Population Ecology of the Dipper (*Cinclus mexicanus*) in the Front Range of Colorado

FRANK E. PRICE and CARL E. BOCK

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DEPARTMENT OF ENVIRONMENTAL,
POPULATION AND ORGANISMAL BIOLOGY
UNIVERSITY OF COLORADO
BOULDER, COLORADO

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Edited by

RALPH J. RAITT

with the assistance of

JEAN P. THOMPSON

at the

Department of Biology
New Mexico State University
Las Cruces, New Mexico 88003

EDITORIAL ADVISORY BOARD

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INTRODUCTION

The major objective of this study was to answer the basic question: What factors influence the dynamics of Dipper (*Cinclus mexicanus*) populations? Detailed objectives were: 1) to measure changes in population size, dispersion, and movements; 2) to quantify available resources; 3) to measure impact of social interaction, especially territoriality, on population dynamics; 4) to measure reproductive success and relate it to other factors, especially territoriality; and 5) to monitor abiotic factors such as weather and stream flow, and to measure their impact on population processes.

BACKGROUND

Despite the importance of understanding population dynamics, the problem of what factors determine sizes of populations is still very much under investigation. Many hypotheses have been proposed, but most concern only one or two factors, and no theory has been, or is likely to be, accepted to the exclusion of others (Watson 1973). For more progress to be made, population studies must become more holistic and measure the constellations of factors which interact in time and space to influence population processes (Southwood 1968, Lidicker 1973, Ehrlich et al. 1975). Field studies on most organisms are unlikely to produce sufficient relevant data without massive, long-term research programs; even then, results may be inconclusive (Chitty 1967). Laboratory systems can be simplified and controlled to the point where clear results are obtained, but these are difficult to apply to nature.

A search for less complex natural systems should prove useful in clarifying population processes (Maynard Smith 1974). As an example, intertidal ecosystems have proven valuable for many types of ecological research (Connell 1961, 1970; Frank 1965; Menge and Menge 1974) because the invertebrate inhabitants tend to be sessile or to move slowly on a two-dimensional surface. Students of vertebrate population ecology have found it difficult to obtain comparable results. Most vertebrates are relatively mobile (hence opportunistic) and potentially interact with a great many resources, organisms, and environments.

An ideal species for studies of population dynamics would have a number of characteristics: 1) individual organisms should be easily observed and censused; 2) social behavior should be observable; 3) populations should be large enough that satisfactory quantities of data can be collected in reasonable time; 4) members of the population should be individually recognizable, or at least easily marked; 5) the species should have a well-delimited habitat so that an entire population can be studied; 6) major resources likely to influence the population should be quantifiable; 7) effects of interspecific competition and predation should either be quantifiable or not significant; and finally 8) the population should be sedentary or have quantifiable immigration and emigration. Obviously, no species outside the laboratory will satisfy all of these criteria, but birds of the Dipper family (Cinclidae) appear to have a relatively simple ecology and hence are especially well suited to studies of population dynamics.

ECOLOGY OF DIPPERS

The four species in the Dipper family are allopatric, occurring in Europe and central Asia (*Cinclus cinclus*), eastern Asia and Japan (*C. pallasii*), western North

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America (*C. mexicanus*) and South America (*C. leucocephalus*) as far south as Argentina (Greenway and Vaurie 1958). The range of the American Dipper (*C. mexicanus*) extends from Alaska to southern Mexico (Bent 1948, Van Tyne and Berger 1959). The family is ecologically homogeneous, with all species restricted to swift, unpolluted, rocky streams. There is only one reference in the literature to an American Dipper more than a few meters from water, and that was of an individual flying across a "Y" in a stream (Skinner 1922).

Dippers establish linear breeding territories because of the nature of their habitat, and all activities take place within the territory (type A territory of Nice 1941). The spatially simple habitat makes it extremely easy to census a population, map territories, and find individuals without territories. The fact that they so rarely fly over land makes it easy to capture almost any individual by placing a net across the stream in its path.

Dippers typically place nests directly over water on ledges of cliffs or bridges that are inaccessible to predators and sheltered from weather. If such sites are not available, Dippers may nest in more exposed sites, such as on large rocks or under tree roots and overhanging banks. Although nests in trees and shrubs away from water have been reported (Moon 1923, Robson 1956, Balát 1964, Sullivan 1966, Trochot 1967), they are rare and we did not see any. Such specialized nest-site requirements make it comparatively easy to find virtually all of the breeding pairs in a given area. Henderson (1908) and Bakus (1959a) give details of nest construction by *C. mexicanus*.

Dippers mostly feed on aquatic insect larvae, but occasionally take other invertebrates and small fish (Mitchell 1968, Vader 1971). Steiger (1940) reports that they eat some plant material, but Mitchell (1968) does not mention any plant material in a detailed analysis of 26 stomachs. Although Dippers do flycatch and glean prey from streamside rocks, most foraging is in water (Sullivan 1973), and even prey taken out of water are likely to have aquatic larval stages. Thus, Dippers are totally dependent on the productivity of streams and rivers. This restricted foraging habitat is more easily sampled for amount of available food than are the habitats of most terrestrial vertebrates.

Dippers are excellent swimmers and many observers (e.g., Muir 1894) have been impressed by their ability to forage in water too deep and too swift for humans to stand upright. Their feet, although large and strong, are not webbed, and they mainly use their wings when swimming in fast water (Goodge 1959). Despite their ability to swim, Dippers more frequently wade in the shallows with their heads submerged, or make short dives into slightly deeper water from perches on emergent rocks. The quality of an area of stream depends on the stream substrate as well as on the amount of food. Favorable bottom consists of rubble (rocks 3–20 cm in size) with many emergent rocks for perching. It is relatively simple to estimate the percentage of a section of stream covered by rubble and thus obtain an index of the physical suitability of that section for foraging. In addition, Dippers' long, unfeathered tarsi and habit of perching on rocks make it easy to read color-band combinations.

Many workers describe Dippers as sedentary residents that occasionally make local altitudinal movements in winter (Bent 1948, Robson 1956, Shooter 1970). However, some Dipper populations are mobile and make regular flights between drainages (Jost 1969, present study). There are no reports of regular, long-distance migrations.

Dippers also appear to be variably territorial in winter. Some workers suggest strong territoriality in winter (Skinner 1922, Vogt 1944, Bakus 1959b), while others report considerable flexibility (e.g., Balát's 1962 report of males foraging within 1 m of each other).

There have been a number of good studies covering different aspects of Dipper natural history. We shall make no attempt to review these further, except as they pertain to specific population processes. The reader who wishes to know more on the ecology of this unique group should consult the following: Bent (1948); Hann (1950); Robson (1956); Bakus (1957, 1959a, b); Balát (1960, 1962, 1964); Hewson (1967); Haneda and Koshihara (1969); Fuchs (1970); Shooter (1970); Sullivan (1973). Murrish (1970a, b) reported on interesting physiological adaptations to temperatures and diving, and Goodge (1959, 1960) discussed locomotion and vision.

For Dippers, as for most vertebrates, predation and competition are among the most difficult to quantify of all population processes. Because of Dippers' alertness, their open habitat, and the inaccessibility of most nests, we do not feel that predation is a major cause of mortality for adults or nestlings. Newly fledged juveniles, however, are more likely to be taken by predators.

Dippers have comparatively few competitors. Belted Kingfishers (*Megaceryle alcyon*) are not common in our study areas (one or two per study area) and are almost exclusively piscivorous (Bent 1940). Trout are more likely to be competitors of Dippers because of overlap in food (Carlander 1969). Rainbow trout (*Salmo gairdneri*) were most common on our streams (biomasses up to 54 kg/ha), with much smaller numbers of brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) (J. T. Windell, unpubl. data). Unfortunately, the extent of niche overlap between trout and Dippers is not known. Data reported by Carlander (1969) indicate that rainbow trout take a wider variety of foods than Mitchell (1968) reported for Dippers, but the data on Dippers are comparatively meager. There are a number of potential differences between the niches of trout and Dippers, such as preferred water depth, substrate, time of feeding, and proportion of prey taken as drift (Waters 1962, Lewis 1969, Jenkins 1969, Jenkins et al. 1970, Griffith 1974). However, more data are needed to clarify the extent of competition between trout and Dippers.

Realizing that Dippers are exceptionally well suited to population studies, we decided to attempt as complete a study as possible of the dynamics of a Colorado Front Range Dipper (*Cinclus mexicanus unicolor*) population. To no one's surprise, we were not entirely successful. We advance this report in the belief that our methods, results and organism have heuristic value. In addition to much intrinsically interesting, basic data on the ecology of *Cinclus mexicanus,* we have two general points.

First, population dynamics of even an ecologically simple species are influenced by many variables. At least *eight* factors significantly affected our populations and at least *four* more remain unstudied. The important factors, actual and potential, ran the gamut from temporal, stochastic, and abiotic phenomena (season, weather, geology), to biota (food, vegetation, predators) and social interactions (mating systems, territoriality).

Second, we encourage other ecologists to choose organisms and/or study areas that, like ours, make holistic studies feasible. Dippers (Cinclidae) are eminently suited to such investigations and will certainly repay further study.

STUDY AREAS

Field work for this study was conducted in the Front Range of the Rocky Mountains near Boulder, Colorado. For general discussions and references on the topography, climate and vegetation of this area, see Gregg (1963), Paddock (1964), and Marr (1967). Dipper populations on two streams, Boulder and South Boulder Creeks, were selected for intensive study (see Fig. 1).

The two study areas are generally representative of Front Range streams; they are fast-flowing, clear, rocky-bottomed creeks. Both flow east from headwaters at 3300–4000-m elevation along the continental divide, dropping rapidly for some 40 km to emerge suddenly from narrow canyons onto the plains at approximately 1650 m. Boulder Creek flows through the town of Boulder, and South Boulder Creek through the small community of Eldorado Springs before they join and eventually enter the South Platte River (Fig. 1). Because Dippers require pristine mountain streams, they do not extend more than a few kilometers onto the plains. Humans have damaged the habitat by mild pollution and some channelization, but have also improved it by constructing bridges which serve as excellent Dipper nest sites, and, on Boulder Creek, by constructing a hydroelectric plant which keep much of that stream ice-free in winter.

The two principal study sites were divided into 400-m segments, which were numbered from downstream to the tops of the study areas (49 for Boulder and 23 for South Boulder). Throughout the rest of this paper we will use "segment" to refer to these divisions of the study sites.

SOUTH BOULDER CREEK STUDY AREA

The South Boulder Creek site extended 9.3 km from the Colorado Department of Water Resources gauging station at 1920 m elevation down to an irrigation ditch at 1670 m (Fig. 2). The stream's drainage basin encloses a total of 308 km². The upper 0.5 km of the study area (segments 23–22) has been disturbed by construction of the Moffat Diversion Dam which backs up a small reservoir for diversion to the city of Denver. There is ample flow below the dam to maintain a natural stream environment.

The next 2.6 km (segments 22–16), from the Moffat Dam to South Draw (Fig. 2), is relatively undisturbed. The slope is 2.3%, the substrate is mostly rubble, and there are many emergent rocks. The banks are extensively lined by willow (*Salix*), alder (*Alnus*), and occasional ponderosa pine (*Pinus ponderosa*) and narrowleaf cottonwood (*Populus angustifolia*).

The section from South Draw 1.0 km downstream to Rattlesnake Gulch (segments 16–14) has been severely disturbed by flood control channelization for a small group of houses and a campground. The slope is still gentle (2.0%), but there is little vegetation along the banks, and the creek bottom is mostly small rubble with few emergent rocks.

The 0.8 km below Rattlesnake Gulch to just above the town of Eldorado Springs (segment 14–12) is steep (10.0% grade) and narrow, with little quiet water. There has been some disturbance of the south bank by road construction, but even on the undisturbed side there is only moderate vegetative cover. The creek bed probably has always been mostly boulders.

