SOCIAL SYSTEM AND HELPING BEHAVIOR IN THE WHITE-BANDED TANAGER (*NEOTHRAUPIS FASCIATA*)¹

MARIA ALICE S. ALVES²

Departamento de Ecologia, Universidade de Brasília, 70910 Brasília, DF. Brasil

Abstract. Banded Neothraupis fasciata were found in both unispecific groups and mixedspecies flocks throughout the year, in cerrado (savanna) near Brasilia, Brazil. Groups with a mean of 3.0 individuals defended permanent territories. Territory size seemed to approach home-range size which was estimated for one group as being 4.3 ha. Some banded nestlings remained with their parents until the onset of the first reproductive season after birth. Pairs were occasionally assisted by helpers, which were either males or females, apparently offspring from prior years. Helpers had multiple roles, such as assisting in feeding nestlings, assisting in territorial defense, and acting as sentinels, which may increase protection against predation.

Key words: White-banded Tanager; Neothraupis fasciata; Thraupidae; social organization; reproductive behavior; helpers; sentinels; mixed-species flocks; cerrado.

INTRODUCTION

Skutch (1961) described helping activities in 130 species, including seven tanagers (Thraupidae). Subsequent long-term studies, many using colored bands, have increased the list of species which show cooperative reproduction (Emlen 1984, Brown 1987). Tanagers are also known to be frequent components of mixed-species flocks of birds (Sick 1985), and may occur as groups within these flocks.

Neothraupis fasciata, the only species of its genus, lives in the cerrados of Central Brazil (Pinto 1944). Its biology was little known until recently. Nest, eggs, and nestlings were described by Alves and Cavalcanti (in press). Silva (1980) showed that *N. fasciata* participated in mixed-species flocks as a central or nuclear species, helping maintain these flocks through movements and vocalizations.

Herein I present data on social structure and cooperative breeding, and describe the sentinel behavior of N. fasciata. Possible advantages of participation in mixed-species flocks for this species and some reasons for its helping behavior are discussed.

METHODS

Neothraupis fasciata was studied at the Ecological Station of the University of Brasilia (UnB), between August 1983 and December 1987. The station is 20 km SW of Brasilia, Brazil, at 15°57'S and 47°56'W and includes ca. 2,300 ha of native vegetation (Ratter 1986). The study area, together with neighboring areas (Ecological Station of IBGE and the Botanical Garden of Brasilia) form a continuous zone of cerrado of more than 10,000 ha. There are two distinct seasons: rainy (October to March) and dry (April to September).

The work has been done in cerrado sensu strictu (Eiten 1984) with little human disturbance. Seventy-six individuals of *N. fasciata* were captured with mist nets and marked with aluminum and color bands (15 nestlings, four fledglings, 14 young and subadults, 28 adult males and 15 females). Observations were along a dirt road of 1,900 m, marked at intervals of 50 m. From August 1986 to July 1987, censuses were made four times a month. Each mixed-species flock found was followed for 10–45 min (generally 20 min) and, sex, age, and color bands of *N. fasciata* recorded.

A grid of 16 ha was marked in quadrats of 25 m to help delimit home ranges. Observations from April to June 1987 resulted in 32 trackings. When a group of *N. fasciata* was detected, its composition and initial location were recorded. Home range was estimated using the Minimum Convex Polygon method (Jennrich and Turner 1969).

¹ Received 19 September 1989. Final acceptance 7 February 1990.

² Present adress: School of Molecular and Biological Sciences, University of Stirling, Stirling FK9 4LA, Scotland.

TABLE 1.	Participation of groups of Neothraupis fas-	
ciata in mix	ed-species flocks and in unispecific flocks.	

	Number of observations				
Group	Mixed-species flocks	Unispecific flocks	Total		
1	2	3	5		
2	13	6	19		
3	10	5	15		
4	8	2	10		
5	13	11	24		
6	12	6	18		
7	9	0	9		
8	15	7	22		
9	11	11	22		
10	1	1	2		
11	11	4	15		
12	1	0	1		

RESULTS

SOCIAL STRUCTURE

Neothraupis fasciata formed unispecific groups of up to six individuals ($\bar{x} = 3.0$, SE = 1.05), which actively participated in mixed-species flocks (Alves and Cavalcanti, unpubl.). Between August 1986 and July 1987, 12 different groups were observed as unispecific groups or in mixedspecies flocks (Table 1), being more frequently in mixed-species flocks (Wilcoxon's test, t = 1.5, P < 0.01).

