BROOD DIVISION IS ASSOCIATED WITH FLEDGLING DISPERSION IN THE BLUETHROAT (LUSCINIA S. SVECICA)

KRISTIN ANTHONISEN, CHRISTIN KROKENE, AND JAN T. LIFJELD[1]

Zoological Museum, University of Oslo, Sars gate 1, N-0562 Oslo, Norway

ABSTRACT.—In many bird species with biparental care, each parent takes the exclusive care of some of the young after fledging. Some of the hypotheses that have been put forth to explain brood division behavior state that it is advantageous for a particular parent to care for a particular "type" of young, e.g. with respect to sex, size, or parentage. Other hypotheses claim a benefit to the parents (e.g. reduced foraging costs or risks of predation) only when the young are spatially dispersed. In this paper, we describe brood division in a Norwegian population of Bluethroats (Luscinia s. svecica). In general, brood division arose once the young became spatially dispersed after fledging. The only exceptions to the rule occurred when the male was polygynous and provisioned the young at a low rate. No brood division was found when the young were still in the nest, nor when they were physically prevented from spacing out by an enclosure around the nest. Young fed by the same parent were more clustered than young fed by different parents. Experimental switching of young among single-parent groups suggested that parents were able to recognize individual offspring outside the nest. However, there were no indications that parents divided the brood by sex, size, or genetic parentage. Our data are consistent with hypotheses that assume a parental benefit from brood division when the young are spatially dispersed. Received 13 September 1996, accepted 7 April 1997.

IN MANY BIRD SPECIES with biparental care, the parents divide the brood after fledging so that each parent takes sole care of some young (Skutch 1976). This phenomenon is known as brood division (Smith 1978, McLaughlin and Montgomerie 1985), and the association between a parent and its young is termed a "family unit" (Nolan 1978). Many reports on brood division are anecdotal and provide no data. However, some studies of brood division are more detailed and well documented (e.g. Smith 1978, Moreno 1984, Harper 1985, McLaughlin and Montgomerie 1985, Kopachena and Falls 1991).

In many altricial species, particularly open nesters, the young leave the nest early (Maher 1964), often before they are completely developed and able to fly (Tinbergen 1939, Skutch 1976, Knapton 1978, Kopachena and Falls 1991). Early nest departure coupled with spatial dispersion of young is viewed as a strategy to minimize the risk of predation (Tinbergen 1939, Maher 1964, Willis 1972, Knapton 1978, Nolan 1978) and/or to help parents reduce the energetic costs of parental care (McLaughlin and Montgomerie 1989a,b). Spatial dispersion