At this point South Boulder Creek emerges from its canyon and for the next
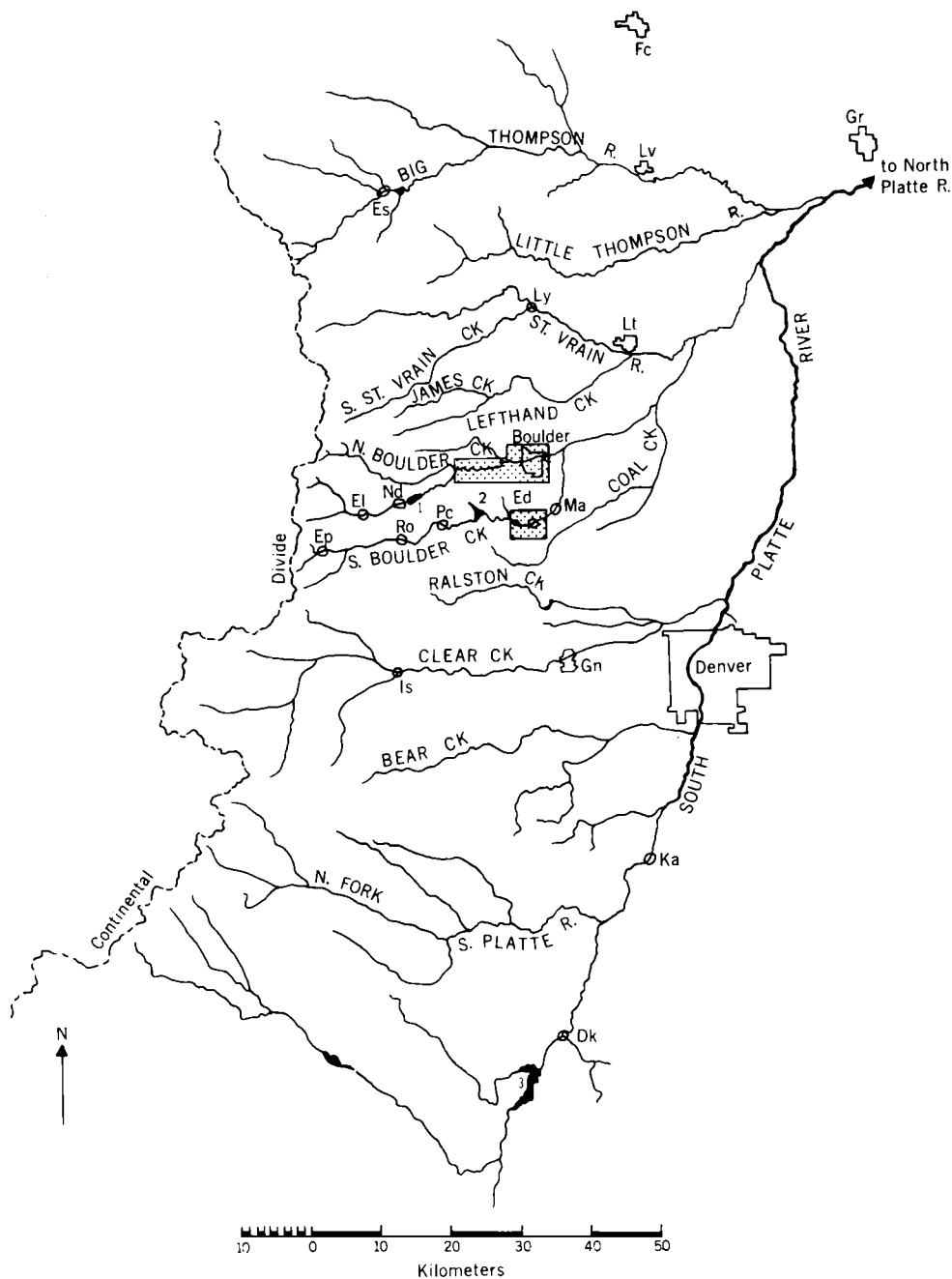
FIGURE 1. General map of study area. Shaded areas enclose intensive study areas shown in detail in Figures 2 and 3. (Abbreviations of towns from north to south: Fc, Fort Collins; Es, Estes Park; Lv, Loveland; Gr, Greeley; Ly, Lyons; Lt, Longmont; El, Eldora; Nd, Nederland; Ep, East Portal; Ro, Rollinsville; Pc, Pinecliff; Ed, Eldorado Springs; Ma, Marshall; Is, Idaho Springs; Gn, Golden; Ka, Kassler; Dk, Deckers. Reservoirs: 1, Barker Reservoir near Nederland; 2, Gross Reservoir near Eldorado Springs; 3, Cheeseman Reservoir near Deckers.)

FIGURE 2. Map of South Boulder Creek study area. (The stream and major tributaries are represented by solid lines, roads by dashed lines, and intermittent streams and irrigation ditches by dashed and dotted lines.)

0.8 km (segments 11–10) flows through the community of Eldorado Springs. Despite some dumping of trash and about 200 m of channelization above the claypit bridge (Fig. 2), the town has relatively little effect on the stream. The bottom is rubble, with many emergent rocks, and the slope is 3.8%. There are small thermal springs at the western end of Eldorado Springs which keep a variable length of stream open and habitable for Dippers in winter.

In the remaining 3.7 km of the study area below the claypit (segments 10–1)

the slope is 1.6%, the bottom excellent, food abundant, and banks almost completely lined by undisturbed riparian woodland of cottonwood, willow, alder, and box elder (*Acer*). There is some residential development along the south bank in the lowest 1.9 km.

Below the study site, irrigation and civic water supply ditches cause severe dewatering except during spring runoff. The remaining 9.7-km section, before South Boulder joins Boulder Creek (Fig. 1), is increasingly inhospitable for Dippers because of dewatering in early spring and late summer, channelization, and subdivision construction.

Width of the stream varies from less than 1 m in the narrow canyon to over 15 m in the bottom section. Depth varies from a few centimeters to more than 2 m. Mean daily discharge during the study ranged from 0.08 m³/sec in late February and early March 1971 to 12.3 m³/sec on 27 and 28 June 1971 (Colorado Department of Water Resources, pers. comm.).

BOULDER CREEK STUDY AREA

The Boulder Creek study area extended 20.0 km from the junction of Middle and North Boulder Creeks at 2100 m elevation down to the Boulder sewage plant outflow at 1600 m (Fig. 3). Area of the drainage basin totals 290 km². The vegetation is similar to that of South Boulder Creek. Boulder Creek has no steep areas comparable to South Boulder Creek and has been more heavily modified by humans.

The upper 2.7 km from Boulder Falls to Black Tiger Gulch (segments 49–43) is the steepest, with an average grade of 7.7%. This area has been disturbed comparatively little, although in places the stream bed was narrowed during road construction.

The 7.6 km from Black Tiger Gulch to the bridge below the junction with Fourmile Creek (segments 43–26) is the least disturbed physically. It has a gentle slope (2.8%) and more rubble substrate than the section above. There is slight pollution from a septic system below Lost Gulch, but this is rapidly diluted.

The 2.4 km from the bridge below Fourmile Creek to the junction of Arapahoe Road and Canyon Boulevard (segments 25–18) is slightly steeper (2.9%) and is severely damaged. Road construction has narrowed the stream bed and filled it with large boulders, retaining walls have been built to retard bank erosion, and several large areas have been channelized and have little streamside vegetation. The first of many irrigation ditches begins dewatering the creek.

Just below the road junction the creek emerges from its canyon and flattens to a 1.4% grade. The city of Boulder occupies 5.3 km of the stream bank. In the 2.0 km above the Broadway bridge (segments 18–14) the creek is in good condition. It runs through a mixture of residential areas and parks and is relatively undisturbed. Just below the bridge, however, an irrigation ditch may almost completely dewater the stream in early spring and late summer. In the 3.2 km from Broadway to the east Arapahoe Road bridge (segments 13–5) Boulder Creek is severely disturbed by polluted drainage from a gas station just below the ditch, and by flood-control channelization. For more than half of this stretch there is no streamside vegetation, the bed is bulldozed, and, except during periods of dewatering, there are few emergent rocks.

In the 1.9 km from the easternmost Arapahoe Road bridge to the sewage outflow
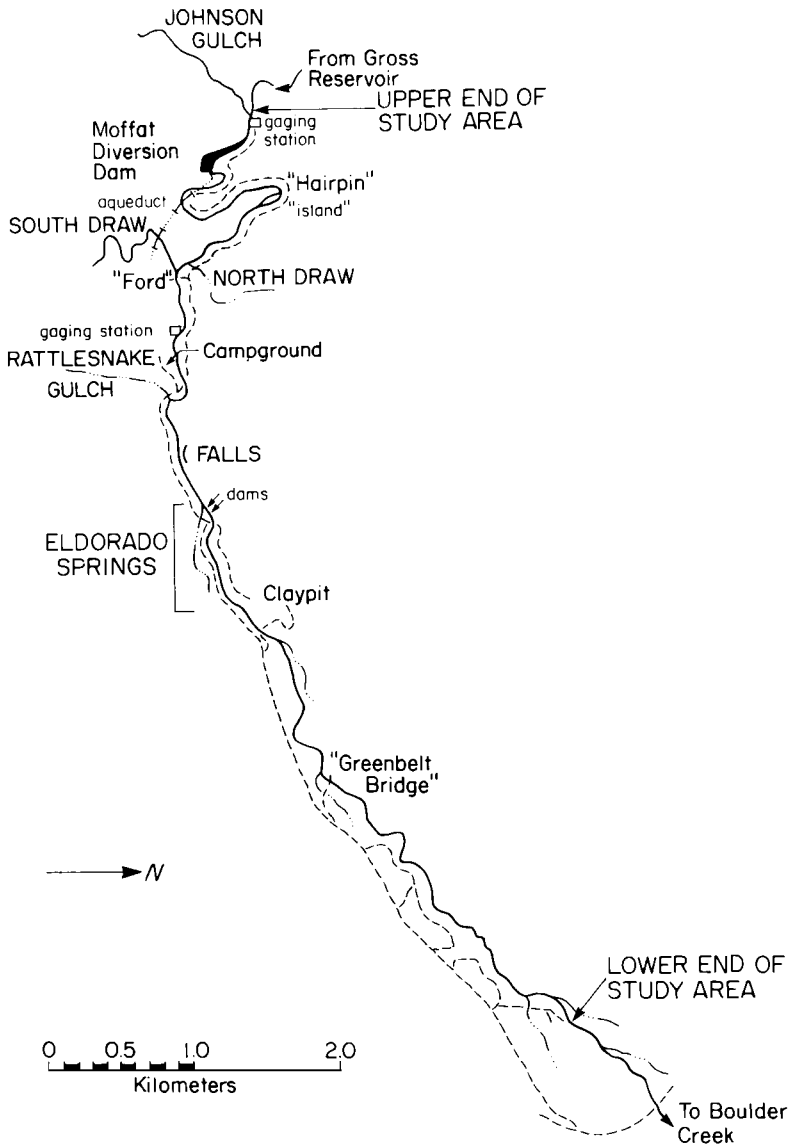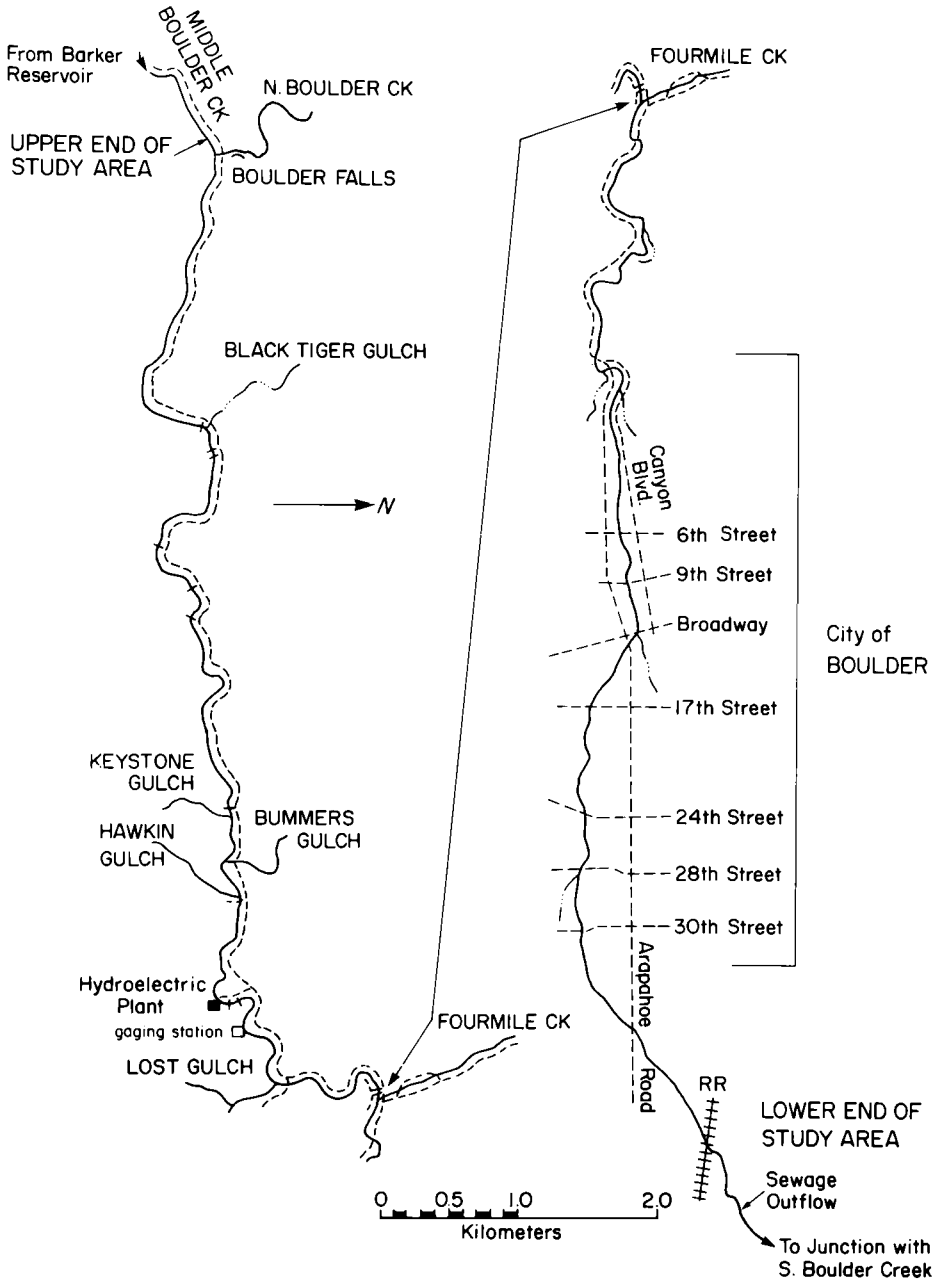
FIGURE 3. Map of Boulder Creek study area. (The stream and major tributaries are represented by solid lines, roads by dashed lines, and intermittent streams and irrigation ditches by dashed and dotted lines. Note that this map has been divided at Fourmile Creek to conserve space.)