The size and composition of groups in the reproductive season are given in Table 2. The commonest social unit was a pair and offspring (nestlings and young) and a pair with another adult and offspring. Occasionally offspring were joined by subadults, that were evidently offspring born in a previous reproductive season (for example, groups 2, 3, and 5 in 1987, Table 2). An adult was sometimes found helping a reproductive couple (n = 3).

Groups were generally stable in composition and home range and changed little between years. Some marked individuals stayed in their areas for more than 3 years.

Home range was delimited only for group 5 (a pair and offspring, Fig. 1). This area, determined from April to June in 1987, was 4.3 ha (n = 30). Six other groups had their home range just partially inside the grid. Home-range areas were essentially territories, because distances between nests ranged from about 200 to 300 m; the area usage was relatively exclusive and fixed; there were hostile interactions between birds of differ-



FIGURE 1. Territory of group 5 of *Neothraupis fasciata*. Six other groups had their home range demarcated partially; based on observations made during line censuses (April–June 1987). Dot-dash line = dirt road; x = nest, discovered in October 1986.

ent groups; individuals approached playback of vocalizations, vocalizing strongly. The group members formed a social unit, feeding within and defending the area together.

REPRODUCTIVE AND SENTINEL BEHAVIOR

In the study area, *N. fasciata* bred during the wet season (September to January). Copulation was observed only once (16 September 1986). The female had nest material in her beak, perched on a tree limb; the male approached from the rear, mounted, and completed copulation in a few seconds.

Only females built the nest, but males accompanied and helped females with feeding the young. Pairs were apparently monogamous. Three of seven (43%) observed nests had helpers, which were either males (n = 2) or females (n = 1). In this last case, the nest had five eggs and the helper did not incubate (Alves and Cavalcanti, in press).

The origin of helpers was not known. However individuals marked as nestlings or fledglings in 1986 were found with their parents in the same areas until the following reproductive season. Of 19 young banded, five were observed for a minimum of 5 months, while three were observed until the the following reproductive season.

Participation of male, female, and helper in feeding nestlings did not differ significantly (Table 3). Besides feeding nestlings, helpers also acted as sentinels and assisted in territorial defense

Group co	ode	2	3	5	6	7	8	9	11
1984									
Α	M F		1 1	2 1		1 1	1 1		1 1
I Y							1		
Y N			1	1		1 3			3
Total			3	1 4		6	3		5
1985			5	7		Ū	5		5
A	м				1				
	M F				1				
I Y N									
Y N					2				
Total					4				
1986									
Α	M F	2 1	1	1	1 1	2 1	1 2	1 2	
	F	1	1 1	1 1	1	1	2	2	
I Y		1				2 *	1		
N		1 2	2	3	2	2	1	2	
Total		6	4	5	4	5	4	5	
1987									
Α	М	1	1	1	1				
.	F	1	1 1 **	1	1				
I	M F	2 (1**)	1 **	1 **					
Y	-			•	1*				
N									
Total		4	3	3	3				

TABLE 2. Composition of marked *Neothraupis fasciata* groups in the reproductive seasons of 1984–1987. A = adult, I = immature, Y = young, N = nestling, M = male, F = female. * = young of the same year, ** = young of the preceding year.

(mainly with the reproductive male, since the female stayed on the nest brooding nestlings, at times for more than 1 hr at a stretch).

Nestlings were not seen flying until 6 days after leaving the nest. During these 6 days, the fledglings stayed on the ground and in low shrubs, calling for food. The fledglings were foraging by themselves in the family groups at a mean of 30 days (n = 3) after leaving nests.

Male and female *N. fasciata* showed sentinel behavior both in unispecific groups and mixedspecies flocks. One individual of the group perched on a bush or tree, above the rest of the group (usually above 3 m high), and turned its head, apparently watching. The rest of the group fed in low bushes and on the ground. The sentinel called when the observer or a predator approached.

Generally sentinels alternated. Occasionally

two individuals were sentinels at the same time. Usually the sentinel called faintly at short time intervals; the sound was hard to locate unless the bird was seen first. When a sentinel changed its perch, it called loudly and frequently and then another sentinel took its place or the group moved elsewhere.

