

definitions of both spacing and migration. The movements of individuals in winter could be regarded as spacing, although juvenile dispersal also was involved.

Movement patterns of organisms, especially juvenile dispersal, have great theoretical importance for population genetics and population dynamics, but are poorly understood (Mayr 1970, Gadgil 1971, Van Valen 1971). Gadgil (1971) has predicted that populations living in scattered patches of habitat with asynchronously fluctuating carrying capacities will show greater dispersal than populations living in stable habitats or in habitats with synchronously fluctuating carrying capacities. He has also suggested that, for many species, a mixture of long- and short-distance dispersal would be the best strategy.

There is some support for these ideas. R. F. Johnston (1961) has indicated that effective dispersal distance of many birds may be bimodal, with a primary mode at a relatively short distance and a secondary mode at a greater distance. Data presented by J. S. Johnston and Heed (1976) suggest a bimodal distribution of dispersal distances for a *Drosophila* species and indicate higher dispersal rates in unstable habitats. Richter (1970) showed that spider species living in abundant habitats (i.e., large, common patches) tended to disperse less than species with scarce habitats.

Dipper habitat obviously is patchy, but it is difficult to document either the extent to which the carrying capacity of a given stream fluctuates or the synchrony of such fluctuations in neighboring drainages (see Effect of Stochastic Events on Survival and Productivity). Robson's (1956) data were gathered in a more stable climatic area than ours (Table 3) and did show shorter average dispersal distances with no observed movement between watersheds. Jost (1969), in a more extreme climate than Robson's, reported finding three of 425 banded adults (0.7%) and nine of 325 banded nestlings (2.8%) on other drainages. Of a total of 55 young that Jost caught more than once, 46 (83.6%) were on their native drainage. Unfortunately Jost did not give data on effective distance of dispersal. Our data, taken from the most variable environment (Table 3), indicate that 10–15% of adults changed drainages, some regularly. At least as many juveniles flew to different drainages, and perhaps as many as 80% may do so.

Although there have been only three studies of movement of Dippers in different habitats (Balát 1962, Jost 1969, present study) they support Gadgil's (1971) prediction that organisms in variable, patchy habitats will have higher dispersal rates than those in stable, extensive habitats. It also is noteworthy that there are differences between separate populations of the same Dipper species (e.g., Robson's 1956 and Jost's 1969 studies on *C. cinclus*) and between *C. cinclus* and *C. mexicanus*.

Mayr (1970) and others have correlated low dispersal rates with high rates of taxonomic divergence. The fact that there is only 1 recognized subspecies of Dipper north of Mexico, compared with 9 of one species in Europe, 13 of two species in Asia (Dement'ev and Gladov 1954), and 7 of three species in Central and South America (Hellmayr 1934), may be indicative of generally high dispersal rates among North American Dipper populations.

POPULATION DENSITY AND DISPERSION

Knowledge of Dippers' movement patterns provides a starting point for analysis of more complex population processes. The major, most immediate effect of population mobility was to produce rapid changes in population distribution and

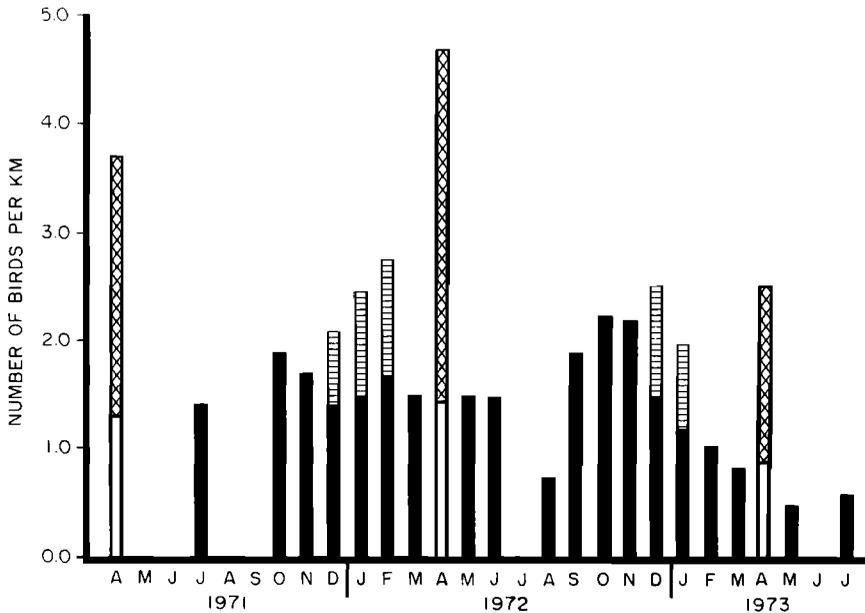


FIGURE 12. Densities observed on Boulder Creek. (Solid black bars indicate number of birds observed on censuses; open white bars indicate density of breeding adults; crosshatched bars indicate nestling density, i.e., total number of nestlings per km in that breeding season; and finely lined bars indicate ecological density in ice-free habitat).

density. These changes modified patterns of resource utilization by the population, and were associated with changes in social structure which had important consequences for population dynamics. We use the term “density” to refer to the number of individuals of a species per unit of suitable habitat (i.e., ecological, rather than crude density, Odum 1971). Density of Dippers is conveniently measured as number of birds per linear kilometer of stream. Population “dispersion” (Berndt and Sternberg 1968, Odum 1971) is the actual pattern of arrangement of individuals in space. Dispersion should not be confused with the terms “dispersal” and “spacing” which are types of population and individual movements that result in dispersion (Berndt and Sternberg 1968).

Figures 12 and 13 show the density of birds on our two study areas. These two graphs illustrate an important difference between the two study areas: except for the 1972 breeding season, mean densities were significantly higher on South Boulder Creek (for all months together, $P < 0.005$, t test). Recall that South Boulder Creek appeared to be superior to Boulder Creek in several factors affecting Dippers (Table 1).

SEASONAL TRENDS IN POPULATION DENSITY

Fall and winter

Effects of migration and winter ice show clearly in Figs. 12 and 13. Although population sizes on both study areas were highest during fall migrations, ecological densities tended to be highest during winters (because of icing) and breeding seasons (because of nestlings). Differences between fall and winter densities were

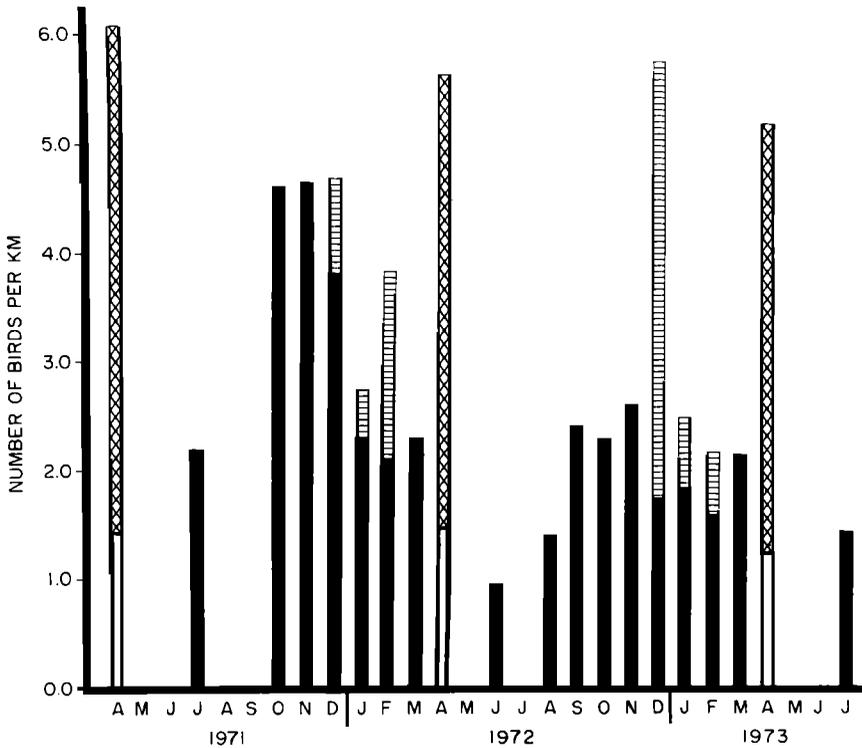


FIGURE 13. Densities observed on South Boulder Creek. (Solid black bars indicate number of birds observed on censuses; open white bars indicate density of breeding adults; crosshatched bars indicate nestling density, i.e., total number of nestlings per km in that breeding season; and finely lined bars indicate ecological density in ice-free habitat).

not always large, but these slight differences were important in the ecology of the populations.

If population density (d) is divided by the carrying capacity of the environment (k), then the ratio (d/k) is an index of the degree of crowding of the population in relation to its resources (Gadgil 1971). One would expect the carrying capacity of a given patch of habitat to decline when weather becomes more severe and birds' energy and shelter requirements increase. Although numerical differences in densities between fall and winter were not great, we would expect the denominator of the crowding index to have decreased in winter and accentuated those differences. Thus, resources were in shorter supply for Dippers in winter than in fall even though the actual numbers of birds per unit area were comparable. Also, fall Dipper populations were so mobile (Fig. 5) as to be dependent on resources in any particular area for only a short time.

Breeding seasons

Adult densities during breeding seasons were not high compared with those found during most censuses (Figs. 12, 13). However, this does not necessarily mean that the populations were not stressing resources. Nestlings and fledglings also used resources, and energy requirements per adult rise during breeding (West

TABLE 5
NUMBER (%) OF MONTHLY CENSUSES WITH RANDOM^a DISPERSION OF DIPPERS

Study area	Season ^b				Breeding
	Summer	Fall	Winter	Spring	
Boulder Creek	3 (100)	3 (60)	1 (17)	1 (50)	2 (50)
South Boulder Creek	2 (67)	4 (80)	3 (50)	3 (100)	1 (100)
Both Study Areas	5 (83)	7 (70)	4 (33)	4 (80)	3 (60)

^a Chi-square test against Poisson distribution; $P < 0.05$ (Zar 1974).