[1] Address correspondence to this author. E-mail: j.t.lifjeld@toyen.uio.no
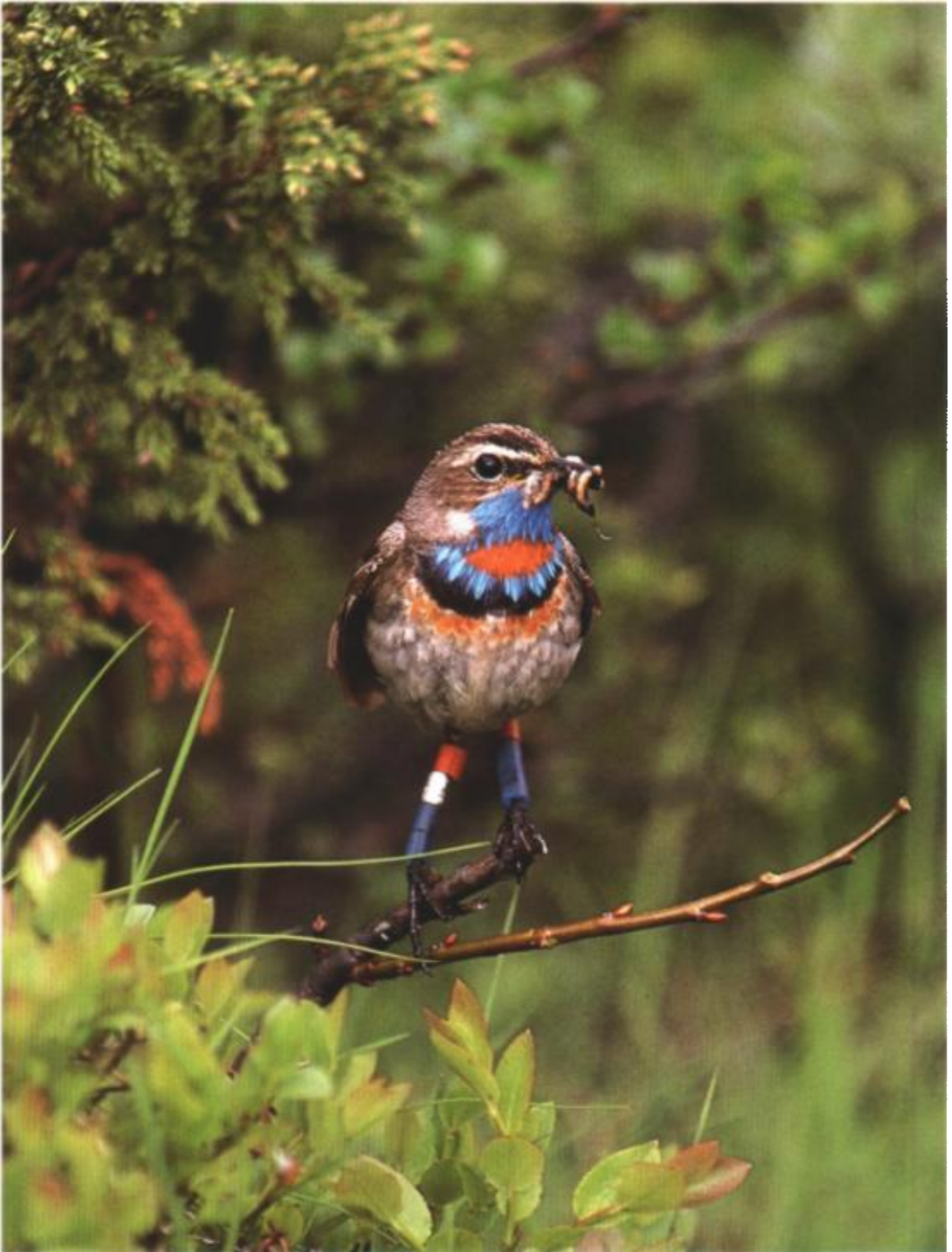
FRONTISPIECE.   A male Bluethroat with food for its young. This male was part of an experimental study showing that the color of leg bands affects the male's mate-guarding intensity during the female's fertile period (Johnsen et al. 1997). Photo by Johnny Steen.

of young after fledging has been reported in several species that exhibit brood division (e.g. Hann 1937, Marler 1956, Nolan 1978, Moreno 1984, Kopachena and Falls 1991), and it could be a proximate factor that initiates brood division (Smith and Merkt 1980, Moreno 1984, Linkhart and Reynolds 1987). It is important to distinguish between dispersion, which is a characteristic describing positions in space, and brood division, which is a behavioral characteristic describing how parents allocate efforts among their young. Hence, brood division does not necessarily require that the young are spatially dispersed.

Several alternative hypotheses have been suggested to explain the benefit of brood division. Some of these assume that the young are spatially dispersed (either singly or in groups fed by each parent), whereas other hypotheses are neutral to any spacing pattern. One hypothesis for dispersed young suggests that parents increase their foraging efficiency when dividing the brood (Simmons 1974, Smith 1978, Moreno 1984, McLaughlin and Montgomerie 1985, Byle 1990), and another states that brood division can minimize the effects of predation (Smith 1978, Harper 1985, McLaughlin and Montgomerie 1985, Byle 1990). Other hypotheses state that it is advantageous for a particular parent to feed a particular "type" of young, i.e. with respect to sex, size, or parentage (Harper 1985, McLaughlin and Montgomerie 1985; see also Price and Gibbs 1987, Byle 1990). Because these hypotheses do not assume anything about the spatial distribution of young, brood division might well occur while the young are still in the nest. No hypothesis has proved to be of general validity, and Harper (1985) pointed out that the various explanations for brood division are not exclusive and do not need to be equally applicable to all species.