ANNUAL VARIATION OF *NEOTHRAUPIS* FASCIATA IN MIXED-SPECIES FLOCKS

Neothraupis fasciata was the nuclear species of mixed flocks (Alves 1988; Alves and Cavalcanti, unpubl.) which were often detected through calls of this species, generally contact calls (Alves 1988). Groups were observed 106 times in mixed-species flocks and 56 times as unispecific groups between August 1986 and July 1987. The participation of this species in unispecific groups showed a peak during the dry season (June), and

Obser- vation Nest time		Birth date of young	Dates of observation	No. visits						
				Parents		Helpers		•		
				М	F	M	F	G	gl	P
1	18	4 or 5 October	6, 7, 13, 14 October	16	17	_		0.06	1	ns
2	18	25 October	29, 31 October 1 November	58	44	_		1.88	1	ns
3	12	14 October	17, 18 October	15	24	_	24	3.54	2	n
4	12	12 November	14, 15 November	24	17	17	—	1.72	2	ns
[otal	60			113	102					

TABLE 3. Parents' and helpers' participation in visits to the nests of *Neothraupis fasciata*. M = males, F = females. * = P < 0.05.

decreased until October (probably due to reproduction). After this *N. fasciata* returned to mixedspecies flocks (Fig. 2). The low participation in mixed-species flocks in January may have been caused by a second nesting of some pairs that lost their offspring in October or November.

DISCUSSION

In Brown's (1987) classification, *N. fasciata* fits among territorial species with cooperative reproduction. Gaston (1978) stated that species with group territories and cooperative reproduction maintain permanent groups of up to 20 birds; generally one couple breeds in each season and groups frequently comprise nonreproductives of both sexes, corresponding to the situation in *N. fasciata*. Pairs of *N. fasciata* were monogamous and this also is frequent in cooperative reproductive systems (Brown 1987).



FIGURE 2. Annual cycle of *Neothraupis fasciata* in mixed-species flocks (below line) and in unispecific groups (above line) from August 1986 to July 1987.

In this study, some young stayed with their parents for a long time (some until the following reproductive season), suggesting that individuals of previous breeding seasons help their parents bring up later broods. Cooperative reproduction is known in some other tanagers, usually with one or two helpers, which may be females (Skutch 1961). Among these, *Habia gutturalis*, a dense forest dweller, can have immatures helping to feed nestlings, and they are probably individuals of previous broods (Willis 1961).

Avian communal breeding systems have a higher frequency in regions where permanent residency on the same territory is common (Brown 1987). Group territoriality is associated with cooperative breeding (Gaston 1978, Brown 1987) which may be viewed as a consequence of the territorial group behavior (Gaston 1978). Among the ecological factors considered to cause selection for group territorial behavior are high survival of adults and saturation of appropriate habitats. Accurate data about adult density and mortality of N. fasciata are lacking, but survival of this species seems to be high, because some marked individuals have been found in the same territories for a minimum of 4 years. Furthermore, a lack of space between territories (Fig. 1) suggests saturation of habitat.

Individuals may use their status as helpers as a step to breeding in their territories or in neighboring areas. This transition has been observed in almost all the territorial species that have been studied for a sufficient time to detect it (Brown 1987). In the case of *N. fasciata*, a male helper changed to a neighboring territory and reproduced after first assisting a breeding couple.

Winterbottom (1943) and Moynihan (1962) stated that a necessary factor in mixed-species flock formation seemed to be an intraspecifically

social species that developed some adaptations to sociality and attracted other species that had not developed these adaptations. Thus intraspecifically social species would become the nuclear species for a mixed-species flock. *Neothraupis fasciata* is nuclear (Alves and Cavalcanti, unpubl.), is intraspecifically social, and shows features of nuclear species (Moynihan 1962) such as neutral plumage and reduced interspecific aggressivity (Silva 1980). The high frequency of participation of *N. fasciata* in mixed-species flocks is related to a reduced sentinel time in these flocks (Alves 1988; Alves and Cavalcanti, unpubl.) suggesting that participation in mixed-species flocks may improve defense against predation.

The fact that *N. fasciata* helpers assist to feed nestlings agrees with previous observations of other species. In most birds with cooperative reproduction, the helpers feed nestlings (Lack 1972, Brown et al. 1978, Wilkinson and Brown 1984) and also help in territorial defense (Verbeek and Butler 1981, Hunter 1985, Brown 1987). In *N. fasciata* helpers not only perform these two tasks but also act as sentinels. This last role may increase protection against predation which is further aided by participation in mixed-species flocks. If helpers perform this task in other Thraupidae as well, its role in the biology of this family may be more pervasive than Skutch (1976) already acknowledges.

