female 28 had demonstrated against him by gaping widely and fluffing her feathers.

Most of the attendants disappeared or bred elsewhere in their second year of life. Male K bred unsuccessfully in his first year. On the failure of one of his nests soon after the young hatched and while his female was rebuilding and re-laying, he attended a nest of his parents, staying to help them in the second year of his life. Attendant Y stayed in the same area until almost 4 years old, attending first his parents and then the pair that had taken their place.

Two birds of doubtful status were in Plot B in different years. Bird G', of unknown origin in the territory of Pair P/B'15 from 1976 to mid 1978, was not recorded attending a nest though it was in the territory or general area of the nests of the breeding pair throughout two seasons. Bird L', in the territory of Pair C'25 in 1979, had probably been reared by Pair C'U in 1978 and was in the area till the end of 1979 but very hard to find. It came to the nest of Pair C' 25 only once when I netted the incubating female. Judged by its unobtrusiveness, it was probably a female, as may have been Bird G'.

In November 1986 I found a nest with 5 eggs, by colour and pattern clearly laid by two females (3 + 2). All eggs hatched about the same time. This helps to explain the RAOU NRS record of two birds sitting on a nest, one on top of the other (Marchant 1984), and perhaps means that, if immature or first-year females remain in or near their natal territory like some first-year males, bigamy or a more complicated relationship may occasionally occur.

Though established pairs remained in the same small area all the year, unattached or attendant birds wandered farther. When chopping wood in Plot B in winter 1977, I found that established birds came to my chopping places only in areas of about 2 hectares, approximately corresponding to their breeding territories, whereas attendants, particularly Y and G', appeared over at least 5 hectares.

My captures of unbanded juveniles when breeding was over showed that these birds dispersed in the first 3 or 4 months of the year and sightings of banded birds up to 4 years old showed that there was another period of dispersal about July (Marchant 1986).

DISCUSSION

Essentially the population of robins that I studied seemed to be of two parts: established pairs that bred year after year with reasonable success and young birds that either acted as attendants or took no part in breeding or bred without success. Of all breeding attempts by birds that I knew or suspected to be in their first year, only Pair U29 in Plot A reared young. Pairs G3, E5 and K11 were certainly first year birds and had 12 nests without success.

It was unexpected to find that the fire in 1980 had no immediate effect on the population and that nests were started at about the same time as in previous years and within a few days after the fire. The population decreased only in the next year and had not recovered by 1985. Destruction of nest sites was probably a less important factor in this decline than growth of a thick grassy ground cover. Yellow Robins have been classed as 'pouncers' (Ford et al. 1986; Holmes and Recher 1986), taking about 70% of their food on the ground by dropping onto it from a perch. Thus the invasion of grasses after the fire probably prevented the robins from foraging in their favoured manner. It may also be remarked that the three pairs that survived best in Plot A after the fire were all experienced established birds.

Attendants were male offspring of the primary pair that they helped or of close neighbours. Female offspring, if they stayed in their natal area during their first year were inconspicuous and hardly ever came to a nest except in an emergency. On the other hand they may have been more prone than young males to disperse after reaching independence before about April each year, which was the usual time that young robins tended to disperse.

Boundary disputes were less frequent and less obvious than in species such as whistlers Pachycephala and thornbills Acanthiza spp. I did not see these disputes end in violence or even come to physical contact between contestants; nor did I note during them the habit of gaping widely, which is quite characteristic of intra-territorial affrays and of defence towards birds of other species that closely approach a female on her nest (Marchant 1986). Territories were defended, as need arose, during the breeding season but it may not be right to regard them as fully defended areas throughout the year. Members of primary pairs were seldom far from occupied nests and females indeed may go no farther than about 25 m from their nests. The nests of adjacent pairs were usually well spaced (Marchant 1986). Thus, encounters between neighbours may not occur often; long-established pairs may not be prone to leave their territories and the dawn-chorus of males may be enough to deter intrusion. In contrast, pairs of inexperienced birds seemed unable to maintain a pair-bond or a territory for more than one season.

Disputes within a territory apparently elicited different behaviour from that shown in boundary disputes. I do not think that these disputes had anything to do with formation or maintenance of pair-bonds, partly because the activity seemed typically aggressive and could end in violence and partly because it included the 'wide gape' response, which in other circumstances was used to repel intruders. I supposed that these affrays represented efforts by primary males to rid themselves of unwanted attendants or by rival youngsters trying to establish themselves in a territory, for which I had one example.

In general, first-year pairs will probably not have attendants and established pairs will have them only if they have reared male offspring in the previous season. Table I shows that Pairs D6 and B15 that had attendants were more successful than Pairs A1/G1 and R/mates that did not. If one assumes that half the fledged young die in the first 6 months after they leave the nest and that half of the survivors are female, it is not surprising that so few primary pairs have attendants. Once endowed with an attendant, a pair has a somewhat better chance of success than pairs without attendants (Marchant 1986) and the system could perpetuate itself. Unsuccessful breeding pairs or ones that produce only female

TABLE 1

Numbers of young fledged annually by four pairs of Eastern Yellow Robins, two with and two without attendants

Pair	Attendants	1975	1976	1977	1978	1979	1980	1981	1982	Total young	Average young per year
D6	+	_	-	2	3-4	4	3			12-13	2
B15	+	-	5	O	3	2	ŏ			10	2
A1/G1	0	0	5	0	0	2	0	2		9	1.3
R / ♀ ♀	0		2	0	0	3	0	3	2	10	1.4

offspring are perhaps less likely to start the process.

Co-operative breeding in the robins seems to be at an incipient stage and not widely spread throughout the population when compared with that in other species of Australian birds (Rowley 1965; Dow 1970, 1980; King 1980). Apart from benefit to pairs with attendants from slightly larger clutches and better development of the young than among pairs without attendants (Marchant 1986), the most readily recognizable advantage of having an attendant is that it reduces the effort of the primary male and could lead to the production of more broods per season. Less easily assessed but perhaps as important, may be the benefit of giving the attendant breeding experience against the time when it can enter the population as a primary male. Male K's behaviour of reverting to help its parents when it was breeding itself seems no different from the incidents recorded by Skutch (1935) and others, in which a bird of one species, having lost its own nestlings, began to feed those of another; probably it has not yet lost the urge to feed nestlings and continues to do so if there is an available opportunity. This certainly does not explain the origination of attendants in the robins because they are nearly always first year birds that have not bred. It may depend on the extent to which primary males will tolerate immatures in their territories. The dispersal of young birds at the end of the breeding season may result partly from aggression on the part of primary and partly from innate wander-lust, which could affect young females more than young males. In whatever way the system originated, it seems well adapted for a species whose individuals are sedentary and long lived when once established as breeding birds in an unpredictable environment.

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