^b Summer, July–Aug.; Fall, Sep.–Nov.; Winter, Dec.–Feb.; Spring, Mar.–Apr.; Breeding, May–June.

1960, Zimmerman 1965, El-Wailly 1966). When nestlings were included, densities were equal to or higher than winter densities.

ENVIRONMENTAL FACTORS AFFECTING DISPERSION

The fact that Dippers were not resident on our study areas made it impossible to follow continuously a discrete population and gather data on such basic processes as mortality. Indeed, the birds' mobility made it impossible to delineate discrete local populations. The only remaining approach to the problem of what "regulated" population dispersion was to make a more detailed study of the distribution of birds along the study streams. The major question became: How does the spacing pattern of individuals along a stream correlate in space and time with the distribution of environmental and social variables?

If population size was close to carrying capacity and if density was in any way "regulated" in relation to resource availability, we would predict closer correlation between important resources and population density in winter and breeding seasons than in fall, early spring, or summer. Close correlations between bird dispersion and certain environmental variables should provide clues to the factors most likely to limit Dipper densities. This assumes, of course, that dispersion was nonrandom.

To determine whether dispersion was random in each census, we tabulated the number of 400-m stream segments with one, two, three, etc., birds, and calculated mean and variance of NUMBIRDS (see Methods section for description of variables and Table 2 for brief definitions). We then did Chi-square tests of these data against Poisson distributions of the same mean and variance (Zar 1974). Table 5 shows the results of this analysis. Summer, spring, and fall had high proportions of censuses with random dispersion, winter had fewest, and breeding seasons were intermediate (although when nestlings were included, dispersion was nonrandom in all breeding season censuses). Environmental factors also did not vary uniformly or randomly along our study areas. We expected to find that dispersion of our Dipper population would correlate most closely with environmental factors in winter and breeding seasons when ecological densities were highest (Figs. 12, 13), and when Dippers were relatively sedentary.

We tabulated the following data for each 400-m segment: 1) width index (WIDTH), 2) bottom-quality index (BOTM), 3) cover index (COVR), 4) sum of qualities of nest sites (TOTSITQL), 5) number of bridges (NUMBRIDG), 6) measured food density (REALFOOD), 7) interpolated food density (INTFOOD), 8) ice index (ICE), 9) index of nest site quality and density (NSQDIST), and 10) density of Dippers (NUMBIRDS, or ESTBIRDS for breeding seasons). Prelimi-

TABLE 6
MULTIPLE CORRELATIONS OF ENVIRONMENTAL VARIABLES WITH DISPERSION IN EACH SEASON^a

Season ^b	Censuses No. ^c (%)
A. Summers 1971, 1972, 1973	3 (43)
B. Falls and springs	5 (33)
C. Winters, 1971–1972, 1972–1973, all segments	11 (92)
D. Breeding censuses ^d	3 (75)
E. Breeding seasons ^e	5 (100)

^a This table summarizes stepwise correlations shown in more detail in Tables 7 and 8.

^b Summer, July–Aug.; Fall, Sep.–Nov.; Winter, Dec.–Feb.; Spring, Mar.–Apr.; Breeding, May–June.

^c Number of censuses on both study areas with significant multiple correlations ($P < 0.05$) in at least one step.

^d Multiple correlation of predictor variables with NUMBIRDS, see Table 2.

^e Multiple correlation of predictor variables with ESTBIRDS, see Table 2.

nary analysis indicated that TOTSITQL, NUMBRIDG, and REALFOOD were each highly correlated with one or more other variables and did not contribute significantly to the multiple correlation with NUMBIRDS; these variables were therefore excluded from further analyses. Because these analyses were designed to determine factors influencing distribution of breeding adults, number of nestlings was not included in breeding season data. (Factors affecting Dipper productivity will be discussed later.) We performed standard stepwise multiple correlations (with NUMBIRDS or ESTBIRDS as the dependent variable) for each census and breeding season. Winter correlations were done on all segments and also on those segments with ICE indices less than 3 (i.e., with open water).

Results from South Boulder Creek generally were less satisfactory and more difficult to interpret than those from Boulder Creek. Several factors contributed to these difficulties. One was that the sample size was less than half that of Boulder Creek (23 vs. 49), and thus it was more likely for chance variations to affect the results. In the 1972 breeding season there was an unusual case of polygyny and a catastrophic decline in food availability on South Boulder Creek. In the 1973 breeding season there again were unusual circumstances in the establishment of breeding territories on South Boulder Creek. Finally, the nine segments below the Claypit bridge (Fig. 2) had very high food densities, which combined with two poor nest sites (Fig. 14) to produce spuriously large negative correlations between INTFOOD and NUMBIRDS.

In spite of difficulties on South Boulder Creek, the correlation analyses reveal much about possible causes of Dipper dispersion patterns. Table 6 is a summary of results from both study areas tabulated by season. Our prediction of high correlations between number of birds per segment and environmental factors during winter and breeding seasons is confirmed. Months with insignificant correlations usually occurred in summer, fall, and spring. Fall and spring censuses, when migrations were occurring (September, October, November, and April 1973), tended to have lower correlations than might be expected from their densities (Figs. 12, 13).

Unfortunately, analysis of all data together was relatively uninformative. The seasons and study areas were too diverse for a single grand multiple calculation to have meaning. Thus, we must discuss each season, stream, and variable in turn. Tables 7 and 8 summarize multiple correlations of census data with Dipper dispersion for each study area; the results for each season are grouped. In order

TABLE 7
RELATIVE IMPORTANCE OF VARIABLES AFFECTING DISPERSION ON BOULDER CREEK
IN DIFFERENT SEASONS

Season	No. monthly censuses (no. signif.) ^a	Mean R^2	Variable ^b	Mean rank	No. signif. correlations ^c	Mean r
A. Summers ^d 1971, 1972, 1973	4 (3)	0.17	BOTM	2.0	1	0.16
			NSQDIST	2.3	2	0.20
			INTFOOD	2.5	2	0.25
			WIDTH	3.8		0.12
			COVR	4.5		0.13
B. Falls ^e 1971, 1972	5 (3)	0.27	INTFOOD	1.4	2	0.32
			NSQDIST	2.8		0.18
			BOTM	3.0	1	0.29
			WIDTH	3.6		0.13
			COVR	4.6		0.18
C. Springs ^f 1972, 1973	2 (2)	0.17	BOTM	1.0	2	0.33
			INTFOOD	3.0		0.31
			NSQDIST	3.0		0.01
			WIDTH	3.0		0.05
			COVR	5.0		0.18
D. Falls ^e and springs ^f	7 (5)	0.24	BOTM	2.4	3	0.30
			INTFOOD	2.4	2	0.31
			NSQDIST	2.9		0.13
			WIDTH	3.4		0.11
			COVR	4.7		0.24
E. Winter 1971-1972 ^g ; all segments	3 (3)	0.57	ICE	1.7	3	-0.45
			INTFOOD	2.0	2	0.46
			WIDTH	3.0	2	0.35
			BOTM	4.3	1	0.24
			NSQDIST	4.3		-0.04
F. Winter 1972-1973 ^h ; all segments	3 (3)	0.36	ICE	1.3	3	-0.44
			NSQDIST	2.3		0.08
			INTFOOD	3.7	1	0.26
			WIDTH	4.0		0.22
			BOTM	4.3		0.16
G. Winters 1971-1972 ^g ; 1972-1973 ^h ; all segments	6 (6)	0.47	ICE	1.5	6	-0.45
			INTFOOD	2.8	3	0.36
			NSQDIST	3.3		0.02
			WIDTH	3.5	2	0.29
			BOTM	4.3	1	0.20
H. Winter 1971-1972 ^g ; open water ⁱ	3 (3)	0.34	INTFOOD	2.3	2	0.43
			BOTM	2.7	2	0.35
			WIDTH	3.0	1	0.41
			NSQDIST	3.0		0.24
			COVR	5.3		0.17
I. Winter 1972-1973 ^h ; open water ⁱ	3 (1)	0.25	NSQDIST	1.0	1	0.37
			INTFOOD	2.7	1	0.25
			BOTM	3.0		0.25
			COVR	4.0		0.15
			WIDTH	4.3		0.14

TABLE 7
CONTINUED

Season	No. monthly censuses (no. signif.) ^a	Mean R^2	Variable ^b	Mean rank	No. signif. correlations ^c	Mean r
J. Winters 1971-1972 ^d , 1972-1973 ^e ; open water ^f	6 (4)	0.29	NSQDIST	2.0	1	0.30
			INTFOOD	2.5	3	0.34
			BOTM	2.8	2	0.30
			WIDTH	3.7	1	0.28
			COVR	4.7		0.16
K. Breeding censuses ^g 1972, 1973	2 (2)	0.36	INTFOOD	1.5	2	0.39
			NSQDIST	1.5	1	0.38
			WIDTH	3.0		0.14
			BOTM	4.0		0.29
			COVR	5.0		0.25
L. Breeding seasons ^h 1972, 1973	2 (2)	0.50	INTFOOD	1.0	2	0.59
			COVR	2.5	1	0.48
			NSQDIST	3.0	1	0.28
			WIDTH	3.5	1	0.24
			BOTM	5.0		0.45

^a Number of months with significant multiple correlations ($P < 0.10$) in at least 1 step.