ACKNOWLEDGMENTS

I thank Roberto B. Cavalcanti for supervision and helpful suggestions throughout the study. The constructive criticism of E. O. Willis greatly improved the manuscript. Fernando A. S. Fernandez and Cláudia A. Magalhães gave enthusiastic support and encouragement, and commented on an earlier draft of the manuscript. Two anonymous referees and D. M. Bryant offered valuable suggestions for improving this paper. Many people assisted in fieldwork, especially Carlos Alves, Maria Gracinda S. Alves, Rita C. S. Medeiros, and Carolyn B. Proença. Paulo T. Z. Antas of CE-MAVE provided suggestions and the loan of mist nets and bands. This work was supported by University of Brasília (UnB) and University of Campinas (UNI-CAMP), with grants from the Brazilian National Research Council (CNPq), Ministry of Education (CAPES), and Fundação M. Brown.

LITERATURE CITED

ALVES, M.A.S. 1988. Organização social e biologia reprodutiva de Neothraupis fasciata (Passeriformes: Thraupidae). M.Sc.thesis, Univ. of Campinas, Campinas, Brazil.

- ALVES, M.A.S., AND R. B. CAVALCANTI. In press. Ninho, ovos e crescimento de filhotes de Neothraupis fasciata. Ararajuba.
- BROWN, J. L. 1987. Helping and communal breeding in birds. Princeton Univ. Press, Princeton, NJ.
- BROWN, J. L., D. D. DOW, E. R. BROWN, AND S. D. BROWN. 1978. Effects of helpers on feeding of nestlings in Grey-crowned babbler (*Pomatostomus temporalis*). Behav. Ecol. Sociobiol. 4:43–59.
- EITEN, G. 1984. Vegetation of Brasília. Phytocoenologia 12:271-292.
- EMLEN, S. T. 1984. Cooperative breeding in birds and mammals, p. 305-339. *In* J. R. Krebs and N. B. Davies [eds.], Behavioural ecology: an evolutionary approach. 2nd ed. Blackwell, Boston.
- GASTON, A. J. 1978. The evolution of group territorial and cooperative breeding. Am. Nat. 112: 1091–1100.
- HUNTER, L. A. 1985. The effects of helpers in cooperatively breeding Purple Gallinules. Behav. Ecol. Sociobiol. 18:147–153.
- JENNRICH, R. J., AND F. B. TURNER. 1969. Measurement of non-circular home range. Theor. Biol. 22: 227–237.
- LACK, D. 1972. Ecological adaptations for breeding in birds. Chapman and Hall, London.
- MOYNIHAN, M. 1962. The organization and probable evolution of some mixed-species flocks of neotropical birds. Smithson. Misc. Collect. 143:1–140.
- PINTO, O.M.O. 1944. Catálogo das Aves do Brasil. Pt. 2. São Paulo.
- RATTER, J. A. 1986. Notas sobre a Vegetação da Fazenda Água Limpa. (Texto no. 3). Editora Universidade de Brasília, Brasília.
- SICK, H. 1985. Ornitologia Brasileira: uma introdução. v. 2 Editora Universidade de Brasília, Brasília.
- SILVA, E.M.D. 1980. Composição e comportamento de grupos heteroespecíficos de aves em área de cerrado, no Distrito Federal. M.Sc.thesis, Univ. of Brasilia, Brasilia, Brazil.
- SKUTCH, A. F. 1961. Helpers among birds. Condor 63:198-226.
- SKUTCH, A. F. 1976. Parent birds and their young. Univ. of Texas Press, Austin.
- VERBEEK, N.A.M., AND R. W. BUTLER. 1981. Cooperative breeding of the Northwestern Crow Corvus caurihus in British Columbia. Ibis 123:183– 189.
- WILKINSON, R., AND A. E. BROWN. 1984. Effects of helpers on the feeding rates of nestlings in the Chestnut-bellied Starling Sprea pulcher. J. Anim. Ecol. 53:301–310.
- WILLIS, E. O. 1961. A study of nesting ant-tanagers in British Honduras. Condor 63:479–503.
- WINTERBOTTOM, J. M. 1943. On woodland bird parties in northern Rhodesia. Ibis: 437–442.