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Co-operative Breeding and Plumage Variation in the Orange-winged (Varied) Sittella

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Observations were made at a nest attended by six Orange-winged (Varied) Sittellas, three of which were colour-banded, near Armidale, New South Wales. The nest was watched for 15 hours, which included late incubation and nestling periods. Only one bird, a female, incubated and brooded. Five group members, including two juveniles from a previous brood in the same season, fed the nestlings and removed faecal sacs. The sixth bird, an adult female, was apparently discouraged from feeding by the incubating bird. The primary pair contributed over half the total feeding effort by the group. Observations at other nests prove that both sexes build, and that incubating females are fed frequently during the incubation period by other members of the group.

Allopreening is described and roosting behaviour suggests the operation of a social hierarchy within the group. The sex ratio of the group studied was even, but males outnumber females in most groups. Sexual dimorphism appears to exist in young sittellas, but adults may be indistinguishable by plumage alone. Juveniles are characterized by white markings on the upperparts but this is lost within the first few months. Buff edging on the wing-coverts, particularly secondary coverts, lasts at least eight months on some birds, and this character is most useful in recognising first year birds.

Apart from Hando's (1970) brief account of three White-headed Sittellas *Daphoenositta chrysoptera leucocephala* feeding young at a nest, there is almost no published information on co-operative breeding of sittellas. Virtually nothing is known of the social organization and behaviour of these birds, and sex ratios of groups are difficult to determine while plumage variation between different ages and sexes is incompletely known.

In January 1979, I watched a group of six Orange-winged Sittellas *D. c. chrysoptera* at a nest in semi-cleared eucalypt woodland about two kilometres north of Armidale, New South Wales. The nest was at ten metres in a Broad-leaved Stringybark *Eucalyptus caliginosa* about 19 metres high. There were four adults and three of these were colour-banded *(Black, Red and White). From observations of copulation and courtship-feeding I established that the Black-banded bird was male and the Red-banded bird, female. The remaining two (unbanded) birds were juveniles, which differed from the adults in having (1) white streaks on the crown and back, (2) pale brown edges to the wing-coverts (visible on the folded wing), and (3) dull, brownish legs and feet. These two juveniles were also easily distinguished from each other

* *Bands used were provided by the Australian Bird-banding Scheme, Division of Wildlife Research, CSIRO.*

(Fig. 2; see Plumage Variation). All three unbanded birds were later collected and sexed internally.

Incubation and Brooding

discovered the nest on 1 January 1979, but few observations were made before 15 January. From 1 to 5 January I noted the Red-banded female ("Red") sitting on five separate occasions. The eggs probably hatched by 6 January, when I saw "Red" take small food items to the nest twice. Both "Red" and "Black" fed the nestlings the following day, but only "Red" was seen brooding them on eight occasions, the last time on 14 January. During a storm at dusk on 15 January, "Red" again brooded the young until the strong winds, causing adjacent branches to rub the nest, drove it from the nest.

In September 1977, I observed another nest (200 metres from the present one) attended by the "Red" and "Black" birds (banded as adults two months previously) and three or four other, unbanded adults. I watched this nest, which contained three eggs, for a total of 90 minutes between 9 and 14 September. On twelve occasions I noted "Red" incubating; no others incubated. Unfortunately, this nest was abandoned by 20 September.

At both nests, "Red" was fed by other adults during the incubation period. In 1979, I saw "Black" and possibly "White" feed it, while at the 1977 nest, I often saw three birds, including "Black", feed it in rapid succession. Sometimes "Red" was fed as it sat, but more often it left the nest on the approach of the rest of the group and scurried over adjacent branches, quivering its wings vigorously and uttering a rapid incessant high-pitched chatter as other members of the group fed it. Such behaviour was typical of incubating sittellas at eleven other nests I have observed in the Armidale region; it was performed while foraging with the rest of the group both in and away from the nest-tree. The constant chattering and wing-quivering of incubating females resembles the food-begging calls and behaviour of fledgeling and juvenile sittellas. Courtship-feeding prior to egg-laying also appears to occur in this species.