In this paper, we report on the occurrence of brood division in the Bluethroat (*Luscinia s. svecica*). In particular, we examined whether brood division was related to the spatial dispersion of young, and we looked at parental provisioning to individual young both in the nest and after fledging. We also carried out an experiment to see how parents allocated their provisioning when the fledglings were prevented from dispersing from the nest. In addition, we examined how broods were divided in relation to various characteristics of young, including genetic parentage.

METHODS

Fieldwork was carried out in 1992 and 1993 in Øvre Heimdalen (61°25′N, 8°52′E), which is located east of the Jotunheimen Mountains in southern Norway at an elevation of about 1,100 m. The vegetation of the study site was dominated by clumps of dwarf birch (*Betula nana*), willow (*Salix* spp.), and juniper (*Juniperus communis*). The open habitat made it relatively easy to locate and observe the parents and their young after nest departure. The estimated breeding density in our study area was 38 breeding pairs per km². For a more detailed description of the study area see Vik (1978).

The Bluethroat is a predominantly socially monogamous, territorial, ground-nesting passerine. Both parents feed and defend the offspring before and after fledging (Cramp 1988). The young leave the nest before they are able to fly (Harrison 1975, Arheimer 1982), at which time they usually become spatially dispersed (Peiponen 1960, Theiss 1973, Koch 1983). Juveniles are sexually monomorphic (Cramp 1988). The species is single-brooded in the northern part of its range, which includes Norway (Harrison 1975, Cramp 1988).

Adult birds were caught in mist nets and given unique combinations of color bands. Eight to 10 days after hatching, nestlings were individually marked with a color band on each tarsus and a spot of acrylic paint of similar color on the forehead. Several morphological measurements were taken of adults and young, including body mass (± 0.1 g), tarsus length (± 0.1 mm), and wing length (± 0.5 mm). We also collected blood samples for DNA fingerprinting analysis. See Krokene et al. (1996) for details on the methods and results of the parentage studies.

To determine whether brood division occurred while the young were in the nest, five broods (four of which reached fledging) were videotaped from 3 to 9 h between day 10 posthatching and fledging. The camera was placed on a tripod 0.5 to 1.5 m from the nest. We recorded identity of the parent and the particular young that received food during all feeding visits. If a parent fed more than one young during the same feeding visit, each feeding was counted separately.

In order to examine whether brood division was a consequence of the young becoming spatially dispersed, enclosure experiments were carried out at three nests. A wire-mesh enclosure, approximately 1 m in diameter and 0.35 m high, was placed around the nests before the young left the nest, preventing them from dispersing after nest departure. Food provisioning to individual fledged young was observed from a blind close to the enclosure. There were two

observation periods per brood, each period ranging from 45 to 155 min. The enclosure was removed immediately after the last observation period, which ended 25 to 50 h after the young left the nest.

After the young fledged we collected data on the parental feeding patterns by observing the parents and their offspring from distances less than 50 m. The first observation period occurred on the day the young fledged (day 0) or the next day. We tried to observe broods on at least three different days. Observation periods ($n = 62$) lasted from 20 min to 4 h ($\bar{x} = 125$ min), which generally was long enough to see several feedings per offspring (average number of feedings per young per observation was 5.75, range 1 to 18).

Observations were performed between 0800 and 2200 h and were carried out by two to five observers. With only two observers we had to follow one parent each. With more observers we were able to monitor each young. Fledglings usually remained at the same location for long periods of time, and they often made begging calls. When we were reasonably sure of the position of a fledgling, we often approached it carefully to determine its identity. Otherwise, we waited until the end of the observation session to avoid disturbing it. When the watch was finished, we estimated all inter-young distances and the distances from each young to the nest.