TABLE 1

COMPARISON OF HABITAT QUALITY AND POPULATION DENSITY OF STUDY AREAS

Habitat measure	Study area	
	Boulder Creek	South Boulder Creek
Mean width index/segment[a]	3.39	3.42
Mean cover index/segment[a]	2.82	3.17
Mean bottom index/segment[a]	2.67	3.47
Mean food density index/segment[a]	3.01	17.22 (segments 1–23)
		5.82 (segments 10–23)
No. quality 3 nest sites/km[a]	0.85	1.86
Breeding density/km		
1971	1.12	1.62
1972	1.47	1.73
1973	0.96	1.40
All years: Mean ± SD	1.18 ± 0.26	1.58 ± 0.17
CV[b]	0.22	0.11

[a] See Methods section for explanation of indices.
[b] Coefficient of variation.

(segments 5–1), Boulder Creek itself is relatively undisturbed. It flows through riparian woodland and has a canopy of cottonwoods, although there are few shrubs along the banks because of grazing by cattle. There is a good rubble bottom and enough groundwater enters the stream bed to maintain some flow even during severe dewatering. From the sewage outflow to the junction with St. Vrain Creek (Fig. 1) Boulder Creek is severely polluted, increasingly sandy, and not Dipper habitat.

Perhaps the most important human influence on Boulder Creek is the Colorado Public Service Company hydroelectric plant in about the middle of the study area (segment 30). That plant, which gets its water via a pipeline from Barker Reservoir (Fig. 1), provides power only during periods of peak demand, during which its discharge may raise the water level of Boulder Creek 0.5 m or more, with a maximum discharge 5.7 m³/sec (Colo. Public Service Co., pers. comm.). These rapid fluctuations in water flow keep the stream ice-free below the plant and provide critical winter habitat that would otherwise be unavailable to Dippers.

The width of Boulder Creek varies from 1.2 m in the upper canyon to over 20 m in the lowest channelized portion. Depth varies from a few centimeters to over 2 m. Mean daily discharge during the study ranged from 0.104 m³/sec on 31 December 1971 to 19.2 m³/sec on 20 June 1971 (Colo. Dept. Water Resources, pers. comm.).

COMPARISON OF BOULDER CREEK AND SOUTH BOULDER CREEK STUDY AREAS

In general, South Boulder Creek had better habitat than Boulder Creek. Table 1 contains summaries of width, bottom, cover, and food-density indices for the two study areas, along with density of good nest sites and density of breeding birds (see section of Methods for definitions of indices). South Boulder Creek clearly was better by all of these measures. Note especially that it had densities of breeding birds that were 34% higher, but only half as variable as those on Boulder Creek.

OTHER STUDY AREAS

In addition to the intensive study areas on Boulder and South Boulder Creeks, portions of both streams up to elevations of 3050 m were visited periodically, especially during the breeding season. Once we discovered that local Dipper populations were more mobile than expected, we made irregular visits to Lefthand, St. Vrain, and Clear Creeks, to the South Platte River below Deckers, and occasionally to the Big Thompson River, Coal and Ralston Creeks, and many small streams near the continental divide (Fig. 1).

METHODS

Principal objectives of this study were 1) to describe population dynamics of the Dipper, especially density, dispersion, territoriality, movements, mortality, and recruitment; and 2) to relate these to quantified resources and environmental variables. Methods used for the first objective were relatively standard: banding, censusing, mapping territories, and monitoring nests. An advantage of studying Dippers is that these methods are less time-consuming than with most species. Resulting extra field time and the nature of the species' habitat and feeding habits made it possible to quantify resources and various factors of the abiotic environment for the second objective.

Data were collected from 7 February 1971 to 27 July 1973 on a total of 472 field-days: 306 and 192 days, respectively, for the Boulder and South Boulder Creek study areas, and 68 days for other areas. Because amount of effort may affect quantity of various data, several indices of monthly effort were tabulated. In most cases amount of effort did not correlate with variation in data. Daily summary maps were prepared, listing observers, areas of stream covered, numbers and identities of birds seen, and status of nests visited. Information on identified birds was transcribed onto individual bird data sheets and maps. Data on nest construction, dates and numbers of eggs, nestlings, and fledglings were tabulated on individual nest summary sheets.

MAPS AND MEASUREMENTS

Study area maps (used for individual records and summaries) were traced from United States Geological Survey 7.5-minute topographic maps. Some distance measurements were made to the nearest 0.1 km on the original topographic sheets with a measuring wheel. Territories were measured in the field using a 50-m steel surveyor's tape. Elevation measurements of nest sites (variable ELEV; see Table 2) were taken directly from topographic maps.

BANDING

Because of the importance of identifying individuals in a study such as this, we made every effort to band as many Dippers as possible. In all, we banded 558 individuals. Of these, 341 were captured on our study areas and 217 at higher elevations on the study streams or on the nearby drainages of Lefthand Creek, St. Vrain Creek, and the Big Thompson River. Adults were captured by chasing them into a mist net stretched across the stream. Nestlings and some females were hand-captured by climbing to the nests with a ladder or rock-climbing equipment. Nestlings were banded before 14 days of age, because older nestlings

frequently left the nest early when startled. A few fledglings were captured with a hand net or by hand. All birds were banded with unique combinations of an aluminum U.S. Fish and Wildlife Service band and various colored plastic bands. Individual birds will be identified in this paper by the last four digits of the federal band number.

After banding, birds were weighed and released. Wing length also was measured in the last spring of field work. Dippers have long, unfeathered tarsi and we could read band combinations from as far as 30 m with 10X binoculars. Few returns were made through the U.S. Fish and Wildlife Service Bird Banding Office and all but five sightings used in this report were made by personnel working on the project and familiar with the color scheme. For each banded bird an individual data sheet and map were kept, and all subsequent sightings were recorded, along with notes on behavior, mates, breeding, plumage, etc.

DETERMINATION OF SEX AND AGE

Although Dippers appear monomorphic, only females incubate (Jourdain 1938, Bakus 1959a, Haneda and Koshihara 1969) and males have longer wings than females (Balát 1964; Andersson and Wester 1971; Price, unpubl. data). Prior to spring 1973, however, we were not aware of the dimorphism in wing length and could sex birds only by observing a brood patch or incubation behavior during the breeding season.

No method is known for aging Dippers after they complete their postjuvenal molt. When ages were used in analysis of factors affecting territory size and fledging success (variables FEMAGE, MALEAGE), the following scheme was used: breeding individuals banded as nestlings or juveniles were given their true age in years. From these individuals, a mean was calculated for each sex. Birds of unknown age when banded were assigned an age equal to the mean for their sex. Unknowns observed again in subsequent years were assigned ages equal to the mean plus one, or mean plus two years. Although this procedure probably underestimated the mean age of unknown birds, we believe it made the best use of our data. Our sample of birds with known ages was too small to evaluate effects of age on territory size and fledging success. Since age may well be an important variable we decided that even an underestimate was useful.

CENSUSING

Throughout the study a complete census was attempted once a month by two or more observers walking the length of each intensive study area. When possible, at least one observer waded. Since a census of both study areas usually required 7–10 days, censuses were not done during the breeding season when other data were needed and the location of each breeding pair was known. Certainly we spent enough time in the study areas during breeding seasons to have found any non-territorial birds.

Dippers are more easily censused than most birds, but there were a number of sources of error associated with this technique. The major difficulty was that some birds remained motionless in hiding until the observers passed. This was especially common in winter when there were air pockets under shelf ice, and in spring when high water made it difficult to see and hear birds (see Bakus 1957 and 1959b for a more detailed discussion). By working down the stream in pairs, throwing rocks

into dense bushes and by ice ledges, pounding on thick ice with poles, and sending one observer back after unidentified birds that flew past, it was possible to see the vast majority of the population. Thus, most inaccuracies mentioned by Bakus were avoided or minimized, and censuses were, to the best of our ability, "true censuses," not "sampling estimates" (Smith 1966).

The number of birds seen on each stream segment was recorded as the variable NUMBIRDS for use in analysis of dispersion. Because few censuses were taken during breeding seasons, an estimate of breeding season density per stream segment was calculated by the formula:

$$D_i = \sum_{j=1,2} (T_j/A_j)P_{ij}$$

where D_i was the estimated density in segment i (ESTBIRDS); T_j was the total number of segments occupied by the territory of female j whose territory included segment i; A_j was the number of adults in the territory of female j (i.e., 2.0 for monogamous and 1.5 for polygynous territories); and P_{ij} was the proportion of segment i occupied by the territory of female j. No segment was ever occupied by more than two females. Our use of this equation assumes: 1) that polygynous males divided their time equally between the territories of two females, and 2) that all parts of a territory were utilized equally. Although it is probable that neither of these assumptions was completely satisfied, we believe that the above formula provides the best possible estimate of ecological density of breeding Dippers. Indeed, these calculations of breeding bird density per 400-m segment probably were more realistic than estimates based upon censuses. Breeding birds were, in effect, "spread" over the sections of stream they used, rather than being placed in a segment where they happened to be seen on a census.

Peripheral areas off the main study areas (see section on Other Study Areas) were spot-checked in nonbreeding seasons, but these data were incomplete. During breeding seasons only potential nesting sites were examined for evidence of breeding activity. Because of the restricted nest site requirements of this species, censuses off the main study areas were reasonably complete for breeding birds, but not for transients.

DETERMINATION OF TERRITORY BOUNDARIES

Most students of Dippers have used chases to determine territory boundaries (e.g., Vogt 1944, Robson 1956, Bakus 1959b, Balát 1962, Sullivan 1973, Sunquist 1976). This method assumes that the birds will go to an end of their territories before turning, but Bakus' (1959b) data and our own indicate that this is not always true. During the first few days of territory establishment, some birds would consistently turn in the same area, but others were never consistent. Later, even individuals that had gone to the boundaries turned at different points, possibly because they were familiar with places to hide within the territory or had become habituated to the chase situation. The best data on the location of territory boundaries came from observing territorial encounters between neighboring birds. Whenever possible in this study, two observers chased birds together to determine where boundaries lay. If this was not possible, the boundary was set where the birds turned around, provided this was consistent two or more times early in the season and neighbors independently turned in approximately the same place.

Encounters between territory holders and wandering individuals were not good indicators of boundaries. Territory owners frequently landed before reaching their boundary and sang while the intruder kept flying. When none of these techniques worked, especially for isolated, open-ended territories without neighbors, only the observed home range (Burt 1943) was mapped. Territory sizes for females were recorded as the variable FEMTRSIZ for use in statistical analyses. Territory-boundary data for the Boulder Creek study area in 1971 were inadequate by these guidelines and were not used in statistical analyses.

MEASURES OF HABITAT QUALITY

Because one objective of this study was as complete an assessment as possible of the components of habitat suitability, a number of additional variables were quantified. The names and definitions of the variables used in analyses are shown in Table 2, and are described below.