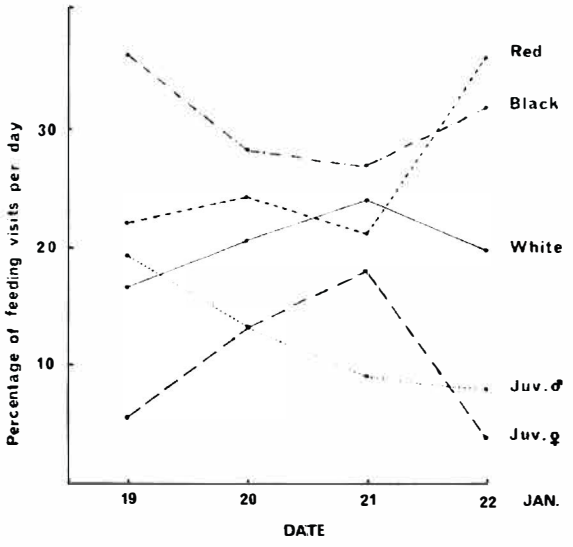
Although building was not observed at either of the Armidale nests, I have seen at least four individuals carrying nest material simultaneously to a nest at Wollomombi Falls (40 kilometres east of Armidale). At other nests attended by simple pairs here, I have observed both members building. Thus it is likely that all members of a group, including both sexes, participate in the building of nests.

Nestlings

I watched the 1979 nest for a total of 15 hours from 7 to 22 January to determine the relative contributions of each of the six group members to the feeding of nestlings. Out of 20 feeding visits witnessed in 2.5 hours of observation between 7 and 18 January, 13 were made by "Black" and another four by the juvenile male. The nest was watched for 30 minute intervals mostly during the morning on 19, 20, 21 and 22 January, for 2.5, 5.5, 3 and 1.5 hours respectively. During these four days, the feeder could not be safely identified in 17 out of 164 instances. The rate of feeding by all birds involved, including unidentified visits, at this stage varied from 12.4 to 18 feeds per hour (mean = 13.1).

The distribution of labour among the five birds feeding at the nest in the last four days is shown in Figure 1. Only visits in which the feeder was positively identified were used in this analysis. Although there is considerable variation in the amount of feeding by each bird from day to day, the efforts of the two juveniles and the supernumerary "White" were usually lower than those of the primary pair, "Black" and "Red". Overall, for the whole period (7-22 January) I saw 167 identified feedings in which the relative contribution of each individual was roughly as follows: "Black" — 35%, "Red" — 23%, "White" — 18%, Juvenile male — 14%, and Juvenile female — 10%. In summary, the primary pair contributed over half (58%) of the total feeding effort by the group.

The unbanded adult female was never definitely seen feeding at the nest. On at least three occasions I saw her approach the nest, apparently without food, but each time she was quickly chased away by "Red". All five feeding birds were also observed removing nestling faecal sacs from the nest but the majority were removed by "Red" and "Black". The sacs were usually



● Figure 1. *Percentage of feeding visits to nest by five Orange-winged Sittellas during four days prior to fledging. Values total 100 per cent; unidentified feedings are omitted. Number of feedings observed for 19, 20, 21 and 22 January was 36, 53, 33 and 25 respectively*

dropped ten metres or more away from the base of the nest-tree. In over 20 instances I noticed birds carrying food in the nest-tree while apparently still foraging, then fly off without actually feeding the young. On four occasions I saw "Red" carrying food for up to 15 minutes and although it perched on the rim of the nest several times, it eventually ate the food itself. All six birds usually flew simultaneously in a tight flock from the nest-tree but the primary pair was usually first to return (with or without food).

Although the group ranged over about 20 hectares throughout the year, much of its foraging during the nestling period was done in the nest-tree itself and in four other trees (three stringybarks and one Rough-barked Apple *Angophora floribunda*), all within 15 metres of the nest-tree. The primary pair spent almost half its time foraging in these five trees during the final stage (43, 45 and 47 percent of time I spent watching the nest-tree on 19, 20 and 21 January respectively). Similarly, at other nests of sittellas I have noticed that incubating birds appeared to forage a great deal in the nest-tree (even on the nest-branch!), before and after sitting. The accompanying "food-begging" behaviour and calls doubtless serve to stimulate others to feed it, but so much activity near the nest could also attract potential predators at times. Certainly most other species of birds I have observed behave far less conspicuously at their nests.