Six of the nests were not found until after hatching. The age of young from these nests was estimated from growth curves (body mass and wing length) drawn from a sample of broods with known hatching dates (Rangbru 1994). Altogether, 58 offspring from 17 broods were observed after fledging, among which 41 offspring from 13 broods were observed for more than one day. Blood samples from 10 of these families were analyzed by means of DNA fingerprinting to assign parentage (Krokene et al. 1996).

Because fledglings are mobile and sometimes mix with other family units, we would expect parents to be able to recognize their young. Hence, we made two experiments with a fledged brood (brood 2/92). In the first experiment, we swapped a male-attended and a female-attended fledgling. The distance between the two positions was approximately 60 m. In the second experiment, one of the female-attended fledglings was first replaced with, and then released together with, an unrelated fledgling from another brood (7/92). Nest 7/92 was located approximately 100 m from nest 2/92, behind a small hilltop.

RESULTS

Provisioning in the nest.—In general, males and females did not differ in provisioning rates, and each parent appeared to distribute food evenly among their young during the nestling period (Table 1). Thus, there was no in-

dication of brood division while the young were in the nest. The only cases where the parents seemed to favor particular young or had different feeding distributions occurred in two nests of a polygynous male (Table 1).

Nestlings left the nest on average 11.6 days after hatching (range 10 to 13, $n = 17$). These are minimum estimates because some of the nest departures may have been induced by us. In three nests, all young fledged during 3, 4, or 7 h, respectively. In four other nests, young left the nest asynchronously, with as much as 48 h elapsing between departure of the first and last young.

Provisioning after fledging.—Most of the Bluethroat parents divided their broods after nest departure (see Tables 1 and 2). Generally, brood division was not observed unless the young were spatially dispersed. In six families where parents and some or all young were observed more than one day after fledging, stable brood division was observed during the first observation period on day 0 or day 1 (family 2/92, 6/92, 13/92, 15/92, 57/92, and 61/93; Table 2). By "stable brood division" we mean that the parental feeding pattern, i.e. which offspring each parent fed, was the same during each observation of that particular brood.

In five other families where parents and at least some of the young were observed for more than one day, stable brood division was not observed until one to three days after fledging. In three of these families, however, broods were divided at the first watch, but the division pattern changed during the following days. The time elapsed until division became stable coincided with increases in dispersal distance from the nest and inter-young distance during the days following fledging. On average, fledglings were located farther from the nest during the last than during the first watch (Table 3). Likewise, the mean distance between young fed by different parents increased significantly with time, and the increase in distance between young fed by the same parent was nearly significant (Table 3).

The mean dispersal distance from the nest did not differ between young fed by male and female parents (Wilcoxon matched-pairs signed-rank test, $Z = -0.87$, $n = 10$, $P = 0.39$; Fig. 1). However, young fed by the same parent stayed closer to each other than to young from the other family unit ($Z = -2.55$, $n = 9$, $P = $

TABLE 1. Provisioning patterns in five Bluethroat families during the nestling period, inside a wire-mesh enclosure, and after dispersal from the nest. Values are total number of feedings observed. Offspring are listed in order of decreasing size.

| Location | Feeding parent | Offspring | | | | | | P^a | P^b |
		A	B	C	D	E	F		
		Brood 14/92 (Primary nest of polygynous male)							
Nest	Female	26	19	19	19	25	9	0.09	
	Male	8	11	10	5	3	11	0.22	0.02
Dispersed	Female	35	11	5	41	0	dead	0.0001	
	Male	0	0	4	0	24	dead	0.0001	0.0001
		Brood 16/92 (Secondary nest of polygynous male)							
Nest	Female	32	22	42	18	—	—	0.007	
	Male	3	1	0	1	—	—	—^{c}	—
Dispersed	Female	19	16	11	dead	—	—	0.34	
	Male	0	0	5	dead	—	—	0.007	0.002
		Brood 17/93							
Nest	Female	30	22	19	26	24	—	0.58	
	Male	14	27	24	15	23	—	0.17	0.75
Enclosure	Female	5	6	4	6	4	—	0.94	
	Male	1	2	1	2	2	—	0.95	0.97
Dispersed	Female	13	0	14	0	17	—	0.0001	
	Male	21	23	0	7	0	—	0.0001	0.0001
		Brood 59/93							
Enclosure	Female	2	5	5	2	6	—	0.48	
	Male	3	8	4	4	2	—	0.29	0.46
Dispersed	Female	0	31	7	5	20	—	0.0001	
	Male	11	0	18	5	2	—	0.0001	0.0001
		Brood 61/93							
Nest	Female	15	22	—	—	—	—	0.25	
	Male	10	10	—	—	—	—	1	0.49
Enclosure	Female	6	5	—	—	—	—	0.76	
	Male	2	2	—	—	—	—	1	0.88
Dispersed	Female	31	0					0.0001	
	Male	0	20					0.0001	0.0001