Food availability

Food availability was assessed using a Surber sampler (Hynes 1970) to estimate biomass of benthic invertebrates. On the Boulder Creek study area, 11–16 stations were sampled in winter 1971–1972 (February), summer 1972 (July), winter 1972–1973 (December), and in spring 1973 (April). Unfortunately, mild spring weather in early 1972 prevented a spring sample in that year and we used the spring food data from 1973 in analyzing all three years' data. In the same months, 9–13 stations were sampled on the South Boulder Creek study area. The sampler was handmade of anodized aluminum and had a sample area of 0.1 m²; the net had a mesh with nine threads per centimeter. Every effort was made to catch organisms on and under rocks, but not to sample deeply buried organisms which would be less likely to be available to Dippers. Six such samples were taken at each station (or three if insects and debris were very abundant) and collected material was preserved in 95% ethanol. Later, organisms larger than 1 mm (mostly insect larvae) were separated by hand. Samples were then air-dried for 5 min and weighed to the nearest 0.01 g. In calculating biomass, each set of six samples from a station was considered to be of 0.5 m² to compensate for losses in sampling, as suggested by Dr. R. W. Pennak (pers. comm.). Because areas with rubble bottom are more productive than areas with boulders, gravel, sand, or silt (Pennak and Van Gerpen 1947), samples were not taken at random. Rather, they were taken in shallow (5–50 cm deep) areas of rubble that experience had indicated were suitable for Dipper foraging. Quantification of relative amounts of rubble in different parts of the study areas is discussed below under bottom-quality index.

Organisms were not sorted into taxa or size classes, nor were stomach samples taken. Work by Mitchell (1968), Thut (1970), and Vader (1971) indicates that Dippers will take almost any animals (within a broad size range) available in the stream. Nor did we sample aerial or terrestrial prey, which Sullivan (1973) found to be the objects of approximately 20% of Dipper foraging maneuvers in spring and summer. Because many insects in the air and on streamside rocks have aquatic larvae, we considered this to be an insignificant source of error.

There is a large body of literature on inaccuracies of available techniques for sampling stream benthos (see Hynes 1970 for a general discussion and references). Our measurements were not intended to be accurate determinations of total ben-

TABLE 2
LIST OF VARIABLE NAMES USED IN THE ANALYSES[a]

A. Variable names used in analysis of dispersion

BOTM	= Bottom quality index of a stream segment
COVR	= Index of percent of stream bank in a segment covered by rocks, vegetation or other things suitable for hiding Dippers
ESTBIRDS	= Estimated density of breeding Dippers utilizing a segment
ICE	= Index of ice cover
INTFOOD	= Interpolated food index for a stream segment
NSQDIST	= Index of quality and distance of nest sites in or near a stream segment
NUMBIRDS	= Number of Dippers seen in a segment on a census
NUMBRIDG	= Number of bridges in a segment
REALFOOD	= Measured stream insect biomass in a segment
SITEQUAL	= Index of nest site quality
TOTSITQL	= Sum of SITEQUAL of all nests sites in a segment
WIDTH	= Width index of a stream segment

B. Variable names used in analysis of territory size and reproductive success

CLCHNUM	= Clutch number, i.e., 1st, 2nd, replacement
D8CUP	= Date inner nest cup was completed; days from 1 January
D8DOME	= Date nest dome was completed; days from 1 January
D8EGG	= Date first egg was laid; days from 1 January
D8FLEDG	= Date nestlings first left the nest; days from 1 January
D8HATCH	= Date eggs hatched; days from 1 January
D8INCUB	= Date incubation began; days from 1 January
D8START	= Date nest construction began; days from 1 January
ELEV	= Elevation of nest site above sea level
FEMAGE	= Age of female parent
FEMTRSIZ	= Size of female's territory
FLOB4CON	= Mean stream flow during the week before D8START
FLONSTL	= Mean stream flow during the nestling period
MALEAGE	= Age of male parent
MEANFOOD	= Mean of interpolated 1973 food samples at 100-m intervals in territory
NOEGGS	= Number of eggs in completed clutch
NOFLEDG	= Number of nestlings fledged
NONESTL	= Number of nestlings
OPNENDS	= Presence of territory boundaries not adjacent to a neighboring territory
POLYGYNY	= Presence or absence of polygynous mate
SITEHITE	= Height of nest site above water surface
TOTAGE	= Sum of FEMAGE + MALEAGE
TOTFOOD	= Product of MEANFOOD × FEMTRSIZ
TPTNINC	= Total precipitation during incubation
TPTNNSTL	= Total precipitation during nestling period
XMNTINC	= Mean minimum daily temperature during incubation
XMNTNSTL	= Mean minimum daily temperature during nestling period
XPTNINC	= Mean precipitation per storm during incubation
XPTNNSTL	= Mean precipitation per storm during nestling period

[a] See Methods section for details on how values of variables were calculated.

thic biomass or of total Dipper food, but rather to be reasonably reliable indices of food availability in different portions of the study areas. A number of samples were replicated after a few days and found to be within 1 g of one another.

Food sample data were plotted against their locations and recorded as the variable REALFOOD for each stream segment from which a sample was taken.

Linear interpolations were made between sample points. In analyzing effects of food availability on dispersion we also took the value of the food graph in the middle of each 400-m stream segment to be representative of that segment and recorded it as the variable INTFOOD. For analyses of relationships between food availability and territory size and placement, we mapped territories along the food graph. At 100-m intervals in each territory the values of the food graph were averaged to obtain an estimate of mean food density in each territory (variable MEANFOOD).

Nest sites

The numbers and qualities of nest sites in each segment were determined. Quality of each nest site (abbreviated SITEQUAL) was graded from 1 (poor) to 3 (excellent) on the basis of four criteria: height above water, ledge width, presence of a sheltering overhang, and security from predators. Quality 1 sites were within 1 m of water level in early April or were easily accessible to predators. Quality 2 sites were high and inaccessible, but lacked a sheltering overhang, or the ledge was less than 10 cm wide. To be rated as quality 3, a site had to satisfy all four criteria.

If Dippers are attracted to nest sites and tend to spend time near them, the probability of our seeing a bird should vary directly with the quality of the nearest nest site and inversely with its distance. An index of nest site quality and dispersion (abbreviated NSQDIST) was calculated for each segment by the formula:

$$I_i = q_1/d_1 + q_2/d_2,$$

in which I_i was the index (NSQDIST) of the ith segment, q_1 and q_2 were the qualities of the nearest nest sites up and downstream, respectively, and d_1 and d_2 were the distances in number of 400-m segments to the nearest nest sites up- and downstream. To avoid division by zero, we gave segments containing a nest site a distance of one; segments lacking a site but adjacent to one with a site were given a distance of two, etc.

Stream quality

To measure additional aspects of stream quality, the center of each stream segment was marked on a map and visited in random sequence by the same two observers. The observers each walked up- and then downstream 100 m from the center and independently rated width, bottom, and cover. Width (WIDTH) of bed (not water) was graded from 1 (less than 4 m) to 6 (more than 20 m). Bottom quality (BOTM) was rated subjectively from 1 (very poor) to 5 (very good) on the basis of amount of bed covered by rubble (rocks 3–20 cm in size), bed profile, depth, and number of large rocks available for perching. Amount of cover (COVR, i.e., large rocks, bridges, and vegetation) along the banks was graded 1 (no cover), 2 (less than 10% cover), 3 (10-to-50% cover), or 4 (more than 50% cover). During winter censuses the amount of ice in each 400-m segment of stream (variable ICE) was rated from 0 (no ice) to 3 (very little open water).

For each segment, the mean score on each variable (WIDTH, BOTM, COVR, and ICE) was taken as representative of the entire segment, and used as an index in statistical analyses. A number of other parameters and rating schemes were evaluated and this sytem proved most reliable (interobserver correlation = 0.83).

Depth could not be reliably rated; because of significant daily fluctuations, many measurements would have been needed at each point and it was judged not worth the time required. Also, general water depth was a component of the bottom evaluation.

Stream flow

Data on mean daily stream discharge were obtained from the Colo. Dept. Water Resources. These data were gathered from gauging stations located just above the campground on South Boulder Creek (Fig. 2) and just below the hydroelectric plant on Boulder Creek (Fig. 3). For each brood, mean stream flow during the week before nest construction started (FLOB4CON) and mean stream flow during the nestling period (FLONSTL) were recorded and used in analyses of reproductive success.

Weather

Data on daily precipitation and daily maximum and minimum temperature were obtained from published U.S. Weather Bureau records for the city of Boulder (U.S. Dept. Commerce, 1971–1973). Although microclimate on the study areas certainly varied from the reported Boulder figures, no better data were available. For analysis of reproductive success, additional variables were computed: total precipitation during incubation (TPTNINC) and nestling period (TPTNNSTL), mean minimum temperatures during incubation (XMNTINC) and nestling period (XMNTNSTL), and mean precipitation per storm during incubation (XPTNINC) and nestling period (XPTNNSTL).

STATISTICAL ANALYSES

Correlation analysis was used extensively in this study. In analysis of dispersion, data on density of Dippers and data on environmental variables for each of the 72 stream segments in each census were punched onto Hollerith cards for input to computer programs. Similarly, pertinent data on each clutch of eggs laid in our study areas were punched onto cards for analysis of territoriality and nesting success. Names and definitions of variables used in these analyses are listed in Table 2. The principal programs utilized were BMD-02R (Dixon 1971) and various SPSS programs (Nie et al. 1975).

ANNUAL CYCLE IN THE COLORADO FRONT RANGE

A brief survey of the annual climatic cycle and its effects on Dipper populations is useful at this point as an introduction to the ecology of the species in our area.

CLIMATE

The climate of the Boulder area is a continental one, with great variations, both diurnal and annual, in temperature and rainfall (Paddock 1964). Figure 4 shows mean monthly temperature and total monthly precipitation in the town of Boulder, and total monthly runoff of Boulder Creek during the study.

Daily temperatures fluctuated an average of 15°C and variations of more than 22°C were not uncommon. Average precipitation was 472 mm per year, but was highly variable, with an average monthly deviation of 25 mm from 30-year means during the study period. The mean annual discharge of Boulder Creek over 63

A. Mean Monthly Temperature

B. Total Precipitation Per Month

C. Total Runoff Per Month
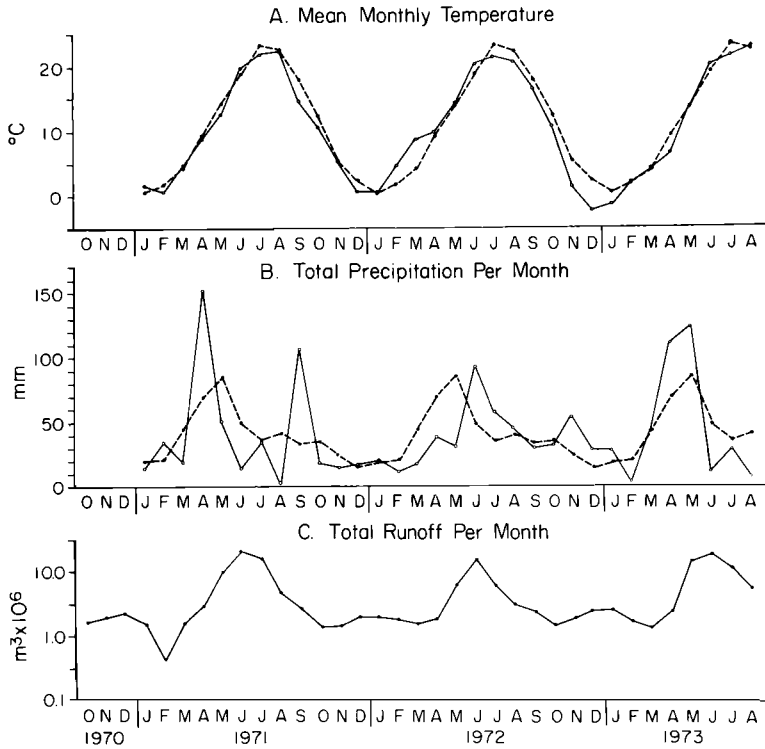
FIGURE 4. Variation of environmental factors in Boulder, Colorado. (Dashed lines show 30-year means, 1930–1960; solid lines, data collected during this study, 1971–1973. Sources: A and B, U.S. Dept. Commerce; C, Colo. Dept. Water Resources.)

years of records has been 8.1×10^7 m^3, with a mean rate of flow 2.6 m^3/sec (Colo. Dept. Water Resources, pers. comm.). Figures for South Boulder Creek are comparable, although more variable. Both streams usually were partly frozen from middle or late December until mid-February.

These average figures do not give a realistic impression of the often extreme environmental fluctuations faced by Dippers. For example, May 1969 was wetter than average (220 mm total precipitation versus a mean of 85 mm), and 87% of the precipitation fell from 3 to 8 May. This storm increased flow in Boulder Creek from 1.0 m^3/sec on 1 May to 25.9 m^3/sec on 7 May, and in South Boulder Creek from 1.7 m^3/sec to 31.7 m^3/sec. Flood damage along both streams was considerable, and effects on the Dipper population undoubtedly were drastic (M. Whitney, pers. comm.). Temperature also may fluctuate greatly. The winter of 1972–1973 was unusually severe, with mean monthly temperature falling below 30-year averages in November, December, and January by 4.1°C, 4.4°C, and 2.0°C, respectively (Fig. 4). One 12-day period in December 1972 had a mean daily maximum temperature of −20°C. The effects of extreme changes in weather are discussed in more detail in the section on survival and productivity.