Fledgelings

The young fledged on 23 January before 07:00 hours, when I noticed the nest was ruined. Thus, the nestling period was at least 17 days. This is consistent with information on two RAOU Nest Record Cards (2/66 and 1/70), which give minimum periods of 17 and 18 days respectively. I found only two fledgelings although there were three young in the nest the previous day. Both days were dull with intermittant rain. One fledgeling (later captured) was perched atop a three metres high *Acacia* shrub, only 20 metres from the nest-tree; the other was about 70 metres from the nest-tree and 20 metres up in a tall stringybark. The group maintained a feeding "shuttle-service" between the two fledgelings, separated by about 80 metres. With the aid of a five metre ladder and a butterfly net, I eventually succeeded in catching the first fledgeling (Fig. 3), which was colour-banded Green and Blue. Upon release this bird flew to the stringybark, in which the other fledgeling and group members were, and at dusk all eight birds clustered to roost on a thin branch at 15 metres in this tree.

On the following day (24 January), the adults continued to feed the fledgelings, now huddled together in the same tree, but by 09:00 hours, 25 January, all eight were almost 300 metres from the nest-tree. The fledgelings were already active, climbing over branches for short distances and flying with the rest of the group. Their almost constant shrill calls and wing-quivering were reminiscent of the incubating parent. It is not known when the two fledgelings reached full independence; adults were seen feeding them occasionally on 13 and 26 March, the latter date over two months post-fledging.

Allopreening and Roosting Behaviour

As is the case in many other gregarious bird species, sittellas frequently engage in mutual or

allopreening. During this behaviour, two or three birds usually cluster together on a horizontal branch, facing the same direction. When three birds cluster, the outer two often preen the middle one simultaneously. I have observed such allopreening in this species throughout the year in many localities around Armidale. In the present group I often saw the primary pair preening each other, in turn. The two juveniles also allopreened occasionally. Self-preening however, was most common and all six birds usually preened and rested simultaneously, each individual separated by one to five metres from the others. Much of the observed preening occurred in a stringybark only 15 metres from the nest-tree. Preening comprised almost 20 percent of the total watching time on 20 January.

McGill (1967) and Beruldsen (1978) described roosting of sittellas but neither re-visited the sites to establish their permanence. I observed roosting of the colour-banded group on 25 nights involving six different trees scattered over their entire home range, the two extreme ones being 700 metres apart. All of the trees were reused, although two different perches were used in two of the trees. All roosting "perches" were thin dead branches, as were the ones described by McGill (1967) and Beruldsen (1978). Three different trees were used on three consecutive nights in April 1979, but in August one site was probably used continuously for three weeks.

Beruldsen (1978) noted that the birds perched head downwards and tail upwards, "at an angle estimated to be between 30 and 40 degrees". However this is not the roosting (sleeping) posture. Groups of sittellas usually go to roost 20 to 30 minutes earlier than most passerines but remain awake in the oblique posture described for up to 50 minutes until it is almost dark (Noske, in prep.). Then one by one the birds tuck their heads over their shoulders, and assume a more or less horizontal pasture over the branch, similar to that seen in most passerines (see plates in Warham, 1957; pers. obs.).

After collection of the three unbanded birds, I watched the remaining five in the group (including the second-brood juveniles) settle to roost on 20 nights. The Black-banded male was always first to arrive, settling near the base of the roost branch. "White" arrived next, and starting at the tip of the branch, it slowly spiralled towards the base, passing underneath "Black". During this movement, "White" continually quivered its wings with head lowered and uttered a soft twitter, behaviour which indicated it was subordinate to "Black". The latter sidled towards the other end of the branch to accommodate "White". Thereafter, each bird arriving at the perch climbed under the branch and squeezed up between the birds present, forcing "Black" to the outermost position. The middle (third) place was used by each of the other three birds (Red-banded female and juvenile male and female). However, the outermost positions were always occupied by the two adult males. This behaviour suggests the operation of some sort of social hierarchy, in which perhaps the oldest individuals protect the others in the group (Noske, in prep.).

