

CO-OPERATIVE PARENTAL CARE; CONTRIBUTION OF THE MALE RIFLEMAN (*Acanthisitta chloris*) TO THE BREEDING EFFORT

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ABSTRACT

A colour-banded population of Riflemen at Kowhai Bush, Kaikoura, New Zealand was studied to determine the contribution of males to the care of young. Parental care and territorial behaviour were qualitatively the same throughout the breeding period. Males fed the females during courtship and in this way contributed the food required to produce the first clutch of eggs. Males made 66% of nest-building visits (early nests), spent 50% more time incubating than their mate by day (both clutches), leaving the females the thermo-insular advantage of incubating at night, always fed young significantly more often than their mate and contributed 55-77% of all food items fed to broods without helpers (the great majority of nests), and shared territorial defence equally with their mate. However, nest-building and territorial defence occupied less than 1% of parents' time early in the breeding season. One widower was unable to fledge young alone. Early season sex ratios for the years studied were (M:F) 22:15, 50:35, 39:37 and 20:21 with extra males sometimes becoming helpers. The male's high parental effort was not reflected in significantly lower survival to the next breeding season. Possible reasons for the large contribution by the male Rifleman to the breeding effort are discussed.

INTRODUCTION

Kendeigh (1952) described the relative contributions of parents to breeding effort in many families of birds. He showed that in passerines males typically did relatively little towards caring for their young compared with their mates. However, this pattern may change with males sharing a more equal burden of rearing young when (1) the confidence of paternity and maternity is high, (2) more male parental care significantly increases productivity and (3) the opportunities for additional matings are limited or absent (Alexander & Borgia 1979).

The Rifleman is an insectivorous, monogamous, hole-nesting passerine. Riflemen have the following features which make them ideal species for studying parental care : (1) they will use nest boxes, (2) they are relatively easy to catch, and (3) they have sexually dimorphic plumage. In this paper I quantitatively describe Rifleman parental care throughout the entire breeding cycle to determine whether the male Rifleman is typical of other passerine males and outlays less effort than their mates caring for young or whether some other pattern is evident. Because territorial defence can be construed as energy spent defending a food resource for young, relative parental effort in defending territory is assessed.

METHODS

A colour-banded population of Riflemen was monitored in an 80 ha patch and a 6 ha patch of kanuka (*Kunzea ericoides*) seral forest near Kaikoura,

on the north-eastern coast of the South Island (42° 43' S, 173° 37' E). The great majority of breeding pairs used nest boxes built to the design of Gray (1969), except that I used elliptical entrances (20 mm maximum diameter hole) to exclude stoats (*Mustela erminea*). The forest is described in detail by Hunt & Gill (1979). Here I give a resumé of already published methods, (Sherley 1985, 1989, 1990a, 1990b, 1993, Sherley & Cunningham 1986) and methods not described elsewhere.

Nest monitoring

All nest attempts in nest boxes (and many in natural holes) were monitored almost daily and so the start of laying, laying interval, clutch size, incubation period, and the nestling period were determined.

Banding

Young were individually colour-banded, usually 4-5 days before they left the nest or occasionally as fledglings. Adults were caught either by flushing them off the nest while brooding about four days after chicks hatched, or by mist-netting adults soon after fledging a brood when adults responded well to tape-recorded calls of juveniles begging. Pair bond formation and mate fidelity could be monitored because >90% of birds were banded in the 6 ha study area and >75% in the 80ha study area.

Territorial behaviour

While studying courtship feeding, I spent 64 hours with pairs for intervals of 20 minutes or more during the pre-lay and laying periods. About 1000 hours were spent in Rifleman territories while checking nest boxes, maintaining tracks and monitoring parental care at nests. Whenever I saw or heard Riflemen, I followed them quietly until they were lost from view. Records were kept of any interactions with other Riflemen, the number of disputes, and which bird of a pair undertook defence under the following categories:

1. The number of disputes where both members of the pair were present and had the option to defend, but only the male chased the intruding bird(s),
2. As for (1) but the female defended,
3. Only the male of the defending pair was present and defended,
4. As for (3) but the female defended.