^b BOTM, bottom quality index of 400-m segment; COVR, cover index of segment; ICE, ice cover index of segment; INTFOOD, interpolated food quality index; NSQDIST, nest site quality-distance index; WIDTH, width index.

^c Number of months in which variable contributed significantly to a step in multiple correlation ($P < 0.10$, F ratio test).

^d July 1971; June, Aug. 1972; July 1973. June 1972 was included because of large numbers of juveniles on study area and the early start of the breeding season.

^e Oct., Nov. 1971; Sep., Oct., Nov. 1972.

^f Mar. 1972, 1973.

^g Dec. 1971; Jan., Feb. 1972.

^h Dec. 1972; Jan., Feb. 1973.

ⁱ Segments with open water (ice index < 3).

^j May 1972, May 1973; June 1972 moved to summer; it was not significant (see footnote^c).

^k 1972, 1973 breeding season summaries; variable ESTBIRDS was dependent.

to indicate importance of the variables, we ranked each by the number of the step in which it entered each multiple correlation and tabled the variables in order by mean rank. For each variable we noted the number of multiple correlations to which it contributed significantly, and its mean correlation coefficient with NUMBIRDS or ESTBIRDS.

Summer

Of seven stepwise correlations run on data from seven summer censuses, three had at least one step which was significant at the 0.05 level (Tables 7A, 8A). Because the bulk of the population had moved upstream beyond our main study areas, our analysis of summer dispersion are unsatisfactory. Nevertheless, the results are relevant to our previous discussion of summer movements. From that discussion, we might expect food and cover to be important determinants of summer dispersion.

If, as suggested by literature on the Cinclidae, the major cause of summer movements was need to find a refuge for molt, we would expect to see strong correlations of NUMBIRDS with COVR in late July and August. Actually, cover was the least significant variable of those we measured (Tables 7A, 8A). However, our data do not conclusively refute the hypothesis. The flightless period is short (from perhaps as little as five days according to Sullivan 1973, to two weeks

TABLE 8
RELATIVE IMPORTANCE OF VARIABLES AFFECTING DISPERSION ON SOUTH BOULDER CREEK
IN DIFFERENT SEASONS

Season	No. monthly censuses (no. signif.) ^a	Mean R^2	Variable ^b	Mean rank	No. signif. correlations ^c	Mean r
A. Summers ^d 1971, 1972, 1973	3 (2)	0.43	NSQDIST	2.3	1	0.35
			INTFOOD	2.7	1	0.23
			BOTM	2.7	1	-0.27
			WIDTH	3.7		-0.15
			COVR	3.7		-0.05
B. Falls ^e 1971, 1972	5 (3)	0.29	BOTM	2.2	2	0.21
			WIDTH	2.2		-0.17
			NSQDIST	2.6	1	-0.00
			INTFOOD	3.4		-0.01
			COVR	4.6		0.11
C. Springs ^f 1972, 1973	3 (1)	0.24	COVR	2.0		-0.26
			WIDTH	2.7	1	-0.09
			NSQDIST	2.7		0.08
			INTFOOD	3.0		-0.20
			BOTM	3.3		0.01
D. Falls ^e and springs ^f	8 (4)	0.27	WIDTH	2.4	1	-0.14
			NSQDIST	2.6	1	0.08
			BOTM	3.1	2	0.14
			INTFOOD	3.3		0.08
			COVR	3.6		0.17
E. Winter 1971-1972 ^g ; all segments	3 (3)	0.75	ICE	1.0	3	-0.76
			BOTM	3.0	1	0.37
			NSQDIST	3.3	1	-0.09
			WIDTH	4.0		-0.23
			INTFOOD	4.7		0.03
F. Winter 1972-1973 ^h ; all segments	3 (3)	0.74	ICE	1.0	3	-0.74
			INTFOOD	2.0	1	0.14
			WIDTH	3.7	1	-0.25
			NSQDIST	4.3		-0.15
			BOTM	4.0		0.44
G. Winters 1971-1972 ^g ; 1972-1973 ^h ; all segments	6 (6)	0.75	ICE	1.0	6	-0.75
			INTFOOD	3.3	1	0.09
			BOTM	3.8	1	0.41
			NSQDIST	3.8	1	-0.12
			WIDTH	3.8	1	-0.24
H. Winter 1971-1972 ^g open water ⁱ	3 (3)	0.80	ICE	1.3	2	-0.77
			BOTM	2.7	2	0.49
			INTFOOD	4.0		-0.11
			WIDTH	4.0		-0.27
			COVR	4.3		0.32
I. Winter 1972-1973 ^h ; open water ⁱ	3 (3)	0.71	ICE	1.0	3	-0.71
			INTFOOD	2.7	1	-0.15
			WIDTH	3.3	1	-0.30
			BOTM	3.7	1	0.39

TABLE 8
CONTINUED

Season	No. monthly censuses (no. signif.) ^a	Mean R ²	Variable ^b	Mean rank	No. signif. correlations ^c	Mean r
			NSQDIST	4.3		0.14
			COVR	5.5		0.17
J. Winters	6 (6)	0.76	ICE	1.2	5	-0.74
1971-1972 ^a ,			BOTM	3.2	3	0.44
1972-1973 ^b ;			INTFOOD	3.3	1	-0.13
open water ^c			WIDTH	3.7	1	-0.28
			NSQDIST	4.7		0.17
			COVR	4.8		0.26
K. Breeding censuses ^d	2 (1)	0.34	NSQDIST	1.0	1	0.65
1972, 1973			WIDTH	2.0		-0.36
			INTFOOD	3.0		-0.02
			BOTM	4.0		-0.31
			COVR	5.0		0.09
L. Breeding seasons ^e	3 (3)	0.68	INTFOOD	2.0	2	-0.73
1971, 1972, 1973			NSQDIST	3.0	3	0.70
			WIDTH	3.7		-0.25
			BOTM	3.7		-0.35
			COVR	4.7		0.00

^a Number of months with significant multiple correlations ($P < 0.10$) in at least 1 step.

^b BOTM, bottom quality index of 400-m segment; COVR, cover index of segment; ICE, ice cover index of segment; INTFOOD, interpolated food quality index; NSQDIST, nest site quality-distance index; WIDTH, width index.

^c Number of months in which variable contributed significantly to a step in multiple correlation ($P < 0.10$, F ratio test).

^d July 1971; Aug. 1972; July 1973.

^e Oct., Nov. 1971; Sep., Oct., Nov. 1972.

^f Mar. 1972; Mar., Apr. 1973; Apr. 1973 included because of late start of breeding season.

^g Dec. 1971; Jan., Feb. 1972.

^h Dec. 1972; Jan., Feb. 1973.

ⁱ Segments with open water (ice index < 3).

^j June 1972; Apr. 1973 moved to spring; it was not significant (see footnote ⁱ).

^k 1971, 1972, 1973 breeding season summaries; variable ESTBIRDS was dependent; NSQDIST forced in all seasons.

according to Balát 1960), and our censuses may have missed the critical periods of many birds. Only four of 17 adults observed on the two study areas in August of 1972 were visibly in molt. All four were in areas with excellent cover, but also near good nest sites.

While we cannot statistically support the older hypothesis that cover is important in summer, our hypothesis about food is another matter. INTFOOD contributed to three of the five significant correlations, while BOTM (a measure of ease of foraging) contributed to two (Tables 7A, 8A).

The only other significant variable, NSQDIST, probably was not important in overall summer dispersion, despite its contribution to three correlations. As we indicated in the section on movements, most Dippers deserted their nests and territories and left our study areas in summer; the majority of birds remaining in late July and early August were recently fledged juveniles and adults with late broods. These individuals would, of course, tend to be near nest sites. If correlations could have been run on entire drainages, NSQDIST might not have been significant.

Fall and early spring

Of 15 correlations done on the fall and early spring censuses, nine were significant (Tables 7D, 8D). The frequent appearance of the bottom quality index in

spring and fall stepwise correlations is logical. Recall that our BOTM index incorporated the amount of rubble, depth, bed profile, and number of perching rocks in an attempt to quantify the ease with which Dippers could forage. Fall and spring were periods when large numbers of birds appeared on our study areas (Fig. 6), and we believe that many were unfamiliar with the habitat. It would be logical for these individuals to use the character of the streams' substrate as a cue for foraging. Indeed, INTFOOD was the only other significant variable in the Boulder Creek study area correlations.

The significant correlations from South Boulder Creek are more difficult to understand, and probably result from the sample size, not real phenomena. NUM-BIRDS correlated significantly with NSQDIST in one fall census (Table 8B). Although roosts (which were common at nest sites) may be important in winter (see below), it seems unlikely that the birds would begin to cue on this resource so early in fall migration. In March 1973, distribution of Dippers on the South Boulder Creek census was significantly correlated with WIDTH, albeit weakly (Table 7C).

Coefficients of determination (R^2) in fall and spring generally were the lowest of the seasonal groups, except for summer correlations on Boulder Creek (Tables 7, 8). This is to be expected because many fall and spring birds were transients and a high proportion of birds seen in summer were juveniles. We could expect to find many individuals moving from place to place and pausing briefly in areas that appeared suitable for foraging. When birds were more sedentary in the breeding seasons and in winter, mean correlation of birds with BOTM declined and mean correlation with actual food density increased.

Winter

Twelve censuses were conducted on both study areas in the winter months and, as we predicted, the analyses showed high correlations between Dipper distribution and the environmental parameters measured. Mean coefficients of correlation in winter were among the highest found and all 12 analyses were statistically significant (Tables 7G, 8G).