Social Organization

There is little doubt that "Black" was male and "Red", female, as I saw them copulating in August 1979. "White", was sexed according to its bill-length (see Table 1). Thus, the sex ratio of the original six group members was even (3:3). However, of 20 birds belonging to four groups collected in north-east N.S.W., only five were female. This suggests a sex imbalance, strongly favouring males. I have collected solitary birds twice and both were female, perhaps indicating that surplus females are not tolerated by the group as much as surplus males. It is significant that the unbanded adult female at the nest I watched was apparently excluded from feeding the nestlings; yet it remained with the group until collected. This is further evidence that adult females other than the incubating (mated) bird are not normally tolerated within a group.

Wilson *in* Frith (1969: 379) stated that *chrysoptera* occurs "always in groups of six to eight birds" but this generalization is unjustified. I have encountered the species in all numbers ranging from one to twelve, and have several records of them breeding as simple pairs. However, group-size is difficult to determine accurately without some colour-banding and undoubtedly the constitution of groups changes within and between years. On one occasion I noted no fewer than 20 sittellas in two adjacent trees, but this had obviously resulted from the

TABLE 1

Field characteristics of the six sittellas in the partly colour-banded group at Armidale. Cheeks refer to the area between the ear-coverts and throat, below the level of the gape.

Name	Sex	Lores and orbital	Cheeks and throat	Wing coverts	Crown and back	Legs and feet
"Black"	male	dark grey	whitish	black	sooty-grey crown; mid-grey back, streaked black	bright yellow
"Red"	female	black	grey cheeks; whitish mid-throat	"	"	"
"White"	male*	dark grey	whitish with grey streaks	"	"	"
Unbanded adult	female	blackish	freckled dark-grey	"	"	"
Juvenile	male	pale grey (white eyebrow)	white	rufous buff edges	white streaks	dull flesh brown
Juvenile	female	blackish grey	freckled dark-grey	"	"	yellowish brown

* Based on bill length. Male sittellas in this region have a significantly longer bill than females (unpubl. data).

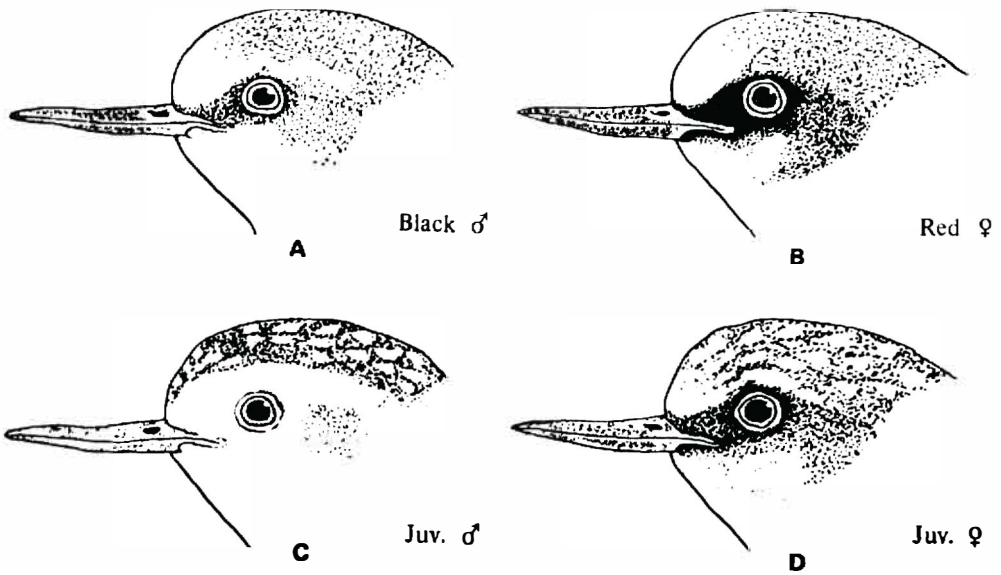
meeting of two or more groups from neighbouring areas. Possibly one of the best methods for establishing group-size and permanency in this species is observation of roosts.