Whenever both male and female attacked, I scored them equally under (1) and (2).

Parental care

Nest-building included recording time spent in the nest and the number of visits with and without building material (Sherley 1990b). During courtship feeding, I calculated the amount of food fed to females as a proportion of (1) the male's and female's total food take and (2) what was theoretically required for the female's maintenance requirements (Sherley 1989). While parents incubated, I recorded the frequency of attentive visits, attentiveness on the nest by day and night, and the relative time available for foraging (Sherley 1990b). When young were cared for, I assessed the

quality of food delivered in terms of type and size of food item, the hourly rate of feeding, and the proportion of time spent brooding by day and night (Sherley 1990a).

Survival

For census purposes, 15 October was taken as early spring; however, any bird not seen on census day, but seen subsequently, was included in survivorship calculations. Parent survival to the following breeding season was calculated for birds of unknown age and birds in their first season of breeding ('yearlings'). For comparing parental survival with respect to relative parental care, a bird was only used once for analysis and must have successfully raised at least one brood. For birds of unknown age, the first season they were observed was chosen to score subsequent survival.

RESULTS

Male and female Rifleman both took part in all forms of parental care and territorial behaviour.

Territorial behaviour

Nine to 15 pairs bred successfully in the 6 ha habitat and 15-17 pairs in the 80 ha habitat. The difference in density may have been related to a large proportion of the bigger forest consisting of an area of unsuitable habitat in which no Rifleman was seen. Rifleman pairs were sedentary year round with young dispersing from their natal "territory" by the onset of winter (Sherley 1985). In five breeding seasons from mid August to late January, 63 territorial disputes were witnessed in which males and females participated equally in territory defence (Table 1). Males and females spent less than 1% of their time in territorial behaviour during the pre-lay and egg-laying periods (Sherley 1989).

TABLE 1 — Sex role partition in territorial defence

Encounters:	Categories of defending territory holders					
	Total involving males + females		Males or females had option to participate		Only one sex present	
Sex:	M	F	M	F	M	F
Frequency :	27*	36*	23	26	4	10
Chi Square :	1.29, P>0.05		0.08, P>0.05		-	-

* males and females both attacked intruders three times.

Pairs were often seen foraging in areas frequently occupied by their neighbours, even above their nest boxes; meanwhile neighbours would often continue feeding young or continue foraging apparently unconcerned.

Courtship feeding

Males progressively gave more food to females as the laying period approached (Figure 1 in Sherley 1989). Overall, they fed 42% (by weight) of the food they collected to females, and this food comprised 35% of her

total intake over the pre-lay and egg-laying periods (Sherley 1989). It was estimated that females caught enough food for their maintenance needs which implied that food required for egg-formation was obtained from courtship feeding.

During the pre-lay and egg-laying periods, pairs were followed for 20 minutes or more, for a total of 64 hours. Males and females spent on average 91.2% (SD = 21.9) of their time within 20 m of each other. Males did not feed females during incubation, or before or during second clutch egg-formation.

Nest-building

Males contributed more than females towards building first clutch nests, taking building material to nests significantly more often than females (\bar{x} males = 8.6 visits per hour, SD = 5.9, N occasions nests watched = 56; \bar{x} females = 4.4 visits per hour, SD = 3.9, N = 57; Wilcoxon matched pairs sign rank test, $Z = 4.27$, $P < 0.001$) and making 66% of the building visits (Sherley 1985; 1989). It was apparently the same building second clutch nests since at one nest, observed on three occasions for 274 minutes, males and females made visits with building materials at a rate of 18.8 and 10.5 visits per hour and stayed in the nest for 16.3 and 2.2 minutes respectively. Nest-building however, was probably a relatively insignificant outlay of energy since less than 1% of male's and female's time was spent building first nests and probably less building second clutch nests since they were significantly lighter (\bar{x} second clutch nests = 37.6 g, SD = 6.7, N = 46; \bar{x} first clutch nests = 40.5 g, SD = 6.7, N = 124; 1-tailed Mann Whitney U test $U = 3436.5$, $P < 0.02$; Sherley 1990b).