ICE was the first and most significant variable in all six winter censuses on South Boulder Creek, and in three of the six Boulder Creek censuses; in the other three winter correlations, ICE was the second variable entered. Ice cover was such an overwhelming factor that we attempted to control for it by running a series of correlations on segments with ice indices of 1 or 2 (i.e., segments with some open water). These analyses showed clear differences between the study areas. On South Boulder Creek ice was still the most important single factor (Table 8J). It was entered first in every correlation except January 1972, when BOTM was first and ICE was second. On Boulder Creek ice was never significant below the hydroelectric power plant (Table 7J), which prevented major ice buildup on the lower part of the study area (Fig. 3).

If food were in short supply, we would expect dispersion to show high correlations with INTFOOD in winter when energy demands were high. This correlation should have been higher on Boulder Creek because stream insect biomass was lower than on South Boulder Creek (Figs. 9, 10; Table 1). Our results (Tables 7H, I, J, and 8H, I, J) support these predictions. Food density contributed to three of four significant stepwise correlations with number of birds on open water along

Boulder Creek, but to only one of six on South Boulder Creek (Tables 7J, 8J). Even when iced-over segments were included, INTFOOD contributed significantly to three of the six Boulder Creek winter censuses (Table 8G).

Hewson (1969) has made a strong case for the importance of secure roosts in the ecology of Dippers in Great Britain, especially in winter, and his arguments should apply equally well in North America. Most nest sites would also make good roosts, although the reverse would not always be true. The correlations of NSQDIST with bird dispersion (Tables 7, 8) tend to support Hewson's hypothesis.

On South Boulder Creek, nest sites did not contribute significantly to any of the analyses of open water areas, although the simple correlation (mean $r = 0.17$, Table 8J) was higher than in fall (mean $r = 0.08$, Table 8J) or in overall winter analyses (mean $r = 0.12$, Table 8G). In the analyses of all winter data, the fact that ice kept the birds on segments with poor nest sites probably resulted in the negative correlation between number of birds and NSQDIST (Table 8G).

As usual, the Boulder Creek results were clearer. On open water of Boulder Creek, nest sites were most important. Although contributing significantly to only one analysis, NSQDIST was consistently the third variable entered in 1971–1972 and first in 1972–1973 (Table 7H, I). Correlation (r) of NSQDIST with NUMBIRDS averaged 0.30 on open-water segments, compared with 0.02 overall in winter and 0.13 in fall and spring (Table 7J, G, D). We would expect roosts to be more important in cold weather, and in the especially severe winter of 1972–1973 (Fig. 4) NSQDIST was the first variable entered in all three Boulder Creek analyses (Table 7I).

On our study areas, then, winter was a period of high bird density and generally high correlations between the dispersion of birds and the environmental variables we measured, especially ice and food density. Winter clearly is a critical period for Dippers, and resources might be expected to be in short supply. This has important implications for winter behavior and will be discussed below.

Breeding season

As indicated earlier, censuses were not done in most breeding season months because of limited time. Censuses which were done (May and June 1972 and May 1973 on Boulder Creek; June 1972 and April 1973 on South Boulder Creek) tended to have low correlations (Tables 7K, 8K). Nevertheless, INTFOOD and NSQDIST, variables one might expect to be critical during nesting, contributed significantly to two Boulder Creek correlations and NSQDIST to one South Boulder Creek analysis; no other variables made significant contributions. As shown in Figures 12 and 13, numbers of birds seen in breeding season censuses were low. Such small sample sizes made correlation of census data with NUMBIRDS a weak analytical tool.

A more realistic approach than using census data would be to recognize that breeding pairs have territories, and to "distribute" territory holders evenly through the segments in their territories. Thus, ESTBIRDS was a better measure of breeding season dispersion than NUMBIRDS (see section on Censusing for details). All analyses with ESTBIRDS as the dependent variable had high coefficients of determination and were significant at or beyond the 0.01 level (Tables 7L, 8L).

Differences between our study areas were clearly apparent in breeding seasons. On the South Boulder study area the correlation of INTFOOD with ESTBIRDS

was very high, but negative (mean $r = -0.73$, Table 8L), because lack of good nest sites below Eldorado Springs prevented more birds from breeding there, despite very high food density (Figs. 2, 10, 14). We avoided this difficulty by having the computer program "force" NSQDIST into the correlation first (Nie et al. 1975). The fact that the initial step of each of these correlations was significant supports our conclusion that the distribution of good nest sites was the major factor in determining breeding dispersion on South Boulder Creek. Because of this confounding effect of nest sites on correlation of food and density of birds, we have no statistically good way to quantify the impact of food on Dipper dispersion during the breeding season on South Boulder Creek, although some evidence will be mentioned below in our discussion of territoriality. On Boulder Creek, INTFOOD clearly was the most important determinant of ESTBIRDS (Table 7L). Several sections of stream had good nest sites, but little food (Fig. 15). NSQDIST was important in one year and COVR and WIDTH in the other.

At this point it is worthwhile to discuss the relationship of breeding density in different years to the results of our correlation analyses. The overall breeding densities on both study areas were highest in 1972, lowest in 1973, and intermediate in 1971 (Figs. 12, 13). Overall densities on South Boulder in 1971 and 1972 were equal (Fig. 13), but the actual arrangement of territories was different and the mean ESTBIRDS per segment was slightly higher in 1972 (0.69 vs. 0.62). Although the five data points (three seasons on South Boulder Creek, two on Boulder Creek) represent a meager quantity of data, it is clear that as breeding density increased, the amount of variance in bird dispersion explained by our variables also increased. In 1973 on Boulder Creek, ESTBIRDS was less than two-thirds the density in 1972 (0.38 vs. 0.60). While NSQDIST was a significant factor in the 1972 correlation, in 1973 it was not, but COVR and WIDTH were significant. This suggests that there were enough good sites to "go around" in 1973 and that birds were free to pick areas of stream that also were wide and had good cover.

Combined data

To conclude this analysis, we ran stepwise correlations for all data on each stream (Table 9). On Boulder Creek INTFOOD was definitely the most important variable (note the F ratios), followed by NSQDIST, ICE, BOTM, and WIDTH (Table 9A). Boulder Creek had lower average food densities than South Boulder Creek in all food samples (Figs. 9, 10), and these differences were significant ($P < 0.005$, t test) in all but the December 1972 samples ($0.2 > P > 0.1$, t test). On South Boulder Creek, ice was most important, followed by width, bottom quality, and nest sites (Table 9). While the Boulder Creek correlation seems to be a reasonable summary, the South Boulder data must be interpreted with care. It is especially odd that width (which contributed significantly to only two census correlations, Table 8) was the second variable entered, although its importance declined as more variables were added. We feel this is a result of the combination of other variables, particularly ice, food, and nest sites. The segments of the study area below the Claypit bridge (Fig. 2) were consistently wide and had high food densities (Fig. 10), yet had few nest sites and were often covered by ice in winter. As a result, WIDTH and NUMBIRDS were negatively correlated, often strongly,

TABLE 9
SUMMARY OF RELATIVE IMPORTANCE OF VARIABLES AFFECTING DISPERSION IN ALL MONTHS

Study area	Step	R ^{2a}	Variable ^b	r ^c
A. Boulder Creek (n = 710)	1	0.17***	INTFOOD	0.41***
	2	0.18***	NSQDIST	0.15***
	3	0.19***	ICE	-0.01
	4	0.19***	BOTM	0.26***
	5	0.20	WIDTH	0.11***
	6	0.20	COVR	0.17***
B. South Boulder Creek (n = 422)	1	0.06***	ICE	-0.25***
	2	0.08***	WIDTH	-0.16**
	3	0.11***	BOTM	0.12*
	4	0.13	NSQDIST	0.09 ⁺
	5	0.13	COVR	0.15**
	6	0.13	INTFOOD	-0.06

^a Significance levels based on *F* ratio of variable in last step; ⁺ *P* < 0.10, * *P* < 0.05, ** *P* < 0.01, and *** *P* < 0.001.

^b BOTM, bottom quality index of 400-m segment; COVR, cover index of segment; ICE, ice cover index of segment; INTFOOD, interpolated food quality index; NSQDIST, nest site quality-distance index; WIDTH, width index.

^c Significance levels as in ^a.

in all but two censuses. Hence, width was not a major factor by itself. In general, the effects of stream width on dispersion of Dippers were complex. A wide section of stream was likely to be shallow and hence to have accessible food. The best nest sites and molting refuges, however, tended to be in steep, narrow sections. We conclude that width per se was probably not a significant factor.

What do these correlation analyses tell us about the factors "limiting" Dipper population density? Clearly they show that food, nest sites, and ice do affect patterns of dispersion, but this does not necessarily mean that they regulate density. Strictly speaking, we detected only correlations between variables, not causal relationships. Although we feel sure that we have delimited the major factors, absolute proof of causal relationships would require experimental manipulation of large sections of habitat. Even granting the validity of our ideas, however, we can only conclude that they have the potential to limit density. Whether they actually do so would depend on whether the habitat is saturated with birds at a given time. This in turn depends on survival and reproductive success in previous seasons.

The only months in which significantly more than half of the variance in population dispersion was accounted for were those winter months in which ice buildup was especially severe. It is particularly significant that much of the variance in dispersion was unexplained during breeding seasons when we expected resources to be in short supply.

There are several possible reasons for these low correlations. One logical explanation is that breeding populations did not saturate available habitat. We will discuss this in more detail later, but we do feel that our populations were at or close to carrying capacity during at least two breeding seasons. A second possibility is that the measurements of variables used in the analyses were subject to large errors. While many of our measurements admittedly were crude, they have proved useful and there are other factors to consider. In particular, the social behavior of the birds might have influenced densities.