Plumage Variation

Boles (1980) has presented evidence suggesting that both sexes of the Black-capped Sittella *D. c. pileata* may possess black faces, contrary to the accepted belief that only females have this character. As the White-winged Sittella *D. c. leucoptera* displays the same variation in head coloration as the Black-capped, with which it interbreeds (Parker, 1970; Ford and Parker, 1974), it can be expected that the assumed sexual dimorphism of this subspecies is also of doubtful reliability. In September 1978, in north-west Queensland, I observed a group of *leucoptera* consisting of three "black-faced" individuals. The preponderance of males in the species generally however, makes it unlikely that all three were females.

McGill (1948: 50) drew attention to four specimens of the Striated Sittella *D. c. striata* in the Australian and National Museums, which were labelled male, yet which possessed the assumed female characteristics of this subspecies *viz.* black face and throat. One recently collected male specimen of this form in the Queensland Museum (0.10411) also has these features, although three others (0.5211-13) which had enlarged testes when collected, have the white or streaked throat "normal" for this sex.

McGill (1948: 49) also pointed out the lack of sexual dimorphism in the White-headed Sittella *D. c. leucocephala.* According to Macdonald (1973: 388) the female of this form has a dusky throat, although the figure opposite depicts dusky ear-coverts and cheeks on the female. H. G. Barnard (*in* North, 1906) suggested however, that "when the head is not pure white in both sexes, it is an indication of youth or immaturity". On 20 May 1979, 30 kilometres south of Mundubbera, Queensland, I collected an adult female



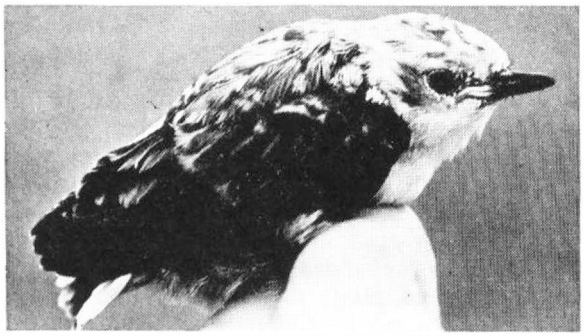
• Figure 2. *Head coloration of four members of the group feeding at the nest: upper left, "Black" (adult male); upper right, "Red" (adult female); lower left, juvenile male; and lower right, juvenile female.*

leucocephala, which had a pure white head, including the throat. Plate 2 in McGill (1951: 15, facing page) shows an incubating or brooding bird, presumably female, which also appears to have a pure white head and throat.

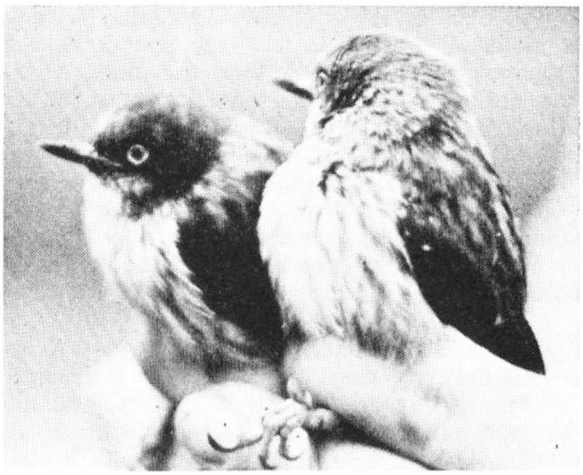
Similar confusion exists in the literature relating to sexual dimorphism in the Orange-winged Sittella *D. c. chrysoptera.* Macdonald (1973) stated that the male has a white throat, while on the female this area is "dusky-white speckled with grey-brown". Slater (1974) described the female as having a "black" throat, while McGill (1948) refered only to a "brown cap and face". Yet in specimens of *chrysoptera* which I have collected in the New England Region, some males had dark-grey spotting on the throat, and some females had whitish mid-throats, with dusky sides and cheeks. North (1906) described female *chrysoptera* as having "the feathers on the head, particularly the lores, orbital region and ear-coverts, darker than in the male". This is an accurate description of most female specimens I have collected, although most also have grey freckled cheeks and throats. It is also consistent with the head pattern of the Red-banded bird at the nest watched (Table 1; Fig. 2b) and the unbanded adult female, which was sexed internally. In contrast, both "Black" (Fig. 2a) and "White" had slightly paler lores, orbital and ear-coverts, and the former had almost white cheeks.