Incubation

During daylight hours, males spent one and a half times longer incubating than females. The median attentiveness (proportion of time spent on the nest) of males and females during first clutch incubation was 48% and 33% (95% confidence intervals 47-52% and 32-35% respectively, 225 one-hour observation periods). For second clutch incubation the corresponding figures for males and females were 45% and 33% (95% confidence intervals 27-42% and 30-35%, 152 one-hour observation periods). The difference in day-time attentiveness allowed females approximately two hours more time than the male for feeding. This may have been related to her requiring extra food to recuperate after egg-laying (Sherley 1990b).

Care of young

Nestlings hatched blind and without down (which did not subsequently develop) and weighed between 1.0 and 1.4 g (Sherley 1985). For the first 4 days they were just able to raise their heads, gape and emit soft peeping sounds to beg. By 10-12 days all the pterylae were developed with feathers just erupting and the eyes were at least half open. By this age, adults had stopped brooding.

Nests were sometimes attended by non-parent adults or juveniles from the current season's first brood helping to feed young. Between 1980 and 1984, 28% of first broods and 52% of second broods had helpers present.

However, helpers contributed significantly to feeding young at only 8% and 4% respectively of first and second clutch nests (Sherley 1990a). Hence presence or absence of helpers does not materially affect comparisons of parental effort.

Males and females gave food items of similar size and type to young (Figure 1 and Table 4, Sherley 1990a). Males fed young significantly more often than females while caring for first clutch nestlings and fledglings, and second clutch fledglings (when helpers were absent). When helpers were present while caring for these young, this pattern persisted for most of the time (Appendix 1, Sherley 1990a). Male parents at second clutch nests without helpers fed young significantly more often than their mates and contributed most of the food items delivered (Table 2).

TABLE 2 — Frequency of parents feeding second clutch nestlings in the absence of helpers (means, standard deviation)

Nesting period days	1 - 4	5 - 8	9 - 12	13 - 16	17 - 20	21 - 24
Males	7.3(4.8)	10.6(7.2)	15.4(7.1)	16.9(8.0)	16.3(10.0)	13.4(7.6)
Females	5.2(3.0)	6.5(4.4)	8.4(5.8)	9.3(6.7)	11.3(6.8)	10.8(6.9)
N ¹	58	59	49	64	64	26
P ²	*	*	*	*	*	NS

Key: 1 - Number of 30 minute intervals spent observing parents feeding young.
 2 - Wilcoxon matched pairs sign-rank one-tailed test (since means for males were larger).
 * - Sign-rank test significant, $P < 0.001$.
 NS - Sign-rank test not significant, $P > 0.05$.

Over the entire second clutch nestling period, males brought 55-65% and females 35-45% of the food items to chicks (data based on observations of at least five different individual pairs within each four-day interval of the nestling period).

Male parents fed second brood fledglings on average 6.0 food items per offspring per hour (SD = 0.8, number of 30 minutes occasions watched = 48), significantly more than females ($\bar{x} = 3.0$, SD = 0.5, N = 48; Mann Whitney U test, $U = 1975$, $P < 0.01$). Male parents contributed 62% and females 38% of all food items fed to fledged young.

One male and one female lost their mate part way through raising their first broods. The male continued feeding the five young until they started to leave the nest, four days later than usual. One nestling died in the nest and the others fledged over two days. Two were unable to fly and none survived to the onset of winter. The female's nest was preyed on before the young could fledge.