SOCIAL FACTORS AFFECTING DISPERSION

All six of the variables used in the correlation analyses were factors extrinsic to the Dipper population. Any effect on dispersion by intrapopulation factors, such as gregariousness and aggression, could not be revealed by this analysis, except as unexplained residual variance. Ultimately, of course, we expect the fitness of social behaviors to be related to environmental factors, but we also expect other variables (e.g., nature of pair bond, amount of gene flow, predation) to affect evolution of social behavior. Social behaviors that evolve in response to selection pressures unrelated to physical environmental factors or to food would tend to lower the observed correlation between bird density and those factors. Since Dippers exhibit strong type A territoriality (Nice 1941) in the breeding season and are at least aggressive in winter, the effect of these social factors may be critical.

Winter dispersion

Dippers on our study areas were not, by strict definition, territorial in winter because they did not defend exclusive sections of stream. Nevertheless the birds were highly aggressive. This behavior may have had a significant effect on population dynamics in winter and thus have been a source of the unexplained residual variance in density discussed above.

Brown (1964) has pointed out that space-related aggressive behavior should be favored by selection when that space contains resources that are in short supply and economically defensible. He noted that defensibility should be thought of in terms of time and energy budgets, not just in terms of physical aggression. Our stepwise correlation analysis suggested that open water, food, and roosting sites might be important for wintering Dippers. In the Colorado Front Range, streams in the foothills-plains interface typically froze and thawed with fluctuations in winter weather. A Dipper that invested time and energy defending a stretch of stream might at any time be forced by ice to leave that area in search of open water, thereby losing its investment. Following this line of thought we hypothesized that Dippers in the Boulder area did not defend winter territories because resources were not constant enough to be economically defensible.

In an effort to test this hypothesis, we placed two and three pans of mealworms (*Tenebrio* larvae) along two open sections of Boulder Creek. We visited them every two-to-five days during December 1972 and January 1973 and refilled them as needed. If the birds' behavior was sufficiently flexible we expected them to respond to augmented food supply by becoming territorial. The birds quickly learned to take the food, and the pans had to be filled (1.5 measuring cups) at each visit. Territoriality did not develop in either case, although many birds were seen taking the food and many aggressive encounters were seen. Dipper home ranges were smaller in areas when feeders were present than in the same areas the previous year and after the feeders were removed, although the differences were not statistically significant (mean home range without food = 394 m, $n = 10$; mean with food added = 224 m, $n = 10$; $0.10 > P > 0.05$, t test), and the effects were more pronounced in the area with less natural food.

These experiments showed that wintering Dippers were sensitive to food supply, but that they did not develop territoriality. Because streams in the Front Range

freeze extensively in winter, there is severe compression of the population on any open water (Figs. 12, 13). These high densities in winter may make strict territoriality unfeasible, regardless of food abundance, because too much time and energy would have to be devoted to defense. Another, less likely, possibility is that the Front Range Dipper populations have lost any genetic tendency to be territorial in winter and could not respond behaviorally to high food densities.

The fact that a resource may be indefensible or unpredictable or both does not preclude the possibility that it may be limiting, however, and that selection might occur for other mechanisms that reduce competition. Maintenance of individual distance, in which individuals are aggressive toward others coming within a certain threshold distance (Conder 1949), is one such mechanism. If individuals maintained a relatively large individual distance they might reduce competition in their immediate vicinity (Marler 1956) and yet be free to move if the stream froze or aggression from other birds became too great. This behavior would result in lower energy expenditures compared with territoriality, where the individual must defend a larger area against all intruders. This is not to imply that individual Dippers did not have relatively fixed home ranges. Although direct evidence is scarce, many possible advantages of site attachment have been suggested (see Hinde 1956: 349–350 for a review). Indeed, some Dippers showed a tendency to remain in one area all winter (Table 4, Fig. 11).

To test the hypothesis that aggression by dominant resident birds caused transient birds to move elsewhere, the following experiments were performed. On 9 and 10 January 1973, 12 birds captured on St. Vrain Creek were released in one 600-m stretch of Boulder Creek below the hydroelectric plant (Figs. 1, 3). Previously the resident population in the area consisted (in order from power plant downstream) of birds 7844 and 1520 (a pair of adults that had bred at the power plant the previous spring), 1489 (first seen and banded in the same area the previous October), and 7928 (a two-year-old bird that had bred at Boulder Falls). When released, introduced birds attempted to preen and bathe. The response of residents to intruders was immediate and aggressive, and intruders were forced to flee or hide.

Aggressive encounters between residents had been infrequent and consisted of calls, posturings, and chases. In three days before the release, we observed one short fight between 1489 and an unidentified bird. Aggressive encounters with the introduced birds were more frequent and more violent. In four days after releases began, 12 fights were observed and residents appeared dominant in 11. Mid-air collisions were frequent, as were fights that continued in the water as the combatants floated downstream. Of 12 introduced birds, only five were seen after the day of release: three one day later, and one was seen after two days. One was found on the second day after its release in a moribund condition, with a body weight 23% below its release weight; it died within five minutes of recapture.

The rapid departure of released birds might have been due to the trauma of capture, transportation, and release, rather than to aggression by resident birds. To control for this possibility, 1520 and 1489 were removed two weeks later, on 26 January (7844 could not be found). Immediately afterward, four St. Vrain Creek birds were released. Unlike the previous experiment, introduced birds were not secretive. They preened for 5–15 minutes and began foraging. Later that day,

7928 was found above her usual home range chasing one of the released birds, and another introduced bird was chased by a resident at Lost Gulch (Fig. 3).

On the following day, one of the introduced birds was seen 600 m below the power plant, foraging 50 m below 7928. The removed residents, 1489 and 1520, were released at the Arapahoe Road bridge east of Boulder Creek. Although subjected to the same handling, these birds were released on another section of their home stream and showed more normal activity soon after release. They remained inconspicuously near the edge of the stream and did not sing, but they did not show submissive behavior near other birds at the release point. This may have been due to past familiarity with the release area (1520's quick return strongly suggests this), or to their having relatively high dominance after a long history of successful aggressive encounters, or both. Two days after the release 1520 returned to the hydroelectric plant and was seen fighting with 7928. The other released bird, 1489, was not seen again until early March, when it was back near the capture point. None of the introduced birds was seen again.

The results of these two experiments are not a clear confirmation of the hypothesis that aggression by resident birds drove other birds out of an area, but the fact that birds released in the second experiment were not immediately attacked and began normal foraging activity suggests that aggressively dominant residents did play a role in causing transients to leave.

This aggression did not produce territories, for birds did not succeed in excluding others. Nor was it defense of an individual space (*sensu stricto*), for birds on their home ranges appeared more aggressive than those off their home ranges. That individual aggression was related to a relatively constant home range suggests that it was advantageous for individuals to stay in one area, but not to defend that area as an exclusive space. The winter social system of the Boulder area Dipper population appears to be intermediate between a fixed and stable territorial system and site-independent dominance hierarchy with individual spaces. Brown and Orians (1970:244) give examples in other species.

Breeding season dispersion

Correlation analysis of factors affecting territory size.—We ran stepwise correlations of female territory size (FEMTRSIZ) with six variables: female age (FEMAGE), male age (MALEAGE), mean food density within territory (MEANFOOD), nest site quality (SITEQUAL), presence of open ends without neighbors (OPENENDS), and presence or absence of polygyny (POLYGYNY; see Methods section for methods of calculating indices and Table 2 for definitions of abbreviations). Results for all territories combined were generally unsatisfactory and gave a multiple coefficient of determination (R^2) of only 0.28. This was probably due to differences in the nature of the Boulder and South Boulder Creek study areas, as discussed earlier. Table 10 shows stepwise correlations for each of the two main study areas. The R^2 values for these correlations were high, but the contributions of the variables were quite different. Territory size was strongly inversely correlated ($r = -0.70$, $P < 0.001$) with food on Boulder Creek. On South Boulder Creek, where food was much more abundant (Figs. 9, 10), MEANFOOD and FEMTRSIZ were positively correlated, but not significantly so. This relationship almost certainly was due to the extraordinarily high levels of stream insect biomass

TABLE 10
STEPWISE CORRELATIONS OF FEMALE TERRITORY SIZE WITH SIX VARIABLES

Data correlated	Step	Variable* added	<i>r</i> of variable	<i>R</i> ² of step	<i>F</i> ratio of step	<i>F</i> ratio of variable in last step
A. Boulder Creek 1972, 1973 (<i>n</i> = 30)	1	MEANFOOD	-0.70***	0.49	26.53***	24.96***
	2	FEMAGE	0.09	0.55	16.58***	4.65**
	3	POLYGYNY	-0.35*	0.62	14.40***	3.71*
	4	SITEQUAL	-0.19	0.67	12.60***	2.64*
	5	MALEAGE	-0.27	0.68	10.30***	1.06
	6	OPENEND	-0.29	0.68	8.27***	0.07
B. South Boulder Creek 1971, 1972, 1973 (<i>n</i> = 27)	1	FEMAGE	0.47*	0.22	7.06*	8.42***
	2	POLYGYNY	0.44*	0.40	8.08**	0.63
	3	MALEAGE	-0.15	0.43	5.80**	3.06+
	4	SITEQUAL	0.11	0.46	4.77*	4.27*
	5	OPENEND	0.27	0.53	4.77**	1.06
	6	MEANFOOD	0.30	0.55	4.06*	0.78

* FEMAGE, age of female; MALEAGE, age of male; MEANFOOD, arithmetic average of interpolated food samples at 100-m intervals in territory; POLYGYNY, presence or absence of a polygynous mate; SITEQUAL, index of nest site quality; OPENEND, number of territory boundaries not adjacent to another territory.