^{a} X^2 test for randomness of feeding by each parent.
^{b} X^2 test for independence of feeding distributions between parents.
^{c} Expected frequencies too small for X^2 test.

0.01; Fig. 2). The idea that brood division was promoted by the spatial dispersion of young was illustrated by the enclosure experiment. In all three enclosed broods, both parents fed all young outside the nest cup, as they had done when the young were in the nest (Table 1). Parents showed no tendency to feed particular young inside the enclosures (Table 1). On the other hand, the parents divided the brood as soon as the young became dispersed after removal of the enclosure (Tables 1 and 2).

A causal link between brood division and brood dispersion also was illustrated by a couple of case studies. In brood 79/92, the whole brood was completely divided between the two parents during the first watch, whereas during the second watch two fledglings were sitting

only 1 m apart and were fed by both parents. In brood 59/93, two fledglings dispersed quickly away from the nest and were fed exclusively by one parent each. The remaining three fledglings did not move very far from the nest or from each other initially, but as the distance among them increased, the feeding pattern changed from no brood division to complete brood division.

Brood division was observed in four other broods (53/92, 54/92, 58/92 and 69/93; Table 2), but none of the young was observed for more than one day after nest departure. In brood 5/92 only one young was seen after fledging, and it was fed by both parents (Table 2). In the secondary brood of the polygynous male (brood 16/92), the male was observed

TABLE 2. Provisioning patterns (no. of young fed by female, male, or both parents) in 17 Bluethroat families revealed during the last observation period of a young.

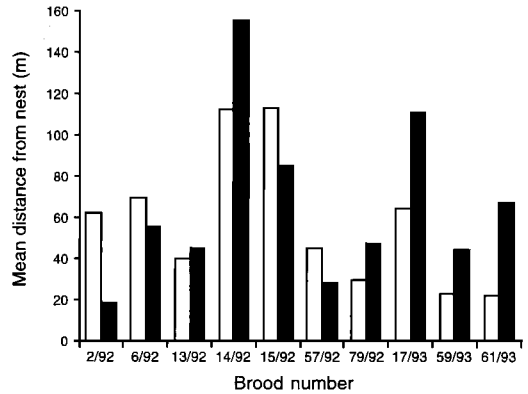| Nest | Parent | | | No. young missing[a] |
	Female	Male	Both	
2/92	2	1	0	0
5/92	0	0	1	4
6/92	3	1	0	0
13/92	2	1	0	0
14/92	3	1	1	0
15/92	2	1	0	2
16/92	2	0	1	0
53/92	3	0	0	3
54/92	0	1	0	5
57/92	1	2	0	0
58/92	3	0	0	4
79/92	3	2	2	0
17/93	2	3	0	0
59/93	2	3	0	0
61/93	1	1	0	0
69/93	3	2	0	1
70/93	2	0	0	2
Total	34	19	5	21

[a] Young not seen after fledging.

FIG. 1. Mean distance between fledged offspring and the nest from all observations of 10 Bluethroat broods. White bars indicate young fed by females, and black bars indicate young fed by males.

providing only five feedings, all to one young, whereas the female was observed feeding all three fledglings, for a total of 46 feeds (Table 1). In summary, brood division was the typical form of postfledging care, and it appeared to be induced by the spatial dispersion of the young.