Overlapping parental duties between early and late broods

The duration of the incubation and nestling periods recorded for Riflemen at Kowhai Bush were similar to those reported by Gray (1969): incubation mean = 19.6 days, SD = 0.8, N = 80 (incubation started upon laying the

penultimate egg-scored as Day 1 and eggs usually hatched synchronously); nestling period mean = 24.0 days, S.D. = 1.2, N = 50 (first and second broods, day of hatching scored as day 0). Of 91 pairs studied, 39 (43%) raised one brood to fledging in a breeding season, 47 (52%) raised two and 5 (5%) laid second clutches having fledged their first brood but did not raise young. The numbers of pairs that were recorded as raising two broods to fledging may have been underestimated because some second broods may not have been found.

Fledglings from first and second broods reached independence four to five weeks after leaving the nest. Because the average time between fledging the first clutch and laying the second was 8.0 days (S.D = 4.0, range = 2-16 days, N = 38) and laying the average second clutch took 3.8 days (S.D = 0.6, range = 5-7 days, N = 41), parents had to feed dependent first brood fledglings for about three weeks while nest-building, laying or incubating the second clutch. This overlap correlated with a lower level of male attentiveness compared with the rest of the time they spent incubating second clutches because male parents undertook most of the feeding of first brood fledglings. During the first four days incubating second clutches, the male's attentiveness was down 10-14%, and the female's attentiveness was 3% higher than her mate's (Sherley 1990a). By half way through incubating the second clutch, first brood young became independent, and the pattern of incubation seen during first clutches was re-established, where the male spent 9-13% more time on the nest than the female.

Early season sex-ratio and pair-bonding

In 1980-81, 1981-82, 1983-84 and 1984-85 the sex ratios (males:females) on or after October 15 were respectively - 22:15, 50:35, 39:37 and 20:21. The totals for 1981-82 and 1983-84 are higher than the others because both patches of forest were studied. Nearly all of these extra males became helpers (see Sherley 1990a). Birds paired at the first opportunity after independence and all combinations of adults and juveniles were observed. Only two "divorces" were observed, one of these involved a bird emigrating. Other birds formed a new pair-bond only after an individual disappeared permanently - presumably dead. Thus unpaired adults at the start of a breeding season were in the main restricted to pairing with that season's fledglings. Some of these adults became helpers and paired with one of the young from that nest (see Sherley 1990a).

Survival of parents

Despite the male contributing most towards parental care, there was no significant difference between parents in their chances of survival to the next season (2 tail Fisher's exact tests; unknown aged birds P = 0.55, yearlings P = 1; Table 3).

TABLE 3 — Number of Rifleman parents that successfully fledged at least one brood in the first year they were studied and survived in the next breeding season.

	Unknown aged birds		Yearlings	
	Males	Females	Males	Females
No. in first study year	34	30	13	22
No. surviving to second study year	25(73%)	16(53%)	11(85%)	19(86%)

DISCUSSION

Throughout the breeding cycle the male Rifleman co-operated with his mate by providing most of the parental care. The importance of courtship feeding to the female is evident since the male's contribution probably supplies the female with the energy and much of the nutrition required for first clutch egg formation. Thus males substantially invested in their offspring before first clutches were laid. Males spent over 90% of their time in their mate's company before and during egg-laying (Sherley 1989) which probably allowed them ample opportunity to prevent cuckoldry. Before second clutches, males were again in close contact with their mate while feeding their first brood. However, there may have been some degree of mixed parentage of offspring since "egg dumping" (unusually large clutches laid in atypically short times) was recorded at three nests (Sherley 1985).

There was strong evidence that territorial behaviour and nest-building were minor components of total parental effort over the breeding cycle. Besides, territorial defence was shared equally by parents. That males undertook most building may have been related to their starting several nests before finally the females joined in, and apparently "decided" which nest to use (Sherley 1985).

If males were truly co-operating in parental care, one would expect their behaviour to be sensitive to competing demands rearing two broods simultaneously, especially if one demand for parental care incurred a greater outgoing in energy. Feeding young demands the greatest rate of energy consumption of all forms of parental care (Ricklefs 1974). Male Riflemen did shift their work-load during second clutch incubation by reducing incubating effort (Sherley 1990b) and bringing most of the food to fledglings of first clutches (Sherley 1990a). Otherwise, the males undertook most of the incubation which probably allowed the female foraging time to recuperate from egg-laying (Sherley 1990b).