It is difficult to compare the annual climatic cycle in Boulder with those of other Dipper habitats. Dippers live in mountainous areas characterized by large differ-

TABLE 3

CONTINENTALITY INDICES AND ELEVATIONS OF STUDIES OF DIPPER POPULATIONS

Cinclus species	Location	Study area elevation (m)	Gorzynski's continentality index[a]	Reference
mexicanus	Missoula, Mont., USA	975–1220	33[b]	Bakus (1957, 1959a, b)
mexicanus	Missoula, Mont., USA	<975–1220+	33[b]	Sullivan (1973)
mexicanus	Boulder, Colo., USA	1600–2100	37[b]	Present study
cinclus	Westmoreland, England	180–550	<10[c]	Robson (1956)
cinclus	Banffshire, Scotland	nd[d]	<10[c]	Hewson (1967, 1969)
cinclus	Peak Dist. Natl. Park, Derbyshire, England	90–370	<10[c]	Shooter (1970)
cinclus	Bern, West Germany	nd	20–30[c]	Vogt (1944)
cinclus	Brno, Czechoslovakia	240–340	25–30[c]	Balát (1960, 1962, 1964)
cinclus	Fulda, West Germany	200–810	15–20[c]	Jost (1969, 1970)
cinclus	Basle, Switzerland	ca. 270	20–25[c]	Fuchs (1970)

[a] Index = $(1.7 \times (A/\sin L)) - 20.4$, where A = annual temperature range (°C) and L = latitude angle (Barry and Chorley 1970).
[b] Calculated from data in U.S. Dept. Commerce (1964, 1965).
[c] Estimated from Barry and Chorley (1970, Fig. 5.1).
[d] nd = data not available.

ences in precipitation and temperature over short distances (Barry and Chorley 1970). However, because published data on the ecology of Dippers frequently appear contradictory, it is necessary to attempt comparisons. Continental climates are characterized by a short time lag between maxima and minima of solar insolation and corresponding maxima and minima of surface temperatures (i.e., rapid spring thaws and fall freezes), as well as great annual and diurnal temperature fluctuations. Climatologists have formulated indices of continentality which can be used in comparing different areas (Barry and Chorley 1970). Table 3 shows such indices, along with the elevations of some areas where Dippers have been studied. Other factors being equal, we would expect areas at high elevations and those with high indices to have less favorable and more variable climates. By either of these measures the Boulder climate is severe.

DIPPERS

As early as the third week in February, individuals that had wintered in areas of open water with suitable breeding habitat began to court and establish territories on their wintering grounds. As the ice melted, nonwintering birds arrived and also attempted to establish territories and find mates. Birds unsuccessful in establishing territories continued to move until they left our study areas.

Both males and females defended territories, although females appeared to choose the actual nest sites. Females performed most of the nest construction, which began 1–2 weeks after territory defense. Nest sites and construction followed the usual cinclid pattern, except that good sites were abundant in our areas and no nests were seen on sites other than cliffs, bridges, and large boulders.

In the three years of our study there was considerable variation in the timing of breeding (see Fig. 5). On the lower parts of the study areas egg laying probably began in early to mid-April in most years, although the start of laying varied from mid-March in 1972 to early May in 1973. From a comparison of Figures 4 and 5 it is clear that Dippers returned to breeding areas and initiated courtship well
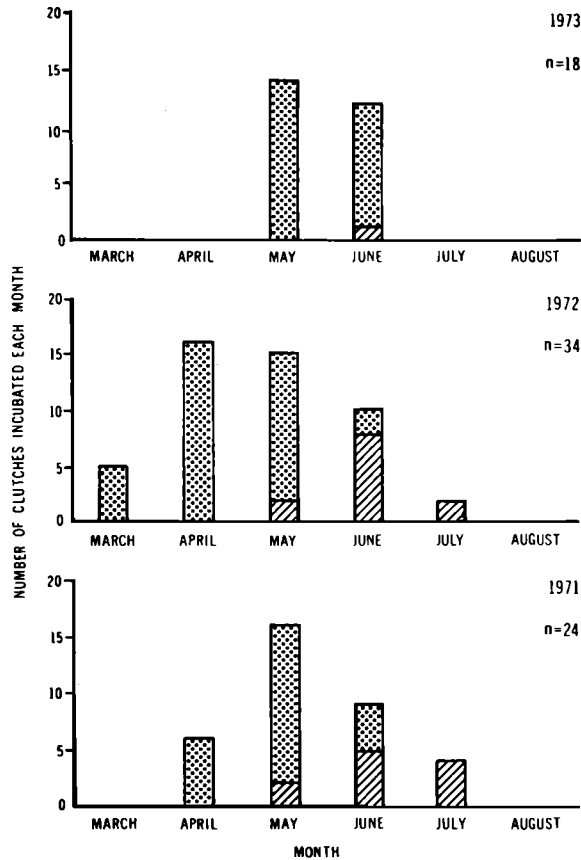
FIGURE 5. Timing and number of clutches being incubated, 1971–1973. (First and replacement clutches are represented by dotted bars; second clutches by bars with diagonal lines.)

before the peak of spring runoff in May and June. Especially in 1972, birds began to appear on the study areas in January even before temperatures rose. The 1973 breeding season was anomalous in this respect, perhaps because of the exceptionally severe winter.

It is adaptive for Dippers to start breeding early because the heavy spring runoff in May drastically reduces food availability (Mecom 1969). While it is true that this means most pairs will be feeding young during the runoff, it is equally true that there would be no more food later in the summer (Figs. 9, 10; Mecom 1969). Egg formation by female birds is energetically expensive (Kendeigh 1963, El-Wailly 1966), and the early start means that most clutches are laid before runoff starts. While incubation also utilizes energy (Kendeigh 1963), the "oven-like," insulated nest which Dippers build is well adapted to reduce heat loss to a minimum. Because of their stringent nest site requirements, suitable nest sites may often be in short supply. It is probable that there has been selection for defense of territories and nest sites by Dippers as soon as ice melts.

Despite this apparent selection for early breeding, winter and spring weather

did appear to affect the start of breeding. Temperatures in February and March 1972 were unusually warm, and incubation started almost a month earlier than in 1971 when temperatures were close to the 30-year means. Temperature and precipitation were again close to normal in February and March of 1973, but incubation did not start until May. It is possible that many birds were in poor condition following the severe winter of 1972–1973 and needed more time to come into breeding condition. Our weight data indicate that in the first four months of 1973, birds averaged 4% lighter than in 1972 (1973 mean = 56.2 g, $n = 25$; 1972 mean = 58.5 g, $n = 31$). While this difference was not statistically significant, these data suggest that adults surviving the winter of 1972-1973 were in poor condition.

Dippers laid one egg per day until their clutches were complete (usually four or five eggs), after which incubation began. The females incubated alone for about 16 days. Although males took no part in incubation, they occasionally fed the females. Clutches of second, polygynous females (Price and Bock 1973) usually were started during laying or incubation of the first females' broods. After eggs hatched, both male and female fed the young for 20–30 days. On the average, fledging occurred 25.4 days after hatching ($n = 51$). After a first brood fledged, about 40% of adults started second broods. Length of breeding season was important in determining the number of second broods (Fig. 5). No second broods were seen above approximately 1830 m elevation, although we did see replacement broods.

After fledging and being fed for from a few days to two weeks, juveniles dispersed, with many crossing over drainage divides to other streams. Most adults left their territories after breeding and moved upstream, with some changing drainages during the summer. During this period in August, adults, but not juveniles, underwent a synchronous molt of flight feathers and could not fly for 5–14 days (Balát 1960; Sullivan 1965, 1973).

Beginning in late August and September, banded birds started to reappear on our study areas, along with unbanded individuals. Numbers increased into October, then declined in November and December. It is unclear where most of these birds went; many probably wandered in search of open water.

By mid- to late December most streams had frozen and the only habitat available, aside from small holes, was to be found in the foothills and high plains. On Boulder Creek the area below the hydroelectric plant (Fig. 3) remained open. On South Boulder Creek a variable length of stream, sometimes less than 1.5 km, was kept open by thermal springs. Since Boulder and South Boulder Creeks drain 290 km² and 308 km² areas, respectively, there was severe compression of the population in winter.

Contrary to other reports (Vogt 1944, Bakus 1959b, Hewson 1967, Sullivan 1973), Dippers on our study areas were not clearly territorial in winter. Although there was much agonistic behavior, there was no clearcut defense of a given space such as occurred during the breeding season. Individuals often exhibited day-to-day movements and left the study areas for a month or more.

In January and February the number of birds began to increase again as the breeding season approached. Individuals seen the previous fall commonly returned, along with large numbers of unbanded birds, and attempted to establish territories.
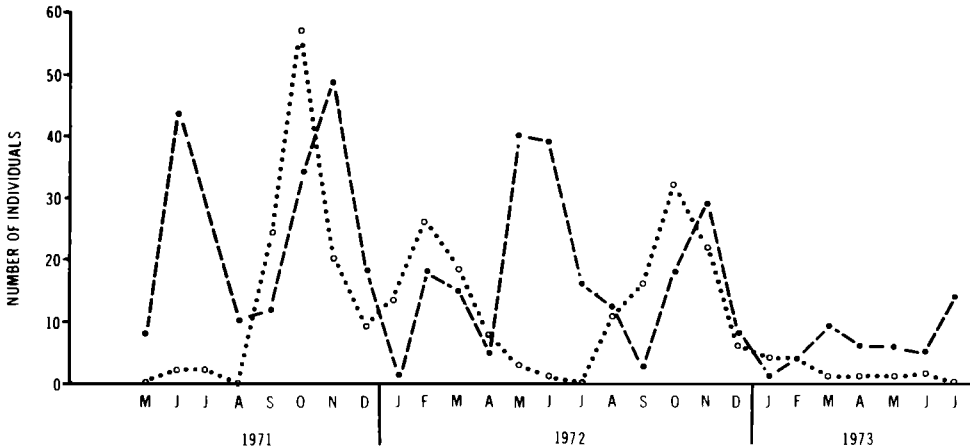
FIGURE 6. Number of banded birds arriving and departing study areas per month. (Dotted line: arrivals, defined as individuals banded in a given month, or previously banded but not seen for at least a month. Dashed line: departures, defined as birds that disappeared and were not observed on the study areas for a month or longer.)

The rest of this paper is an elaboration and documentation of this overview of the yearly cycle of the Dippers in the Front Range.

POPULATION MOVEMENT

The Dipper population in the Boulder area was more mobile than others reported in the literature, with the possible exception of *Cinclus cinclus* in Switzerland (Jost 1969). These movements greatly affected population density and distribution.

SEASONAL MOVEMENT IN ALTITUDE

Movement of Dippers to different elevations for breeding and wintering has been reported for both American and European species of Dippers (Vogt 1944, Bent 1948, Bakus 1959b, Balát 1962, Fuchs 1970, Whitney and Whitney 1972). However, detailed observations on the movements of a large number of banded individuals have been scanty, especially for *Cinclus mexicanus*.

Figure 6 shows numbers of banded individuals leaving and entering our study areas in each month. Clearly the number of Dippers moving onto and off of the study areas fluctuated seasonally. Numbers increased in January, February, and March as individuals began to move upstream in search of breeding territories. This movement in late winter was most obvious in 1972. After the hard winter of 1972–1973 the population was small and few birds returned. Movement declined in April when adults had either found territories or moved off the study areas. The considerable variation in the timing of breeding in the three years (Fig. 5) affected the number of juveniles and adults leaving the study areas in the late spring and early summer. Juveniles began to fledge and move off the study areas in June of 1971, May and June of 1972, but not until July of 1973. From a low level in summer, the number of birds moving onto our study areas increased in fall as indigenous adults and juveniles returned, along with unbanded birds from
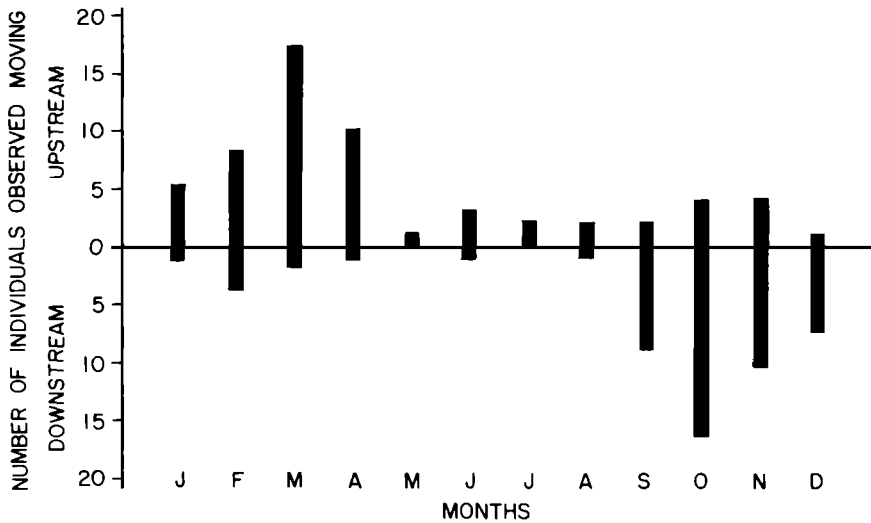
FIGURE 7.   Mean number of banded Dippers moving more than 1.6 km on study areas per month (April 1971 through March 1973.)

other areas. Following another low in mid-winter, the number moving again increased in spring.