No clear division rules.—Among monogamous pairs, males tended to care for fewer fledglings than did females ($Z = -1.85$, $n = 15$, $P = 0.064$; Table 2). However, this result should be treated with caution because in each of four broods one parent and several young were not found, and we are not confident that they were not present. When excluding these cases, we found no indication that males cared for fewer fledglings than did females ($Z = -1.16$, $n = 11$, $P = 0.25$).

Within each brood, the offspring were ranked according to four size categories: body mass, wing length, tarsus length, and the three measurements combined (i.e. mean rank). No significant differences were found between female-attended and male-attended offspring (Wilcoxon tests, Z-values between -0.83 and -0.27, all $Ps > 0.40$). Thus, we conclude that the parents did not divide the brood according to size of young. In four cases the identity of the first young to fledge was known. In two cases the fledgling was subsequently fed by the female, in the two other cases it was fed by the male. Hence, at least within this restricted sample, there was no indication that one sex was more likely than the other sex to take care of the first young to fledge.

A few offspring were recaptured and sexed, according to Lindström et al. (1985), before they left the breeding site in late July or early August (T. Aarvak pers. comm.). As a result of these recaptures, we know that two sons were fed by their mother, whereas one daughter was

TABLE 3. Distances (m) between nest and offspring and between offspring from the same and different family units in Bluethroat broods; values are $\bar{x} \pm SE$.

| Distance between | Observation | | Z^c | n | P |
	First[a]	Last[b]			
Nest and offspring	36 ± 5	116 ± 19	-3.20	14	0.001
Offspring from same family unit	33 ± 5	53 ± 8	-1.84	9	0.07
Offspring from different family units	51 ± 7	94 ± 19	-2.31	10	0.02

[a] 0 to 3 days after young left nest.
[b] 3 to 15 days after young left nest.
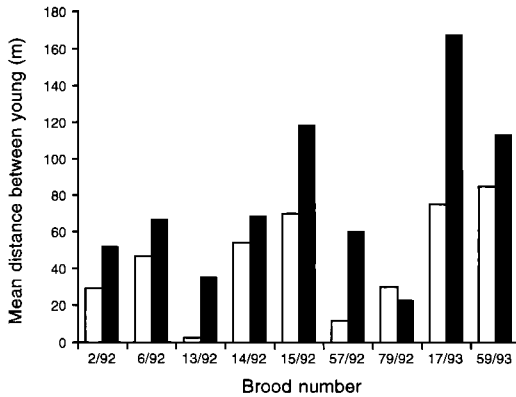[c] Wilcoxon matched-pairs signed-rank test.

FIG. 2. Mean distance between fledged offspring from all observations of nine Bluethroat broods. White bars indicate offspring belonging to the same family unit, i.e. fed by the same parent, and black bars indicate offspring belonging to different family units within a brood, i.e. fed by different parents.

fed by her father and another by her mother at the stage of brood division. Due to the small sample size, these findings preclude a firm conclusion about brood division by the sex of offspring, but at least they indicate that parents do not divide the brood strictly by sex.

In three broods with known parentage (Krokene et al. 1996), some or all extrapair offspring were seen after fledging. In one brood (13/92), the female took exclusive care of the only extrapair offspring. In another brood (15/92), the male fed only one fledgling, which was one out of four extrapair offspring. Only one offspring in that brood was sired by the resident male, and it was fed exclusively by the female. In the third brood (5/92), the only offspring seen after fledging was the only extrapair offspring in that brood, and it was fed by both parents. Thus, in two cases a male fed a fledgling to whom he was not genetically related, and in one case he took exclusive care of such an offspring.

Offspring-recognition experiments.—The two switching experiments were carried out with a brood that had showed stable brood division for two days. In the first experiment both parents, after approximately 1 min of hesitation, adopted the "new" young that previously had been fed by the other parent. In the second experiment the female clearly refused to feed the unrelated young for 25 min, whereafter the young started to beg intensively and was fed

several times in rapid succession. There was no such hesitation in feeding after the release of her own young. The next day we observed the female feeding only the two young from her own nest, whereas the young from the other nest was fed by its own father. Evidently, he had recovered his lost young.