Male parents displayed little aggression towards non-paired adult helper males which, when they were present, started feeding young after the fourth day of the nestling period (Sherley 1990a). Some of these helpers (termed "regulars") contributed a significant amount of food to the young (in and out of the nest) without the total volume of food to these broods being increased. Instead the male parent's feeding rate dropped significantly compared to male parents without regular helpers (Sherley 1990a). The opportunism exhibited by male parents accepting relief from parental duties was matched by that of their helpers, some of whom paired with female offspring from the nest they helped. One even paired in the same season with a breeding female when her mate died (Sherley 1990a).

It is hard to argue that surplus males early in the season accounted for the observed high degree of male parental care. This is because the sex ratio was not consistently different from unity and in two of the four seasons studied it differed only slightly (Sherley 1990a). While a long-term study could resolve this issue, and one cannot completely dismiss the influence of limited opportunities for additional matings, it is probably a minor component compared to the advantages of co-operative parental care which must have maximized efficiency and, ultimately, productivity. The suggestion that productivity was improved with co-operative parental care

was supported by the inability of the lone male parent to successfully fledge its offspring. Similarly, Smith *et al.* (1982) found that the young of unaided female song sparrows (*Melospiza melodia*) grew more slowly, more young died, and fewer offspring survived than offspring from broods where both parents fed.

One cannot conclude that because male Riflemen undertook most parental care they experienced the greatest cost in terms of survival. In fact, the evidence is that there was no concomitant increase in mortality due to the male's high parental effort (Table 3). There may be some unaccounted for (and impossible to measure) equalisation of parental effort with the stress involved in egg-formation. However, there remains no doubt that Riflemen display a highly co-operative system of parental care.

Do other small native passerines in New Zealand display co-operative parental care? Within the family Acanthisittidae, Rock Wren (*Xenicus gilviventris* - a 13-15g hole-nester) which lives permanently in the sub-alpine zone in the South Island, is territorial with the male sharing equally in nest-building, incubation, brooding and feeding the young (Michelson-Heath 1990). Further, by feeding their mates, males "made a significant contribution to the food supply of the female at all stages of the breeding cycle" (Michelson-Heath 1990).

Studies of four other passerines at Kowhai Bush showed that males of these species also contributed a great deal towards parental care and territorial defence (Table 4). Thus, there seems to be a pattern of high male parental care in at least the small insectivorous New Zealand passerines, especially if one accepts that territorial defence may be interpreted as defending a food resource for the male's young and his mate. My comparison of Riflemen with these species is not confounded with any of them being polygamous or migratory.

TABLE 4 — Role of male parents of five passerines at Kowhai Bush in parental care and territorial defense

Behaviour	Species				
	Rifleman ¹	Grey Warbler ²	Fantail ³	Brown Creeper ⁴	Robin ⁵
Territorial defence	2	3	2	2	2
Courtship feeding	3	0	3	0	3
Nest-building	2	1	2	2	1
Incubation	3	1	2	1	1
Incubating bird					
Fed by partner	0	0	3	3	3
Feed nestlings	3	2	2	2	2
Feed fledglings	3	2	2	2	2
Mean body weight (grams, sample size)	5.5-7.0,53	6.4,7	7.9,17	13.4,51	34.9,27

Key: 0 = none occurs, 1 = bulk or all done by female parent, 2 = shared with female parent, 3 = bulk or all done by male parent.

Note: I have observed incubating fantails being fed but have not known the sex of either bird.

Authorities: ¹ - this study, ² - Gill (1980), ³ - Powlesland (1982), McLean (1980),

⁴ - Cunningham (1983), ⁵ Powlesland (1980).