The data in Figure 6 document large numbers of birds moving onto and off of the study areas, but do not show directions of movements. Figure 7 shows the mean number of banded individuals that made well-documented movements of at least 1.6 km up- or downstream on the study areas. Most birds moved upstream in March and downstream in October.

Although the majority of our population moved, a number of individuals stayed in or near their breeding territories most of the year. Such "resident" birds tended to be absent for short periods in summer and winter, but did not follow the typical migratory pattern. Possible explanations for summer absences will be given later; winter absences usually appeared to be caused by extensive ice formation. Overall, individuals that bred on sections that did not freeze remained on our study areas in winter significantly more often than did birds from territories that froze (14 of 27 vs. 6 of 34, Dec. 1971–Feb. 1973; $P = 0.04$, Fisher's exact test).

Altitudinal movements in spring (up) and fall (down) are of obvious adaptive value: they enable Dippers to avoid frozen habitat in winter, yet disperse as widely as possible for breeding. However, migration is energetically expensive (Berger and Hart 1974), and, although direct evidence is scarce, it is possible that birds that remain resident in one area become familiar with food sources and refuges from predators (Hinde 1956). Because of the increased risk and metabolic cost of migration, one might expect Dipper populations to be resident in areas that do not freeze.

Indeed, there are many reports of resident populations of *Cinclus cinclus* in ice-free habitat in Europe (Robson 1956, Balát 1962, Hewson 1967, Shooter 1970). Balát (1962) reported both migratory and resident birds in one area of Czecho-slovakia, with the latter occurring on streams fed by warm springs.

Altitudinal migration in the American Dipper also appears to be facultative, with individuals that breed in habitat that is ice-free in winter tending to remain resident. Bakus (1957, 1959a, b) described an annual pattern of movement in Montana similar to that reported here, and his data (1957) show at least two banded individuals returning to the same wintering areas two years in a row. Sullivan (1973), in a more extensive study on the same Montana streams, observed only a few instances of adult Dippers being forced from their territories by ice. Sullivan (1973:151) concluded that such cases were rare and that "observations of . . . transient juveniles . . . are probably responsible for the so-called 'altitudinal migration' associated with this species in the literature." This statement certainly does not apply to the Dipper population in the Front Range of Colorado.

While the ultimate causes of altitudinal migration seem clear, proximate cues for altitudinal movements are unknown. In spring most birds appeared to follow upward movement of open water as ice thawed. Given strong selection for early territory establishment, one would expect Dippers to move into habitat as soon as it became available. However, actual loss of habitat was unlikely to have been the proximate cue for downstream movement. Downstream migration in fall began before any but the very highest tributaries started to freeze. Thus, there may be different cues for movement in spring and fall.

POSTBREEDING MOVEMENT OF ADULTS

After young became independent, usually in June or July, adults often could not be found for several months. The numbers of breeding birds present on our study areas dropped to a low in August, rose in fall, dropped again in winter and rose again in spring (Fig. 8). Although some adults did remain on their territories, data indicate that most moved.

Of 76 individuals that bred on the study areas in 1971 and 1972, only 7 (9.2%) remained within 1 km of their breeding sites, 7 are known to have moved upstream, and 62 (81.6%) were not observed for a month or more. For both years, the average period of summer absence was 1.8 months ($n = 50$). There was no apparent difference in the behavior of the sexes. As the lower end of the Boulder Creek study area marked the lowest extent of suitable habitat, it is likely that most birds that disappeared moved upstream off the study areas.

One possible explanation for this summer exodus is that the birds sought refuges for molting. For a 5–14-day period during their postbreeding molt, adult Dippers are flightless and seek out refuges of tangled logs and brush (Balát 1960; Sullivan 1965, 1973; Hewson 1967). Sullivan (1973) attributed the majority (78%) of his sightings of birds off their territories to need to find a molting refuge. During this time Dippers are secretive and might have been missed by our censuses.

A few of our birds did appear to seek out refuges for molt. In our study areas there were few dense tangles of debris suitable for hiding and few areas of dense brush. We searched such areas carefully during July and August when the water levels were low enough to walk through most of them. Only a few molting birds were seen. The molting individuals seen on Boulder Creek were not far below the junction with North Boulder Creek (Fig. 3). This area offered the best cover on the study area and was least disturbed by human activity. On the South Boulder Creek study area the sections above North Draw and between Eldorado
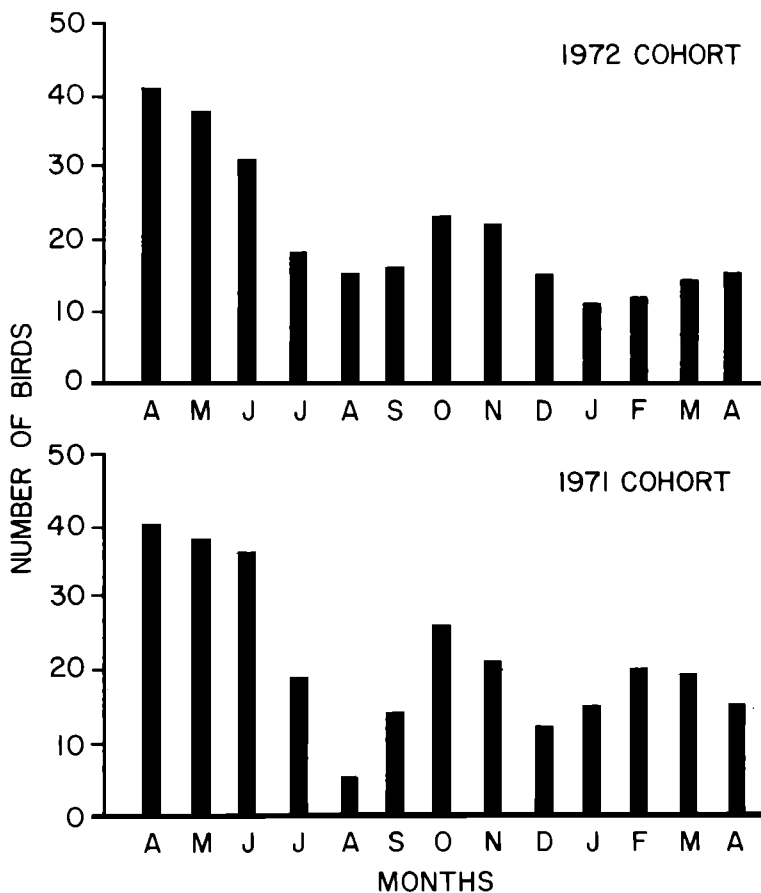
FIGURE 8. Numbers of 1971 and 1972 breeding birds present on study areas in each month after breeding.

Springs and Rattlesnake Gulch (Fig. 2) were more suitable than some others, and several birds were seen in these areas during the molting period. Three birds that did not move had bred on territories with good refuges nearby.

Despite the attractions of this hypothesis, there are several reasons why molt probably was not the only cause of postbreeding adult movements. If it were, most individuals should have gone only as far as the first good refuge, and have been absent only for the two weeks of the flightless period. Birds were absent for an average of seven weeks and most observed movements were for distances greater than necessary to reach a refuge. The longest observed movement during this period was approximately 25 km and some birds even changed drainages. On the South Boulder Creek study area the section downstream of the Claypit (Fig. 2) had the most dense brush and was least disturbed by man, yet no adults were seen there in mid-summer. If birds were aggressive during this period, one might expect long movement, but no aggression was observed.

Another possible cause for the observed upstream movement after breeding was a decrease in food availability. Figures 9 and 10 show our data on stream
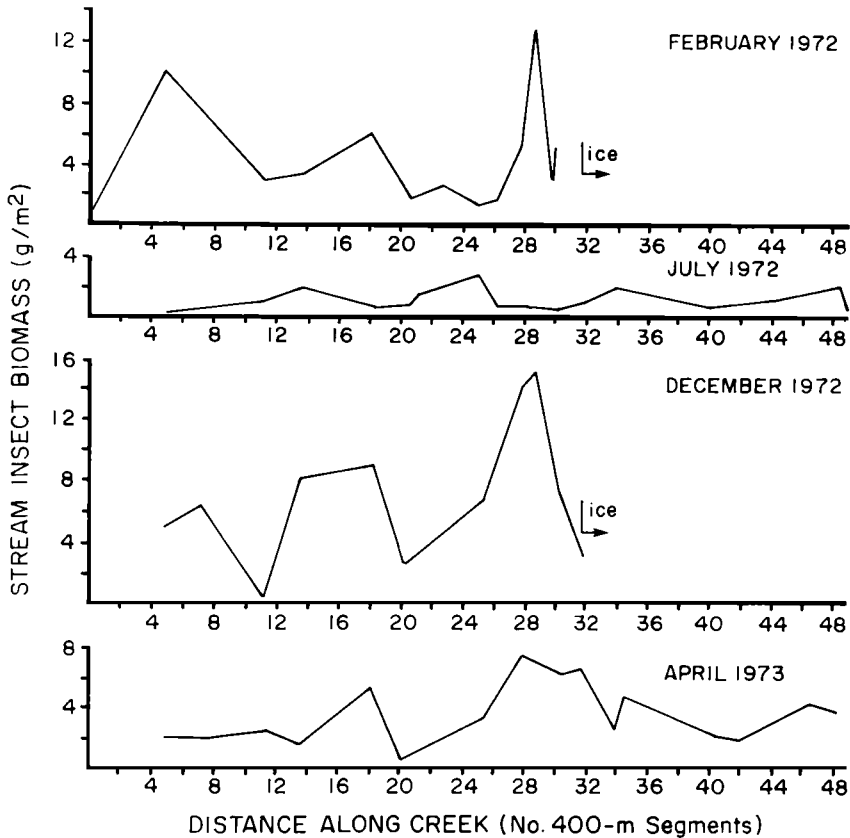
FIGURE 9.   Boulder Creek food samples.

insect biomass. Collections in December, February, and April averaged 10.0–15.2 g/m² on South Boulder Creek and 3.5–7.0 g/m² on Boulder Creek. The samples taken in summer averaged only 3.1 and 1.1 g/m², respectively. The differences between the July samples and all other series on each stream were highly significant ($P < 0.001$, t test).

There are reasons for believing that food may have been more available at high elevations during summer, although no quantitative samples were taken above the study areas. Casual turning of rocks in streams at high elevations in July and August revealed more large specimens (>5 mm in length) of Trichoptera, Ephemeroptera, and especially Plecoptera than were present at lower elevations. Because of the short and delayed growing season at higher altitudes, more adult insects emerge in July and August and more insect species have two-year larval periods than at lower elevations where a life cycle may be completed in one year (Mecom 1969, Hynes 1970). Consequently, when benthic insects at lower elevations had emerged and only eggs or small instars were present in the stream, insects at high elevations were ready to emerge or were only part way through larval development.

Abundant food at higher elevations could explain 1) the long movements observed in some adults and hypothesized for those that were absent for several
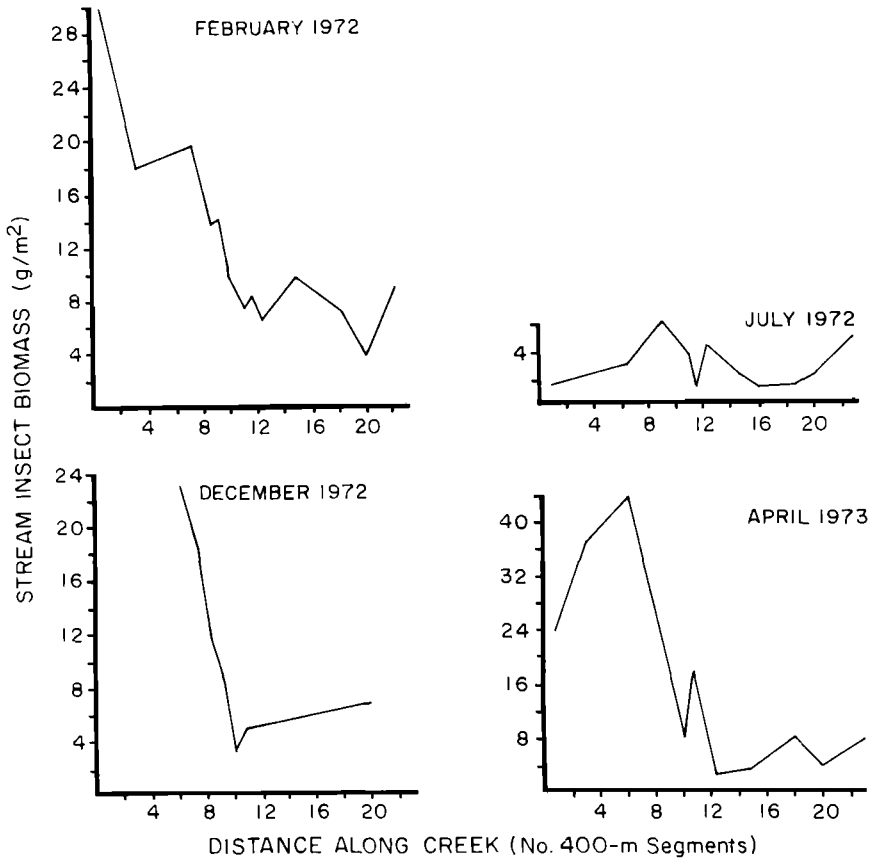
FIGURE 10. South Boulder Creek food samples.

months, 2) the tendency to move upstream observed even in individuals moving short distances, and 3) the failure of birds to use seemingly excellent molting refuges low on South Boulder Creek. On the basis of our data, neither molt nor food hypotheses can be preferred as the major cause of an upward movement of adults after breeding. Since molt is energetically expensive (Payne 1972) as well as dangerous for Dippers, the birds probably searched for areas with both good cover and abundant food.