There are few satisfactory descriptions of juvenile sittellas. Again North (1906) provided the most detailed and accurate account: "the feathers of the head, mantle and back (are) tipped with a dull white sagittate marking . . .; the greater (primary) wing-coverts . . . tipped with dull whity-brown [sic] . . .; the white tips of the lateral tail feathers have a rufous wash; and the underparts are white . . .".

White mottling on the dorsal surface, buff edging to the wing-coverts, and white, almost unstreaked, underparts were discernible on the first-brood juveniles feeding at the nest, in addition to dull legs and feet. Yet these two young birds, later found to be opposite sexes, possessed obviously different head patterns (Fig. 2c,d), which suggested that sexual dimorphism in this species exists at an



● Figure 3. *Fledgeling male Orange-winged Sittella on the day it fledged. Note pale appearance of head and underparts, as well as pale (rufous) edging to wing-coverts.*



● Figure 4. *Two Sittellas mist-netted at Wollomombi Falls, 40 km E of Armidale, N.S.W. The bird on the left is probably an adult female, with dark face and cheeks, and pale mid-throat (similar to "Red"). The bird on the right is immature as pale spots can be seen on the edges of some lesser and secondary coverts.*

early age. On 25 February 1979, one month after fledging, the two "fledgelings" (second-brood juveniles) also had noticeably different head patterns. The colour-banded bird was pale-faced, with a broad white eyebrow and pale grey streak through the eye resembling but paler than the first-brood juvenile male (Fig. 2c). The other was dark-faced, almost black on the lores, orbital region and part of the ear-coverts; it therefore was female, similar to the first brood bird (Fig. 2d). Bill length measured when these two birds were mist-netted six months later confirmed that the colour-banded bird was male, and the other, female (12.0 and 10.7 millimetres, respectively). At Wollomombi Falls I found another group feeding two fledgelings (later collected and found to be opposite sexes), which had probably fledged less than one week before and yet possessed different head patterns, similar to the ones just described. It is possible therefore, that some sex differentiation in plumage occurs even before the young leave the nest. I have found that at least three species of treecreepers (Climacteridae) can be sexed as nestlings (unpubl. data).

On the day it fledged, the colour-banded fledgeling (Fig. 3) possessed a white-streaked crown and back, prominent rufous-buff margins on all the median and secondary coverts and some lesser coverts; a wholly black (short) bill, dark brown irides, greyish orbital skin, a whitish gape, and dull, flesh-brown legs and feet. The bill, eyes, gape and orbital probably assumed adult colours within the first month post-fledging. The white markings on the upperparts were lost after about three ($\pm$ one half) months, and disappeared from the back first, then the crown. The buff edging on the secondary coverts was still present on both "fledgelings", when mist-netted on 21 August 1979 (eight months post-fledging) though much reduced on the colour-banded male. This character was in fact, quite noticeable on the female in the field at this time, but had apparently disappeared on the male only three and a half months after fledging. The legs of both birds, particularly those of the male, were also duller than in the adults. In head colouration, the two birds were still remarkably different, the female having a greyish throat and blackish "face", while the male had a prominent whitish eyebrow, pale grey lores and orbital, and white throat.

Presumably the retention of juvenile characteristics varies considerably among individuals of the same age, as can be seen from the amount of buff on the wing-coverts of the two second-brood juveniles just mentioned. The white marks on the dorsal surface disappeared on the male at least two weeks before they did on the female;

in the case of the first-brood juveniles feeding at the nest, the female had less white streaking (confined to the crown) than the male, which was presumably the same age. However, by 26 March (two months after the second brood fledged) these two first-brood juveniles were indistinguishable from adults, even though they were probably less than six monhts old at this time. Juvenile characteristics may therefore endure longer on late broods, than they do on early brood birds.