DISCUSSION

We found no evidence for brood division while the young were still in the nest. Moreover, parents distributed food evenly among brood members. Our findings are consistent with the general pattern for birds with biparental care, although in some species females have been reported to feed the smaller young in the nest preferentially (Gottlander 1987, Stamps et al. 1987, Lifjeld et al. 1992). Almost no studies have reported strict division of broods during the nestling stage, as pointed out by Reed (1981) and Weatherhead and McRae (1990). Apparently, the only indication of brood division in the nest occurred at a Great Tit (*Parus major*) nest where the male and female parent fed the nestlings from different positions in the nest on the last day of observation, and as a result the brood became divided (Bengtsson and Ryden 1981).

In most of the Bluethroat families, the parents divided the brood after nest departure in such a way that each parent fed certain young almost exclusively. Among the few exceptions was the secondary brood of the polygynous male, where complete division of the entire brood was not observed, probably because the male provided very little care. Another exception was a brood where probably all but one young were depredated. Consequently, brood division after fledging appears to be the rule in Bluethroats. These results are in accordance with many detailed studies that have found brood division to occur in nearly all broods, e.g. Northern Wheatears (*Oenanthe oenanthe*; Moreno 1984), Lapland Longspurs (*Calcarius lapponicus*; McLaughlin and Montgomerie 1985), Flammulated Owls (*Otus flammeolus*; Linkhart and Reynolds 1987), American Robins (*Turdus migratorius*; Weatherhead and McRae 1990), and White-throated Sparrows (*Zonotrichia albicollis*; Kopachena and Falls 1991). Other studies have reported brood division in only some of the broods, e.g. in Eu-

ropean Robins (*Erithacus rubecula*; Harper 1985), Medium Ground-Finches (*Geospiza fortis*; Price and Gibbs 1987), and Cactus Finches (*Geospiza scandens*; Price and Gibbs 1987). In species with more than one nesting attempt per season, brood division tends to occur mostly in broods that are not followed by another breeding attempt, e.g. Five-striped Sparrows (*Amphispiza quinquestriata*; Mills et al. 1980), European Robins (Harper 1985), Eurasian Blackbirds (*Turdus merula*; Edwards 1985), and Northern Mockingbirds (*Mimus polyglottos*; Zaias and Breitwisch 1989).

The onset of brood division in the Bluethroat varied between nests and among young from the same nest. Some broods were divided on the day of fledging, and others were not completely divided until four days after fledging. The time between fledging and stable brood division ranges from 0 to 4 days in Dunnocks (*Prunella modularis*; Byle 1990), 0 to 5 days in Song Sparrows (*Melospiza melodia*; Smith and Merkt 1980), 3 to 8 days in Northern Wheatears (Moreno 1984), 0 to 10 days in Eurasian Blackbirds (Edwards 1985), and less than 1 day in Prairie Warblers (*Dendroica discolor*; Nolan 1978) and Lapland Longspurs (McLaughlin and Montgomerie 1985).

In our study, the onset of brood division seemed to be closely coupled to the spatial dispersion of young. Stable brood division was observed only when the young had become spatially dispersed, as demonstrated in the enclosure experiments. Likewise, brood division could be relaxed or changed if two young fed by different parents came into secondary contact. These observations strongly suggest a causal link between brood division and the spatial organization of the young, an idea that previously was put forth by others (Smith and Merkt 1980, Moreno 1984, Linkhart and Reynolds 1987).

We did not attempt to explain why Bluethroat fledglings become spatially dispersed after they leave the nest, but other workers (e.g. Tinbergen 1939, Willis 1972, Knapton 1978) have suggested that such behavior is an antipredator strategy and/or helps parents reduce the energetic costs of parental care (McLaughlin and Montgomerie 1989a,b). In our study, predation was high during the nestling period (8.2% nestlings lost per day), and losses appeared to decrease after nest departure

(4.8% fledglings lost per day). In our estimate of predation rates, all young that disappeared were presumed dead; consequently, the predation rate after fledging may have been overestimated. Thus, shortening of the nestling period may yield considerable fitness benefits, which probably explains why the young leave the nest before they are fully capable of flying. A study of another open nester in our study area, the Willow Warbler (*Phylloscopus trochilus*), indicated that a major function of male parental care is to promote early fledging (Bjørnstad and Lifjeld 1996).