DISPERSAL OF JUVENILES

Dispersal of juvenile Dippers from their nests and ultimately to their own breeding territories was difficult to quantify. Most fledglings disappeared and were not seen again. In most cases we could not determine whether individuals died or moved. In the Boulder area most juvenile Dippers that survived their first year probably dispersed away from their native areas.

Dispersal could not be followed directly, but a rough estimate of the magnitude of juvenile dispersal from the study areas can be made. Of 40 adult Dippers that bred on the Boulder and South Boulder study areas in 1971, 21 were known to be alive in 1972. Since the total 1972 breeding population was 44, there were 23

new breeders on the study areas in 1972. Five of these 23 were 1971 juveniles, and 18 were immigrants. Let us make the admittedly tenuous assumptions that 1) the 1971 population produced enough surviving young to exactly account for new breeders in 1972, and 2) survival and dispersal rates were comparable everywhere along the Front Range. If these assumptions were true, then 23 of the 1971 young survived, but 18 emigrated and balanced the 18 immigrants. Although not reliable in detail, this line of reasoning suggests that roughly 80% of young Dippers that survived their first year left their native area. Clearly, dispersal of juveniles is a major factor in the dynamics of the Dipper population near Boulder.

Most juveniles, like their parents, moved upstream. Of 147 fledglings banded on or near our study areas in 1971 and 1972 we have data on postfledging movements (i.e., within three months of fledging) of only 42 (29%). Seven (17%) moved less than 1 km. Of the remaining 31, 10 (24%) moved downstream and 14 (33%) upstream. Eleven birds (26%) were observed to change drainages. Because birds that changed drainages probably moved upstream (see below), approximately 60% of observed juvenile movements were upstream. This was significantly more than would be expected if juveniles moved up- or downstream at random ($P < 0.005$, normal approximation to the binomial test; Zar 1974). By the same test, there was no significant difference in frequency of north or south movements ($0.1 < P < 0.02$).

This distinct upstream orientation of dispersing Dippers might seem an exception to the usual random dispersal of most animals (Berndt and Sternberg 1968, Dow and Scott 1971). However, this probably is an artifact of the short period after fledging used to define the data set. It is likely that juvenile Dippers, like their parents, moved upstream to reach better foraging areas. After approximately three months, immature Dippers became part of fall migration and moved downstream.

Duration of the dispersal period and speed of movement were variable. Some fledglings reached their eventual breeding areas in as short a period as three months; others did not settle in over 11 months. Some Dippers remained close to their nests for several weeks (one fledgling moved only 1.2 km in 29 days) while others moved more rapidly (e.g., 8.1 km in 22 days). Balát (1962) observed Dippers moving as far as 3 km per day, but did not state their ages.

Movement of juveniles was not affected by adult territoriality. Sullivan (1973) observed adults chasing "strange" juveniles out of their territories; this would tend to force juveniles to move rapidly. However, we observed two instances in which adults tolerated, but did not feed, begging juveniles that were not their own, and one case of an adult feeding a strange juvenile. Balát (1962) also noted juveniles crossing territory boundaries with impunity.

Data on effective distance of dispersal (the shortest distance in an air line between site of birth and site of breeding; Johnston 1961) were difficult to obtain. Mean distance for 16 observed individuals was 17.8 km; mode and median, 10 km ($n = 3$); range, 2–74; SD, 20.0. Because our data were biased toward smaller distances, we conclude that our Dippers dispersed farther than those reported in the literature. Balát (1962) observed juveniles 25 and 42 km from the nearest breeding sites, but these were unbanded birds that had moved to nonbreeding habitat; the effective distance may have been less. Robson (1956) analyzed 34 recoveries from almost 3000 British Trust for Ornithology records on banded

Cinclus cinclus and found a maximum effective dispersal distance of 19.3 km; the mean of six females' dispersal distances was 6 km. Shooter (1970) ringed 215 birds and 7 were found, all within 8 km of their nests. Hewson (1967) suggested longer distances, as no young bred on 11 km of stream under periodic observation around one site. The available data are insufficient to determine whether the effective distance of dispersal of Dippers shows the bimodal frequency curve found in other organisms (Johnston 1961).

MOVEMENT IN WINTER

As noted above, the literature describes Dippers as either residents on breeding territories or as altitudinal migrants with winter territories. Our birds were far more mobile than this suggests.

The majority of workers mention winter territories or note many chases and aggressive interactions between wintering Dippers (Skinner 1922; Vogt 1944; Penot 1948; Bakus 1957, 1959b; Hewson 1967; Holmbring and Kjedemar 1968; Fuchs 1970; Sullivan 1973). Only two previous papers suggested that Dippers may not be territorial in winter. Balát (1964) observed few interactions in *Cinclus cinclus* and even saw two males foraging within 1 m of each other, but he also noted that individuals stayed on a 100–200-m stretch and could not be chased from it. Also, Whitney and Whitney (1972) observed as many as 15 individual *C. mexicanus* on one 800-m section of a Colorado stream, and mentioned two distinct groups of seven and two birds each.

Patterns of movement

The vast majority of Dippers that we saw in fall and winter were mobile and left the study areas for at least part of the winter. Of 181 banded birds seen in the falls of 1971 and 1972, 140 (78%) were not seen for at least one month during the following winter. Since all of the available Dipper habitat on Boulder Creek and most of the habitat on South Boulder Creek was under observation, it must be concluded that virtually all of these individuals moved to other drainages.

Table 4 shows some of our data on winter movements of four typical birds. Some individuals (7806, see also Fig. 11) appeared to be resident or to move as little as necessary to find open water. Several gave indications of making regular trips to wintering areas (7803, 7823). A few birds stayed mostly on the study areas, but wandered seemingly at random (7809). Finally, a large number were absent for 1–5 months during fall and winter (7852). The mean length of absence for birds that left and returned was 2.0 months ($n = 41$), the modal absence was 1.0 month. This seems too short a period for birds to have migrated great distances.

A major effort was made in the winter of 1972–1973 to find these absent birds. Accessible open water areas were checked on St. Vrain Creek, Lefthand Creek, South Boulder Creek from Marshall to Boulder Creek, Coal Creek, Ralston Creek, Clear Creek and the South Platte River from below Kassler to Cheeseman Dam and Buffalo Creek (Fig. 1). In addition, a number of flowing irrigation ditches and open lakes from Boulder and Lyons east to the South Platte River were checked. Over 120 sightings of individual Dippers were made, but only two individuals (both on South Boulder Creek below Marshall) had been banded. Because 14.5% of the banded birds that had left the study areas in winter 1972–1973 returned in the spring, mortality cannot have been solely responsible for our lack of success.

TABLE 4
EXAMPLES OF WINTER MOVEMENTS

Bird No. and sex		Date	Study area and notes
7803	F	13 Mar. 1971	BC[a]; 24th St. bridge
		16 Mar. 1971	BC; 24th St. bridge
		—[b]	Absent during 1971 breeding season and summer
		7 Oct. 1971	BC; Broadway bridge
		26 Oct. 1971	BC; 9th St. bridge
		Nov. 1971	Location unknown
		3 Dec. 1971	BC; 24th St. bridge
		9 Dec. 1971	SBC; "Greenbelt bridge"
		12 Dec. 1971	BC; 24th St. bridge
		18 Dec. 1971	BC; 17th St. bridge
		—	Absent during rest of winter, 1972 breeding season, summer, and fall
		14 Dec. 1972– 1 Feb. 1973	BC; 24th St. bridge, 5 sightings
		22 Mar. 1973	SBC; "Greenbelt bridge"
		23 Mar. 1973– 29 Mar. 1973	BC; 24th St. bridge, 3 sightings
		Spring 1973	BC; Bred at Broadway bridge
7809	?	8 Oct. 1971	BC; W. Arapahoe Rd. bridge
		15 Oct. 1971	BC; 250 m below W. Arapahoe Rd. bridge
		3 Nov. 1971	BC; railroad bridge east of city of Boulder
		5 Nov. 1971	BC; 6th St. bridge
		19 Nov. 1971	SBC; 2.4 km above junction with BC
		3 Dec. 1971	BC; E. Arapahoe Rd. bridge
		Jan. 1971	Location unknown
		22 Feb. 1972	BC; below E. Arapahoe Rd. bridge
		8 Mar. 1972	BC; above 6th St. bridge
		—	Not seen again
7823	M	27 Mar. 1971	SBC; Eldorado Springs
		Spring 1971	Bred at junction of Fourmile Creek and BC
		21 Oct. 1971	BC; junction with Fourmile Creek
		10 Nov. 1971	SBC; 500 m below Claypit bridge
		8 Dec. 1971	SBC; Eldorado Springs
		Jan. 1972	Location unknown
		22 Feb. 1972	BC; 28th St. bridge
		—	Not seen again
7852	F	29 Sep. 1971	BC; 1.1 km above Keystone Gulch
		Oct. 1971– Jan. 1972	Location unknown
		3 Feb. 1972	BC; 9th St. bridge
		9 Feb. 1972	BC; 6th St. bridge
		20 Mar. 1972	BC; on breeding territory 1.3 km below Black Tiger Gulch

[a] BC = Boulder Creek; SBC = South Boulder Creek; See Figures 2 and 3, respectively.
[b] Dashes = location uncertain during nonwinter period.

There are two possible explanations for our failure to find these birds: either most birds traveled beyond areas we checked, or the number of banded birds was such a small fraction of the total that chances of seeing a banded bird were very small. Without more data it is difficult to be sure which of these hypotheses is

correct, but we are inclined toward the latter. Some indication of the "dilution" of banded birds in the unbanded population may be gained from data collected on 21 November 1971 on a census of 6.4 km of South Boulder Creek below Gross Reservoir. This area was upstream of the regular study area and no banding was done there; however, 26 individuals of all ages had been banded higher on the stream between Pinecliff and Rollinsville (Fig. 1) and 66 had been banded on the study area. Of 28 birds seen in the 6.4-km census, only two (7%) were banded. It is not surprising that no marked birds were seen on drainages more distant from the banding areas.

This is not to say that some individual Dippers do not move far in winter. Bent (1948) referred to Dippers seen on the plains of Canada 80 km away from mountains. Muelhausen (1970) and Green (1970) reported a Dipper along streams on the northwest shore of Lake Superior in Minnesota, approximately 1400 km from the nearest breeding habitat in the Black Hills of South Dakota.

Taking into account the strong tendency of many birds to remain on the study areas, the short-distance wandering observed in others, the short duration of many absences, and the large number of unbanded birds in the area, it is most probable that there was no regular, long-distance winter migration by our population.

Winter movements of juveniles

Our data suggest the greater mobility of juveniles continued in winter. Although we cannot be sure that no. 7803 (Table 4) was a juvenile when banded, she was clearly older and more sedentary in winter 1972–1973 and spring 1973 than in 1971 and 1972. Statistically, of 179 banded birds seen on the study areas between September and November of 1971 and 1972, 72% of the adults and 90% of the juveniles and birds of unknown age were not seen for at least a month between December and February. This difference is significant at the 0.005 level (Chi-square test). Among birds that left in winter and then returned the following spring, juveniles and unknowns were gone significantly longer than adults (mean absence of 21 juveniles and unknowns = 2.3 months vs. 1.7 months for 28 adults; $0.05 > P > 0.02$, t test).

Lack of winter territoriality

Preliminary field work for this project in winter 1970–1971 indicated that our Dippers were extremely aggressive. However, detailed observations on banded individuals in the winter of 1971–1972 indicated that, at best, winter territoriality was only poorly developed.