+ $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

at the lower end of the South Boulder Creek study area, where scarcity of nest sites resulted in only two very large, open-ended territories (Fig. 14).

POLYGYNY was positively correlated with territory size on South Boulder Creek, whereas on Boulder Creek these two factors were negatively correlated. In general we would expect polygynous females to have small territories because two females are within a male's territory. On South Boulder Creek, however, there was a polygynous male at the top of the study area in 1971 and 1972 and another polygynous male at the lower end in 1972 (Fig. 14). Both of these males, but especially the lower one, had unusually large territories because of the absence of a competing pair at one end. Thus, the positive correlation of polygyny and female territory size on South Boulder Creek probably is an unusual case.

NSQDIST was only weakly related to territory size and the signs of the correlation coefficients were opposite on the two study areas. Recall that availability of nest sites was a very important factor in determining overall density and dispersion of breeding Dippers (Tables 7, 8). Once a Dipper selected a nest site, however, the size of its territory was not related to the quality of that site (Table 10).

Older females tended to occupy larger territories, although the correlation was significant only on South Boulder Creek (Table 10). The data indicate a weak negative correlation between territory size and male age. We have no ready explanation for this seemingly paradoxical situation. Larger sample sizes and better estimates of ages will be necessary to resolve the relationship between age and territory size.

Analysis of local situations affecting territory size.—Certain environmental variables might be critical in determining territory sizes in some places and not at all important in others. Stepwise correlations for entire heterogeneous study areas, such as those combining both study areas, are likely to obscure such relationships.

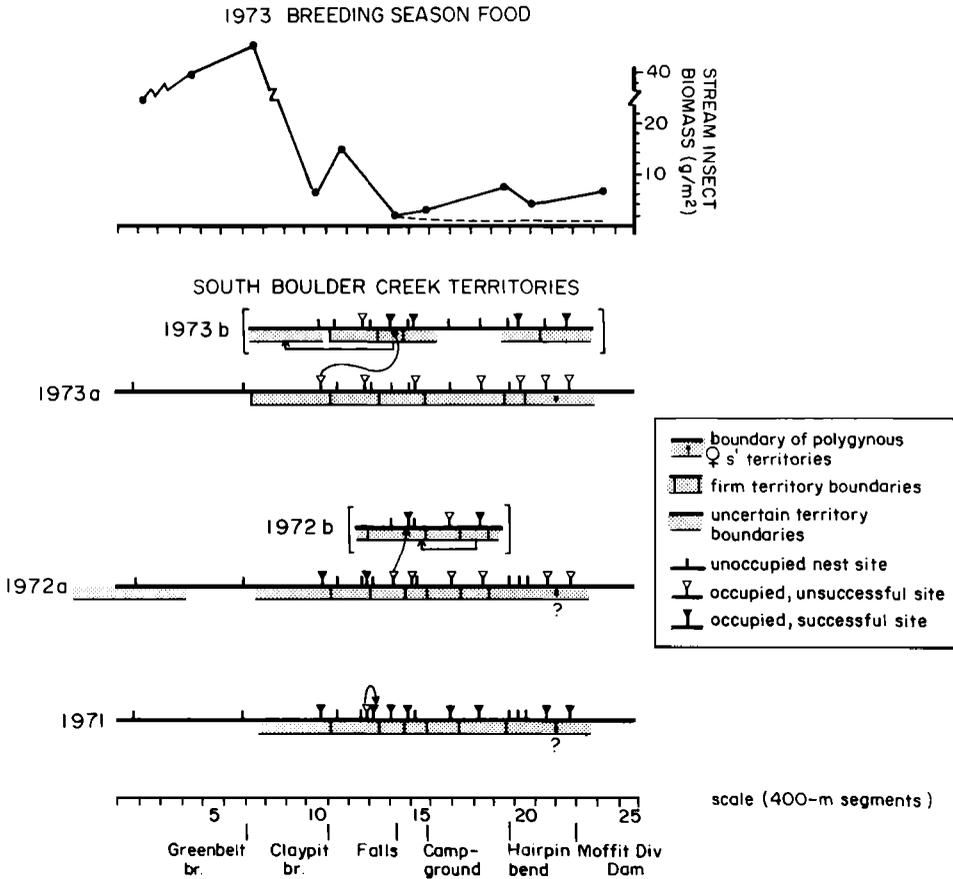


FIGURE 14. Breeding territories, 1971–1973, and 1973 breeding season food on South Boulder Creek. (Horizontal axes of both graphs indicate 400-m segments with upstream to the right. Short segments labeled 1972b and 1973b show changes that occurred after territories were established; arrows show movements by breeding females or movement of territory boundaries. The dashed line on the food graph indicates estimated 1972 breeding season food.)

Consequently, we must examine specific parts of our study areas, and the variables that appeared to operate in them.

Figures 14 and 15 are maps of territories on the two study areas in each of the three breeding seasons studied; food samples from the 1973 breeding season are shown to the same horizontal scale above the maps. The shorter maps labeled 'b' show changes that occurred after initial establishment of territories.

Effect of nest site quality on placement of territories was most apparent on South Boulder Creek (Fig. 14). The lowest 10 segments of the study area had the highest food density on our study areas (Figs. 9, 10) and abundant cover, yet were occupied only once in three years. The three potential nest sites in this area were: 1) on the low flood gate of a diversion dam for an irrigation ditch, 2) on the wooden "Greenbelt" bridge, and 3) in a small culvert under the Claypit bridge. None was of high quality. Indeed, broods of two females nesting in this area were flooded early in incubation. Significantly, this low area was occupied only in 1972,

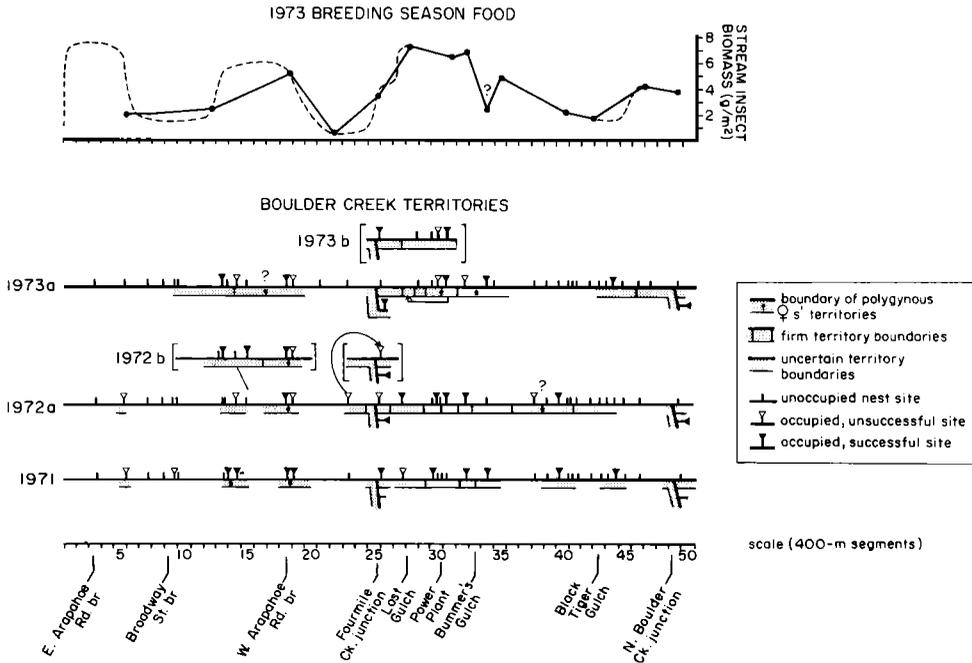


FIGURE 15. Breeding territories, 1971–1973, and 1973 breeding season food on Boulder Creek. (Horizontal axes of both graphs indicate 400-m segments with upstream to the right. Short segments labeled 1972b and 1973b show changes that occurred after territories were established; arrows show movements by breeding females or movement of territory boundaries. The dashed line on the food graph indicates estimated 1972 breeding season food.)

the year of highest population density (Figs. 12, 13; Table 11), and both females were in one male's territory. The fact that one male was able to maintain a territory over 3 km long in a year of high population suggests that there was little competition for these sites.

Segments 38–42 on Boulder Creek had 12 potential sites (Fig. 15), but only two were of high quality. Although birds were seen investigating seven of these sites in the three years, nests were started at only three, and young fledged from only the two best sites. Figure 16 shows the number of nests of high and low quality occupied as a function of total number of sites occupied. As one would expect, optimal sites were occupied first, but only up to a point, whereupon suboptimal sites were chosen. Nest site quality could not have been the only factor in nest site choice, however, since in every year some apparently high-quality sites were not utilized.