Despite this variation, buff edging to the wing-coverts always persists long after the white markings on the upperparts are lost; it is probably the most reliable indicator of immaturity in all sittellas. Indeed, near Kyogle, New South Wales, eight (five male; three female) out of 31 specimens collected in mid-July 1979, showed traces of buff on the wing-coverts. These specimens also had duller legs and smaller gonads than most of the adults in the sample.

Variation in head colouration of sittellas may be age-related. It has been shown for many sexually dimorphic Australian passerines, that males do not attain full adult plumage until two or more years old (e.g. Golden Whistler *Pachycephala pectoralis*, Grey Shrike-thrush *Colluricincla harmonica*, Satin and Regent Bowerbirds *Ptilinorhynchus violaceus* and *Sericulus chrysocephalus*, and possibly some *Petroica* robins; see Disney, 1976 and Disney *et al.*, 1974).

I suggest that young female sittellas acquire dark head colouration rapidly (within the first few months?), but males retain a pale face, in their first year (or possibly longer in some forms). This differential development of adult head plumage by the sexes could explain the abundance of "white-faced" males of the western forms, *pileata* and *leucoptera*, particularly if sex ratios favour males. In fact the head of juvenile male *chrysoptera* (Fig. 2c) bears some resemblance to "white-faced" *pileata* when the crown loses the white markings and becomes dark grey. In conclusion, it appears juvenile *chrysoptera* may be sexed on the characteristics of the head, but that this dimorphism is not so obvious in adults. Whether or not the two sexes eventually have identical (monomorphic) head plumages remains to be resolved.

Conclusions

Both Hando (1970) and Cameron (1971) suggested that the offspring of one brood of sittellas assisted in the feeding of later broods, but neither mentioned the important features separating juveniles from adults. I have shown that the white markings on the upperparts of juveniles are lost within three months after fledging. The two unbanded juveniles feeding at the nest I observed must, therefore, have belonged to a brood raised by the four adults earlier in the same season. In the multi-brooded Superb Fairy-wren *Malurus cyaneus*, "nest-helping" was performed by juveniles only 58 days old (Rowley, 1965).

It seems only one female normally incubates in the sittellas; this is typical for most Australian co-operative breeding passerines studied to date. However, in the Superb Fairy-wren (Rowley, 1965), Yellow-rumped Thornbill *Acanthiza chrysorrhoa* (Ford, 1963) and Noisy Miner *Manorina melanocephala* (Dow, 1977) it was found that males rarely, if ever, fed the incubating female. Yet such behaviour is quite characteristic of Orange-winged Sittellas and all species of treecreepers prior to and during incubation (Noske, 1980 and unpubl. data).

There is little published information on the distribution of labour among individuals of co-operative breeding species. At the nest of sittellas studied, the primary (mated) pair contributed over half the total feeding effort of the group. Dow (1970) found that most activity at one nest of Noisy Miners was by two birds, although there were at least eight other visitors. The incubating female showed the highest rate of feeding visits to nestlings at this nest (Dow, 1970; Fig. 2). However, in a later study of this species, Dow (1978) found that the average contribution by males at each of 21 nests varied from 64 to 84 percent. The contribution by the single most active male at each nest averaged 17 to 29 percent, but as many as 14 males visited some nests.

Comparisons between miners and sittellas are naturally limited because of their differing social organizations. Miners do not live in discrete groups but in large colonies composed of small contiguous groups of males which collectively defend an exclusive area (Dow, 1978). My

observations of four groups of sittellas at Wollomombi Falls (some colour-banded), indicate that each group lives in a large but quite discrete territory, although considerable overlap occurs. The constitution of these groups however, varies within and between years with adult mortality and the annual increment of young. Males outnumber females in most groups collected to date.

Head colouration may not be a reliable guide for distinguishing the sexes in adult sittellas (see also Boles, 1980). In *chrysoptera*, adults of both sexes may possess dark (spotted) throats and blackish faces, although the latter is apparently less frequent in males. However, evidence presented here suggests that young birds (up to at least eight months old) are sexually dimorphic in head colouration: males are pale-faced with whitish eyebrows and throat, while females have dark faces and throats. It is not known whether males eventually develop plumage identical to the female; clearly more work, particularly observation of known-age colour-banded individuals, is necessary to solve the complexities of plumage variation in this species.

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