Gill (1982) postulated that the Rifleman and other Kowhai Bush passerines have longer laying intervals, incubation and nestling periods than Northern Hemisphere passerines because food is scarcer in New Zealand and does not allow faster development. Niethammer (1970) reported that Northern Hemisphere passerines introduced to New Zealand have lengthened their breeding cycles or reduced their clutch sizes. If food scarcity is important, this added constraint would add to the advantage of Rifleman adopting a system of co-operative parental care.

An alternative explanation for the male Rifleman's large contribution to rearing offspring may relate to the small body size of the species (at 5.5 - 7.0 g it is one of the smaller passerines). Allometric equations relating diminishing body size in birds to biophysical parameters predict an increasing rate of energy consumption (Calder 1974), shorter physiological life span (Calder 1974, Kendeigh *et al.* 1977), a reduced ability to store energy (Walsberg 1983) and the need to maximize efficiency ratios (such as work output to energy intake), an increase in the rate of basal metabolic rate per unit mass (Kendeigh *et al.* 1977), increasing rate of heat loss (Kendeigh *et al.* 1977) and energy stress. When the evolution of small body size is coupled with the requirements of endothermy, extended postnatal parental care and altriciality have resulted (Hopson 1973; Case 1978). These factors which characterize small endotherms must influence each other. For example, the need to maximize efficiency should be related to parental care.

The need to maximize efficiency should be greatest in small passerines. One method to increase efficiency and decrease the biophysical limitations imposed by very small body size could be to (1) co-operate in parental care and produce altricial young which would enable greater investment cost-sharing (Case 1978) and (2) form monogamous pair bonds. Evidence for these characteristics has already been described. For example, care of young by male Goldcrest (*Regulus regulus*) facilitates double brooding because the male feeds first brood young while the female is incubating the next clutch (Haftorn 1986). That male parental care is necessary for reproductive success has been shown by experiments in which the male is removed (e.g. Weatherhead 1979, Smith *et al.* 1982, Lyon *et al.* 1987, Alatalo *et al.* 1988).

The fact that the male Rifleman undertook most parental care, unlike many other passerine male parents, is made more exceptional because they weighed on average 1.5g less than females (Sherley 1993) and must have been under tighter energetic constraints such as higher rate of heat loss, less ability to store food and higher basal metabolic rate.

If energetic considerations influence parental behaviour then breeding behaviour should be correlated with climate, especially temperature. Finch's (1984) study on Abert's Towhee (*Pipilo aberti*) showed that 78% and 28% of the variation of the female's daily energy expenditure over the incubation and nestling periods respectively was explained by mean daily air temperature. That air temperature significantly influenced Rifleman behaviour was supported by the significant negative correlation of attentiveness with increasing ambient temperature over the second half of incubating the first clutch and the entire incubation of the second clutch (Sherley 1985).

In small passerines which display high male parental care, the pattern of male parental care is more likely a product of necessity rather than poor mating opportunities (eg. Brunton 1988; Alexander & Borgia 1979). The other explanation for male parental care (apart from an increase in offspring success) that has been given is a high confidence of paternity (Brunton 1988). While it has been shown that mixed parentage happens in other small birds, high male parental care and consequent attendance at the nest and on the female (eg. courtship feeding in Rifleman) must minimize the risk of cuckoldry and at least pay off with improved productivity.

While other factors such as feeding ecology and food availability are undoubtedly implicated in the evolution of the extent of male parental care, the energetic constraints associated with endothermy, small size and altriciality, and the concomitant need to maximize efficiency have had an influence, and evidence for this is apparent in New Zealand's smallest passerine - the Rifleman.

ACKNOWLEDGEMENTS

The research was funded by a New Zealand Government Wildlife Service Scholarship and a New Zealand Royal Forest and Bird Protection Society Stokker Scholarship.

For their support and advice, I thank John Warham, Ian McLean, Ian Stewart, Peter Horn, Jack van Berkel, and Brenda Sherley. Thanks to Ian Flux, Don Newman and Mike Fitzgerald for critical review of the text.

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