In 1972 a fortuitous, sharp drop in stream invertebrate biomass clearly demonstrated that food also was important in determining territory size. In late January 1972, just before territory establishment on South Boulder Creek, the lake behind Moffat Dam (Fig. 2; most of segment 23, Fig. 14) was drained, and accumulated sediments bulldozed up and removed. As a result, a large amount of sand moved downstream and covered virtually all good foraging areas in segments 17–23 to depths of 1 m or more. Effects of silting did not extend below

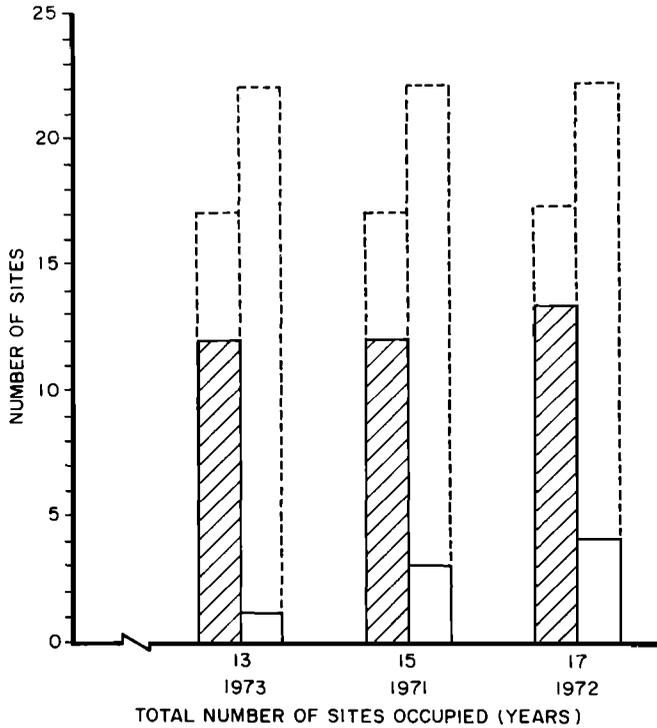


FIGURE 16. Total number of optimal and suboptimal nest sites occupied at differing population densities on Boulder Creek. (The crosshatched bar indicates the number of occupied optimal sites, SITEQUAL = 3; the open bar the number of occupied suboptimal sites, SITEQUAL = 2 or 1; and dotted lines the number of potential sites of either type.)

South Draw (segment 15) before the end of the breeding season. By late July, insect breeding and drift from above the study area was replenishing the benthos (Fig. 10, McLay 1970).

In 1972 the uppermost two territories (upper 3 nests) were held by the same five birds as in 1971, yet the upper (polygynous) territory was over 300 m longer in 1972 (Fig. 14). The fact that the upper male's territory was enlarged during a period of low food (and high population density) is circumstantial evidence that food played a role in determining territory size. Significantly, even with the larger territory, the second (polygynous) female's nest was not completed until over a month after construction started (the only time we observed nest construction lasting so long), and her four nestlings died within a week. Only one nestling hatched in the uppermost nest, and it died when water spraying from a sluice gate inundated the nest. In 1973, after the sand dispersed and stream benthos recovered, the upper (same male's) territory was even smaller than in 1971 (Fig. 14). In 1972 the second male's territory (segment 18, Fig. 14) was already established and the adults were feeding nestlings when sand covered most of their foraging areas. This pair succeeded in fledging four young, but were often seen flying downstream and foraging near the boundary of the next two territories

below theirs (see 1972b, Fig. 14). The third male's nest was flooded in 1972 and the nestlings died.

It is highly significant that the only other case of adults foraging outside their own territory occurred on South Boulder Creek in the territory with the lowest measured food density in 1973 (see 1973b on Fig. 14). This territory was established in the narrow canyon above Eldorado Springs where food density was approximately 2.5 g/m^2 (segment 14, Fig. 14). The female had had a nest flooded out at the Claypit bridge (segment 10), moved upstream, and re-nested in the territory of a previously mated male. In late July, toward the end of the nesting period, both she and her mate were seen foraging in her old territory from the Claypit bridge to the Greenbelt bridge where food was more abundant than in the precipitous canyon (Fig. 10).

Unfortunately, mild spring weather in 1972 resulted in early runoff and a breeding season food sample could not be taken. Consequently, the magnitude of the food decline caused by the silting on South Boulder Creek could not be quantitatively assessed. There is no doubt, however, that many centimeters of sand killed most stream insect larvae (Mecom 1969) and resulted in a catastrophic decline in Dipper food.

There are indications that food also was limiting on several parts of Boulder Creek. Figure 15 shows that sections of stream with less than 2.5 g/m^2 stream insect biomass in 1973 were not occupied by Dippers. In addition, the smallest territories on Boulder Creek occurred in areas with the highest food densities, as measured in 1973 (Fig. 15, segments 28–35). The dashed line in the food portion of Figure 15 is an estimate of biomass trends in 1972. Winter 1971–1972 samples indicated higher food densities in segments 2–7 and 13–18 than in 1972–1973 (see Fig. 9) and in 1973 a combination of late runoff and severe dewatering for irrigation resulted in the lowest water levels during the study below segment 13. We assume, therefore, that breeding season food densities were higher in 1972 than in 1973. In 1971 and 1972 when food was probably more abundant below segment 6, Dippers attempted to breed under the Arapahoe Road bridge (segment 5, Fig. 15).

Effects of a number of other factors were less clear-cut than those of nest site quality and food availability. As shown previously, amount of cover and stream width probably contributed to quality of territories, but were of secondary importance. Direct human disturbance (other than habitat modification) was severe along portions of the two streams, but was low in intensity during the period of territory establishment. Human activity probably had little to do with establishment of territories, although a few nests were destroyed.

Does territorial behavior limit breeding density?—The role played by territorial behavior in determining breeding dispersion and density, and the ultimate adaptive value of territoriality, have been debated for many years and continue to be enigmatic and controversial (Huxley 1934; Nice 1941; Kluyver and Tinbergen 1953; Lack 1954, 1966; Hinde 1956; Wynne-Edwards 1962; Brown 1964, 1969b; Brown and Orians 1970; Fretwell and Lucas 1970; Watson and Moss 1970; McLaren 1972; Wilson 1975; Verner 1977; Hailman 1978). Unfortunately, suggested crucial tests of the major hypotheses require uniform habitats and/or painstaking quantification of resource availability (especially food) in relation to ter-

ritory owners' needs (Brown 1969b; Fretwell and Lucas 1970; Verner 1977; Hailman 1978). We find it difficult, at least with Dippers, to test these hypotheses. Estimates of total food per territory (Figs. 14, 15) do suggest that our birds theoretically had access to enormous stream insect supplies. However, the critical variable is not simply the amount of food in the stream, but the amount of food sufficient for reproduction plus the rate and ease with which Dippers can harvest the food. Therefore, food could be limiting (by rates of harvest and delivery to nests), even if the birds take only a fraction of what was in the stream.

Leaving aside the question of ultimate causes, we can state that territoriality did limit breeding densities on our study areas. Brown (1969b) suggested three criteria to be met in proving that territoriality limits breeding densities. First, it must be shown that individuals are prevented from breeding (i.e., there must be a surplus of nonbreeders). Second, it must be demonstrated that it is aggressive behavior on the part of territory holders that prevents surplus birds from breeding. Observation of individuals being prevented from settling in previously claimed areas by aggressive behavior of owners obviously is important. Brown also suggested systematic removal of territory owners and observation of replacement. Third, if information is desired on whether total reproduction is limited, it must also be proved that territoriality prevents some females from breeding. In addition, Brown (1969a, b) also noted (following Kluyver and Tinbergen 1953), that territoriality should "buffer" density in good habitat.

It is clear that aggression by territorial Dippers did prevent some birds from establishing territories in our study areas. We made many observations of territory holders interacting with intruders (see Sullivan 1973 for descriptions of agonistic postures and behaviors). The question arises as to whether birds driven out by territory holders were physiologically capable of breeding (Brown 1969b). Direct evidence of this is scarce, but we observed six males and five females to breed in their first year, and believe it is a reasonable assumption. We also noted three instances of Dippers interacting with territory holders, then breeding successfully elsewhere. In 1972, for example, a male held a territory above the hydroelectric plant on Boulder Creek for two weeks before he was driven out by an intruder; he eventually bred on Lefthand Creek (Figs. 1, 3). We made no direct observations of floaters (birds without territories) once breeding was well underway, because individuals that did not establish a territory moved off the study areas.

In an attempt to estimate the number of birds prevented from breeding we compiled the data shown in Table 11. We reasoned that individuals seen attempting to breed at a site, but that did not lay eggs, may have left either because the site was not suitable or because of competition from other birds. If another bird bred that year at the same site, we regarded the site as suitable and the replacement as an indication of a surplus bird. This assumes that all birds were uniform in their evaluation of nest sites and that birds that failed to breed did not die (the one case where we know this to have occurred is not included in Table 11). Lack of a mate is not likely to have caused abandonment of a site. In 1973 both males and females were observed to remain near suitable sites for as long as three weeks in the absence of a mate. We believe that the birds we saw attempting to breed were a representative sample of the total population and that the estimated surplus in our sample was comparable to that in the total population (13.0–28.6%, Table 11).

TABLE 11
NUMBER OF BREEDING ATTEMPTS AND EVIDENCE FOR POPULATION SURPLUS

	Boulder Creek				South Boulder Creek			
	1971	1972	1973	Mean \pm SD	1971	1972	1973	Mean \pm SD
A. No. adults seen on study area	44	55	30	43.0 \pm 12.5	27	34	32	31.0 \pm 3.6
B. No. observed attempting to breed ^a	29	40	23	30.7 \pm 8.6	19	22	21	20.7 \pm 1.5
C. No. failing to breed ^b	8	12	5	8.3 \pm 3.5	4	7	10	7.0 \pm 3.0
D. No. failing and replaced at observed site	4	11	3	6.0 \pm 4.4	3	5	6	4.7 \pm 1.5
E. % observed attempting to breed ^c	65.9	72.7	76.7	71.8 \pm 5.5	70.4	64.7	65.6	66.9 \pm 3.1
F. % failing and replaced (estimated surplus) ^d	13.8	27.5	13.0	18.1 \pm 8.2	15.8	22.5	28.6	22.3 \pm 6.4

^a Attempt defined as one or more of the following: song, inspection of a nest site, aggressive interaction with one or more other birds, and carrying of nest material.

^b Breeding defined as laying eggs.

^c (Row B/Row A) \times 100.

^d (Row D/Row B) \times 100.