The main predator on Bluethroat nestlings was the adder (*Vipera berus*; T. Amundsen and J. T. Lifjeld unpubl. data). Many snakes use olfaction to locate prey (Dowling 1986). Because the odor probably is stronger when the young are gathered, it may be more profitable for young to become spatially dispersed than to stay together after nest departure. Moreover, spatially dispersed young are less conspicuous than gathered young, regardless of whether they are detected by sound, sight, or smell. Therefore, spatial dispersion of young may reduce the risk of predation from other potential predators as well. For instance, we witnessed a stoat (*Mustela erminea*) take only one fledgling when several others from the same brood were in close proximity. The stoat searched the area for at least 30 min without detecting any of the other brood members.

Brood division assumes that parents are capable of some sort of offspring recognition (Horsfall 1984, Edwards 1985, Kopachena and Falls 1991). It has been suggested that parents can recognize fledglings from their begging calls (Smith and Merkt 1980, Harper 1985) or from the actual location of the fledglings (Harper 1985, Kopachena and Falls 1991). Our switching experiments suggest that parents use both individual begging calls and location of dispersed young as cues for offspring recognition. However, the fact that one female started to feed a foreign young suggests that the recognition is not perfect and that the cost of refusing to feed one's own offspring is higher than the cost of feeding an unrelated individual. Moreover, parents often had difficulty finding a particular fledgling when it had moved between two visits and did not make begging calls when the parent came to feed it.

Our data on brood division with respect to

offspring sex, size, and paternity were few; consequently, no strict conclusions can be drawn. However, we do know that the parents did not divide the brood strictly according to these characteristics. Because brood division seemed to occur in response to spatial dispersion of the young, it is likely that brood division is beneficial only when the young are dispersed.

Two major hypotheses concerning brood division are based on the assumption of spatial dispersion. The Predation Hypothesis states that brood division can prevent loss of the entire brood when the male-attended and the female-attended young are widely separated (Harper 1985, McLaughlin and Montgomerie 1985; see also Byle 1990). Thus, at best, a predator that tracks a parent to its young will find only half the brood (McLaughlin and Montgomerie 1985). This explanation seems plausible provided that the brood members tended by one parent are clustered. If, on the other hand, the group members are spatially dispersed, as in the Bluethroat, the antipredation benefit is less obvious. In addition, both parents may defend all of their young even if they feed only some of them (Willis 1972), so that predators should have no difficulty locating both parents as long as the parents detect the predator. This was probably the case with the Bluethroats in our study. The reduced predation rate after fledging may have resulted from spatial dispersion of the brood rather than brood division per se.

The Improved-Foraging Hypothesis states that parental foraging is more efficient when broods are divided. First, it may be easier for parents to locate individual young, and thereby spend less time searching for them (Smith 1978, Harper 1985, McLaughlin and Montgomerie 1985, Byle 1990). Brood division also may enhance foraging efficiency by reducing the parents' foraging route or travel costs (Moreno 1984, McLaughlin and Montgomerie 1985). For instance, if food items are patchily distributed and different patches do not contain enough food to sustain all of the young, then dividing the brood may help parents to reduce their travel time and become more efficient providers (Moreno 1984, Byle 1990). Such a division would result in young fed by the same parent being more aggregated than young fed by different parents, as we found for Bluethroats and

as has been reported in other species (Nolan 1978, Moreno 1984).

We conclude that brood division is the typical form of postfledging parental care in Bluethroats. Brood division occurred once the young became spatially dispersed. In this setting, brood division is likely to enhance the foraging economics of the parents. Our study did not reveal any rules as to how the male and female parents divided their broods.

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