We would expect the surplus to increase disproportionately as total population increased, and this was confirmed on Boulder Creek. The total potential breeding population was 55 in 1972, 25% higher than in 1971, and 83% higher than in 1973. The estimate of the percentage surplus approximately doubled in 1972 compared with 1971 and 1973 (Table 11). The difference between the number of failures that were replaced in 1972 and in the other two years was significant ($P = 0.04$, Fisher's exact test). On the South Boulder Creek study area the difference between the total population in 1972 and in the other two years was not as great as on Boulder Creek and the difference between the estimated surplus in 1972 and the other two years also was not significant ($P = 0.54$, Fisher's exact test).

The data in Table 11 demonstrate that nest sites abandoned by Dippers often were reoccupied or appropriated by other individuals. In the absence of systematic removal experiments, these data provide strong evidence for a population surplus of Dippers in the Front Range.

A natural removal experiment occurred in 1972 on Boulder Creek. A polygynous male established a territory containing four potential nest sites in the town of Boulder in 1971 (segments 13–15, Fig. 15). In 1972 another male established a monogamous territory covering the same area, with one of the 1971 females (1972a, Fig. 15). This female disappeared during a snowstorm in March and was not seen again. The male obtained another mate within 10 days, but this female built her nest under the downstream nest site (1972b). The male apparently abandoned the upper portion of the territory. Three days after the replacement female started her nest, another pair had moved in, established a territory, and was building a nest at the uppermost site (segment 16, 1972). This episode suggests that there was surplus of both sexes in 1972.

It is worth noting at this point that the breeding density of Dippers in good habitat appeared to be "buffered;" breeding density in good habitats remained relatively constant, while densities in poorer habitats fluctuated with changes in

total population size (Kluyver and Tinbergen 1953; Brown 1969a, b). The South Boulder Creek study area was better Dipper habitat than the Boulder Creek study area. South Boulder had higher indices of width, bottom, and cover, and higher food and nest site densities than Boulder Creek (Table 1). It also had a significantly higher mean density of Dippers ($0.05 > P > 0.025$, one-tailed t test). The variation in breeding density per segment on the South Boulder Creek study area was approximately half that on the Boulder Creek study area, although this difference was not significant ($P > 0.25$, variance ratio test, Zar 1974). Comparison of areas of good habitat on each study area (e.g., segments 10–25, Fig. 14; segments 25–35, Fig. 15) with areas of poor habitat (e.g., segments 1–10, Fig. 14; segments 1–13, 20–23, 35–48, Fig. 15) shows that densities were buffered within study areas as well. A graph of the number of high- and low-quality nest sites occupied on Boulder Creek versus population size (Fig. 16) resembles Brown's (1969b) illustration of the relation between population size and density in different habitats.

To summarize, our data strongly indicate that all of Brown's (1969b) criteria were satisfied for our populations: 1) there were more potential breeding birds on our study areas than could breed there, 2) territorial behavior was important in preventing many of these individuals from settling, 3) at least some of the surplus birds were females, and 4) densities in good habitat were buffered. The problem remains as to whether or not the situation on our study areas was representative of other areas in the Front Range. Without continuous records through the breeding season on at least one floater we cannot offer direct evidence that a regional surplus existed. However, the main difference between our study areas and other areas was the large number of man-made nest sites. In more natural areas in the Front Range, where nest sites were less plentiful, territoriality probably produced larger surpluses and had even greater effects on population density and dispersion.

There are suggestions in the literature that surpluses exist in other Dipper populations. Shooter (1970:160) recorded that in one year "several surplus pairs were attempting to set up new breeding sites between existing long-established territories, causing considerable disruption." None of these pairs was successful. Fuchs (1970) reported that a nonbreeding bird was in his study area through the breeding season and remained as a "molting guest." Hewson (1967) saw one case of a male being replaced within three days of its disappearance in the spring, although a female that disappeared after laying eggs was not replaced until October. Sullivan reported five "surplus nests" in poor sites when all of the good sites were occupied, and stated that nest sites were "the critical resources for Dippers" (1973: 83). It is not clear from his account whether there were many unused sites within territories. His maps and those of Bakus (1957) suggest that there may have been territories encompassing more than one site, although Sullivan reported only one such case.

The proximate determinants of territory size have yet to be identified. Territory size may well be a direct function of the owner's aggressiveness (Watson and Miller 1971). Suggested determinants of aggressiveness include genotype, hormone balance, previous experience, seasonal factors, population density, food, visibility, and others (King 1973). Lacking direct measures of aggression, genotype, and other variables, we nevertheless observed that territories were larger for older females and in the absence of competition (i.e., presence of "open ends"), and smaller where food was abundant and competition high (Table 10).

Irrespective of factors determining aggressiveness, territoriality may or may not influence breeding population size, depending on the chance arrangement of suitable nest sites. As will be seen in the next section, nest site quality is an important factor in a Dipper's reproductive success and the birds do discriminate between sites (Fig. 16). The quality of a site is not its only characteristic, however; its position in space relative to other sites is at least as important. Other factors being equal, the spacing of breeding Dippers will be determined by the spacing of nest sites. Other factors are never equal, of course. Territoriality becomes important in restricting the number of breeders when sites are close enough in space that more than one satisfactory nest site occurs in a territory. When this happens, territoriality prevents some individuals from breeding. The fact that Dippers can be polygynous (Price and Bock 1973, Galbraith 1979) may blunt the effect of territoriality in this respect, but females also are territorial and exclusion of females does occur.

Now we begin to see the complexity of the situation. With a given series of potential nest sites of specific qualities and spacing, territoriality may well affect the number of Dippers that breed in an area. But it is not correct simply to say that territoriality "limits the size of the breeding population," because size of territories will in turn be influenced by distribution of nest sites and food, overall number of competitors, and other factors.

Brown's (1964, 1969b) theory that territoriality will evolve when defensible resources are in short supply is most attractive. However, we must not take up Occam's razor too quickly and assume that there are only one or two critical resources, that those resources are the same for all populations of a species, or the same in all parts of one local population's range, or the same from year to year. There also is no reason why more than one benefit should not accrue to a territorial individual, including indirect benefits gained by preventing other birds from breeding (Verner 1977).

DISCUSSION OF DENSITY AND DISPERSION

The basic question addressed in this section is: How does spacing pattern of individuals along a stream (and hence population density) correlate in space and time with the distributions of environmental and social variables? We have shown significant correlations of bird distribution with six variables that quantified aspects of the environment extrinsic to the Dipper population itself. Taken together, these six factors explained as much as 50% of the variation in the number of Dippers per stream segment in winter and breeding seasons when the population was near carrying capacity (Tables 7, 8). By contrast, birds during fall and spring were often dispersed randomly (Table 5) and their locations were not highly correlated with the variables used in the analysis (Tables 7, 8).

Data also showed that social behavior, specifically aggression related to individual distance, had a significant impact on winter movements and density (Fig. 11). Some birds were forced to move off our study areas, reducing density and producing more even dispersion than would otherwise have been the case. Data for the breeding seasons showed that territoriality reduced the total number of Dippers breeding on our study areas and produced a surplus of individuals of both sexes that were not permitted to breed there (Figs. 14, 15; Table 11).

Our analysis of social factors affecting dispersion was hindered by lack of a

technique to quantify their impact. This has been a major difficulty with studies of territoriality, which it is not a variable, but a constant within a given population. Consequently we may never be able to say that territoriality accounts for $x\%$ of the variance in population size, or that environmental factors account for another $y\%$. It is not enough to ask, "Does territoriality regulate population size?" Phrased in this fashion, the question is heuristically useless. Evolution has shaped the behavior of animals to permit flexible responses to ecological situations. As for our population, we conclude that social behavior in general, and territoriality in particular, had an impact on the number of Dippers on our study areas. The role of behavior on different sections of stream in different years was itself affected by feedback loops with other factors such as food, nest site quality and dispersion, age of birds, and total population size. Future studies must dissect these various relationships.

As King (1973) has noted, the proximate determinants of agonistic behavior are a complex series of interactions between intrinsic and extrinsic factors. Interrelationships between aggressive tendencies, population density, and environmental resources in the Dipper are not understood. We cannot say, for example, whether an individual Dipper was more or less aggressive in the presence of high food density, whether availability of roosts changed thresholds of agonistic behavior, or whether an abundance of cover allowed subordinate individuals to remain nearer dominant individuals. Dippers would be excellent subjects for experimental studies on the relationship of environmental variables to population density and aggression, but such studies remain to be done.

SURVIVAL AND PRODUCTIVITY

So far we have discussed population movements and the factors related to Dipper density and dispersion. During the breeding season these factors determined how many birds bred in an area and where they bred. However, they did not necessarily determine the actual size of the population. As Brown (1969b) has observed, the total size of a population may continue to rise by the addition of individuals to the floating component, even if the number of breeders remains fixed. Neglecting movements, the total size of the population is determined by the number of births minus the number of deaths in each year.

SURVIVAL AND MORTALITY

Survivorship and mortality rates are among the most difficult of all population parameters to study because of the confounding effects of dispersal. We had hoped that our populations would be relatively sedentary, but this was not the case. Our best estimate of adult survival comes from data on the number of breeding birds surviving from one breeding season to the next. Most nonbreeders present in the early spring months were in all probability first-year birds, and could not be relied upon to return the next year, even if they survived. Since none of the Dippers that bred on our study areas was ever observed to breed off the study area in subsequent years, we assumed that breeders had died if they were not observed the following year.

Our data on survival and estimates of survival rates are shown in Table 12. Survival of juveniles was estimated by assuming: 1) that just enough young survived to equal the number of new breeders on the study areas the following year,