Figure 11 shows home ranges and aggressive interactions noted on six days through the winter 1971–1972 in one area on Boulder Creek. Data for 22 October, 5 November, and 3 February were collected by teams of 9–14 observers sitting quietly along the edge of the stream watching overlapping sections of creek for the times indicated. Other data were taken from censuses. Clearly, most individuals did not remain in and defend exclusive areas. Although many aggressive interactions were observed, they were not predictable. On 3 February, for example, a female (7806) attacked and displaced a female and a bird of unknown sex (7952 and 7813, respectively), yet a few minutes later foraged within 3 m of another female (7980) without attacking. It is also worth noting that of 12 individuals seen on the days tabulated, only five were seen on more than one day and only
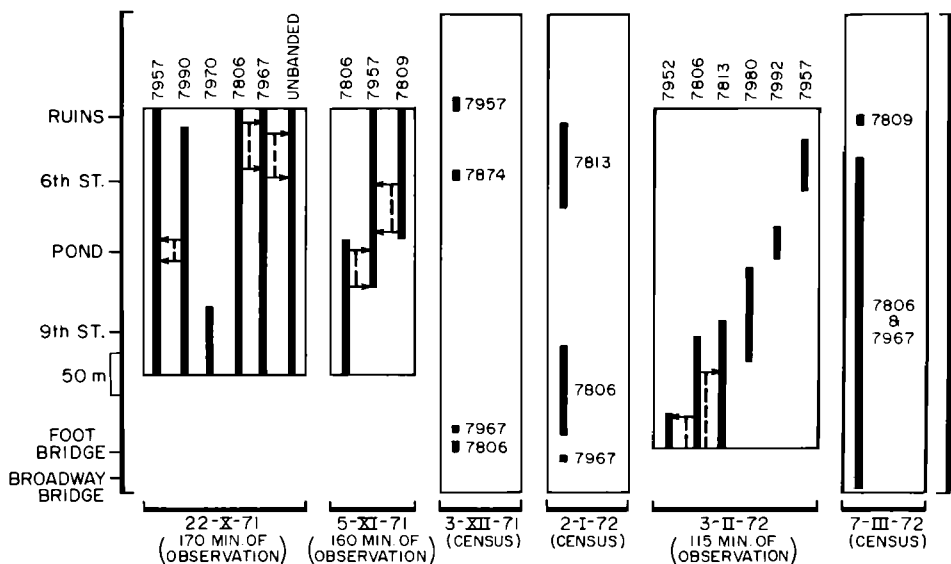
FIGURE 11. Home ranges and observed interactions of wintering Dippers on six days in the winter of 1971–1972. (Areas under observation are enclosed by rectangles; observed ranges of individual birds are shown by heavy vertical bars; areas of stream where aggressive interactions occurred are shown by horizontal arrows pointing toward the subordinate bird.)

one was seen on all six days. Similar data from other areas revealed the same pattern of high turnover, high levels of aggression, and few relatively sedentary birds. Significantly, most of these "resident" birds later bred near their wintering grounds. Individuals 7957 (female) and 7967 (male) were seen on four days each; the former eventually bred 1100 m above the "ruins" indicated on Figure 11, and the latter bred with 7806 under the 9th Street bridge. By 7 March 1972, 7806 and 7967 had established their breeding territory and were looking for a nest site.

Brown and Orians (1970) identified the essential characteristics of a territory as 1) a fixed area that may change slightly over time, 2) on which occur acts of territorial defense, which may be actual defense or behaviors such as song that identify the owner and elicit avoidance by rivals, so that 3) the area becomes exclusive with respect to those rivals. Although most dippers did not occupy fixed areas, female 7806 and male 7967 (Fig. 11) came close to satisfying these criteria. Both occupied relatively fixed areas and exhibited aggressive behaviors and song throughout the winter. The third criterion was not fulfilled as other birds were in the area all winter.

MOVEMENT BETWEEN DRAINAGES

In discussing individual movements we have frequently mentioned movement between streams. Although interdrainage movement was not a separate phenomenon and occurred during all types of movements, a few comments should be made. Most authors appear to make a tacit assumption that Dippers do not fly over land. There have even been statements in the literature that they never do (Steiger 1940). Robson (1956) observed no movement between streams 13 km

apart after banding 219 birds. The only over-land flight reported to date for the American Dipper is Skinner's (1922) observation of a bird flying 400-m across a 'Y' in a stream. However, Jost's (1969) paper on the palearctic *Cinclus cinclus* thoroughly documented movement between watersheds by juveniles, and his observations from Switzerland indicated that adult Dippers may make regular migrations across the high Alps where the lowest passes are over 2000 m.

Of 558 individuals banded in our study, 58 were observed on another drainage. Fourteen were observed to make more than one interdrainage movement, and three made three movements each. Most of our data are, of course, on movements between Boulder and South Boulder Creeks, but longer movements were not uncommon. For example, one bird was banded as a nestling in Pinecliff and two weeks later was found in Idaho Springs, a 22 km straight-line distance (sld.). Still another, banded as a nestling on our South Boulder Creek study area, was found breeding in Estes Park a year later (ca. 55 km sld.). Our longest observed movement was by a bird banded as a nestling 10 km up Fourmile Creek and found two years later breeding 13 km above Kassler on the South Platte River (ca. 75 km sld.).

Although there were water connections between all drainages studied (Fig. 1), we believe our birds flew over ridges between drainages. Connections between streams occurred east of the mountains in areas unsuitable for Dippers because of pollution and lack of a rubble substrate. It is far more likely that birds flew the shorter distances over ridges, especially during spring, summer, and early fall when the birds were at high elevations. For example, a Dipper that flew from Boulder Creek up Hawkin Gulch (Fig. 3) could stay over water until it was within 400 m of another stream that descended into South Boulder Creek (Fig. 1).

We made one direct observation that tends to support the overland-flight hypothesis. On 24 October 1971 on South Boulder Creek between Rollinsville and East Portal (Fig. 1), three Dippers had been involved in a series of agonistic encounters for several minutes near a bridge. One, after being repeatedly displaced, continued to fly downstream after its pursuer landed. Instead of remaining within a few feet of the water and landing quickly, it continued to fly and climbed higher. Because of this unusual behavior we continued to observe it through 10× binoculars. The bird climbed for about 30 sec until it was approximately five times the height of the telephone poles alongside the stream; it then made a 90° turn to the left (north). We watched it for another 10–15 sec before losing sight of it against a forested hillside. We estimated it to be over 60 m in the air when last seen, the highest flight we saw in three years. There are tributaries to South Boulder Creek in the vicinity so we cannot be certain that the Dipper did not remain over water while we watched. Indeed, the long straight flight and sharp turn suggest that it did follow water. Nevertheless, the fact that it continued to climb indicates that it was not making a typical flight and we believe that it was going to fly over the ridge to the Boulder Creek drainage near Eldora. If this was a typical interwatershed flight it is not surprising that Dippers have never been reported flying over land. At a height of several tens of meters they would be indistinguishable from many other passerines, as well as totally unexpected. Jost (1969) reported Dippers being caught in mist nets above tree line in the Swiss Alps, so such flights may be common.

From our data, there was no preference for north or south movements. There were approximately equal numbers of flights in both directions in all seasons.

Cross-watershed movements appeared to be an integral part of movements described earlier, and the seasonal distribution of interdrainage flights was similar. Of 29 interdrainage movements that could be dated within specific months, eight occurred in February, March, and April, three in June and July, 15 in September and October, and three in December. The two months with most records were March ($n = 5$) and October ($n = 8$), peak months of general spring and fall movement (Figs. 6, 7).

To clarify possible age and sex differences in tendency to change drainage, a subset of the data was analyzed. Because birds banded late in the study were not observed for as long as birds banded earlier, statistics were calculated on individuals banded in the first year of our study. Of 213 birds in this group, 32 (15.0%) were observed to change drainage at least once. There appeared to be no sexual dimorphism in tendency to make interdrainage flights. From our data on juvenile dispersal we expected juveniles to change drainages more often than adults. Although our data support this hypothesis (14.4% of 97 juveniles changed drainages, compared with 12.2% of 74 adults), the difference was not statistically significant. In all probability the difference was biologically significant, for our data were biased toward within-drainage movements. Also, our sample size was small because we had to exclude many birds of unknown age.

HOMING BY ADULT DIPPERS

An experiment conducted in May and June 1973 to evaluate aspects of territoriality yielded results that bear on movement. Four females and one male were moved from territories on South St. Vrain Creek to Boulder Creek; two breeding pairs were moved from James Creek to Boulder Creek (Fig. 1). Of the St. Vrain birds, one female returned 23 km sld. to breed near her first nest, and a second female moved 21 km sld. up Boulder Creek. All of the James Creek birds returned to their nests (12.4–12.9 km sld.). Because of the high mobility of our population and the high site fidelity of adult Dippers it is not surprising that they can home, although such homing has not previously been reported in the Cinclidae.

DISCUSSION OF MOVEMENT

It is clear that our Dipper population was far more mobile than previous reports on *Cinclus* have indicated. The expected altitudinal migration in spring and fall did occur, along with extensive movement of adults after breeding and of all ages in winter. Juveniles dispersed far greater distances than expected and most appeared to move to different watersheds. Movement of both sexes and all ages across divides between drainages was common.

Movements to small tributaries because of high water have been reported previously (Balát 1962, Sullivan 1973) but were not seen in our study. Our intensive study areas were on comparatively small streams and no really high water occurred during our study. Because turbidity kills many stream invertebrates (Mecom 1969), we expect that severe flooding would provoke such movements in our population.

Comparison of our results with those of others reinforces the idea that there may often be considerable differences between populations of the same or similar species. The only other major study on the ecology of *Cinclus mexicanus* is that

of Sullivan (1973). He banded 154 birds, gave no quantitative data on juvenile movements, and made no mention of cross-watershed movements. However, from his data it appears that adults were more sedentary than those in our population. Marked adults were off their territories in only 12.1% of over 666 observations by Sullivan. He attributed the majority of absences (78%) to need to find a refuge for molt. Other causes were mate-seeking (3.8%), high water (6.3%), and freezeup (12.5%). In 1198 observations of 67 adults banded in the first spring of our study, 20.4% of the sightings were of birds off their breeding territories. It is difficult to compare our data with Sullivan's because such data inevitably are biased toward territorial sightings by the large number of visits to nest sites during breeding seasons. Of 382 sightings we made between September and February, 42.7% were of birds off their breeding territories. Sullivan's study areas were at lower elevations than ours (Table 3) and streams never froze completely during his study (Sullivan, pers. comm.). Thus the differences between Sullivan's results and ours are reasonable. As mentioned previously, Bakus (1957, 1959a, b) described movements similar to those reported in our study. Because Bakus and Sullivan worked in the same area, it is difficult to reconcile their opposing conclusions. The discrepancies may be due to the fact that Sullivan studied a much larger area, or perhaps Bakus' area was not typical of the region as a whole, or the two winters when Bakus did his field work were unusually severe.

Studies of the European *Cinclus cinclus* show a similar pattern of sedentary populations in stable habitats (Balát 1962, Hewson 1967, Shooter 1970), and of migratory populations in habitats susceptible to freezing (Vogt 1944, Balát 1962, Holmbring and Kjedemar 1968, Fuchs 1970). Fuchs (1970), in particular, reported what he called "fall and spring passers-through," "winter-guests," and "molting-guests." For a group of species as well suited to a cold, wet environment as the Cinclidae (Murrish 1970b), one would expect the evolution of a flexible response to freezeup to be adaptive, and such evolution appears to have occurred.

Data on juvenile dispersal are not adequate for firm conclusions. Our fledglings initially tended to move upstream, but eventually dispersed randomly to an effective distance of probably over 20 km. The few data from other studies on *Cinclus* (Robson 1956, Balát 1962, Hewson 1967, Shooter 1970, Fuchs 1970, Sullivan 1973) suggest that our populations have the highest dispersal rate yet reported.

There have been a number of attempts to define types of population movements. Berndt and Sternberg (1968) and Dobzhansky (1973), along with others, have defined migration as a synchronous movement, usually periodic or seasonal, by many individuals of a population in the same direction, from one area to another. By this definition the movement of Dippers from low to high elevations in spring and the reverse movement in the fall clearly are migratory movements. The postbreeding adult movements could also be regarded as migratory.

Dispersal is commonly regarded as the randomly directed movement of young individuals from place of birth to place of breeding (Johnston 1961, Dobzhansky 1973). Juvenile Dippers showed this type of behavior. Pielou (1969) referred to random movements by birds of any age as "diffusion," but this seems too vague a term for a discussion of specific movement patterns. Spacing is the movement forced upon an individual by factors which will not allow it to establish itself in an area, and which results in the dispersion of individuals in space (Johnston 1961, Berndt and Sternberg 1968). Upward movement of breeders in spring fits

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
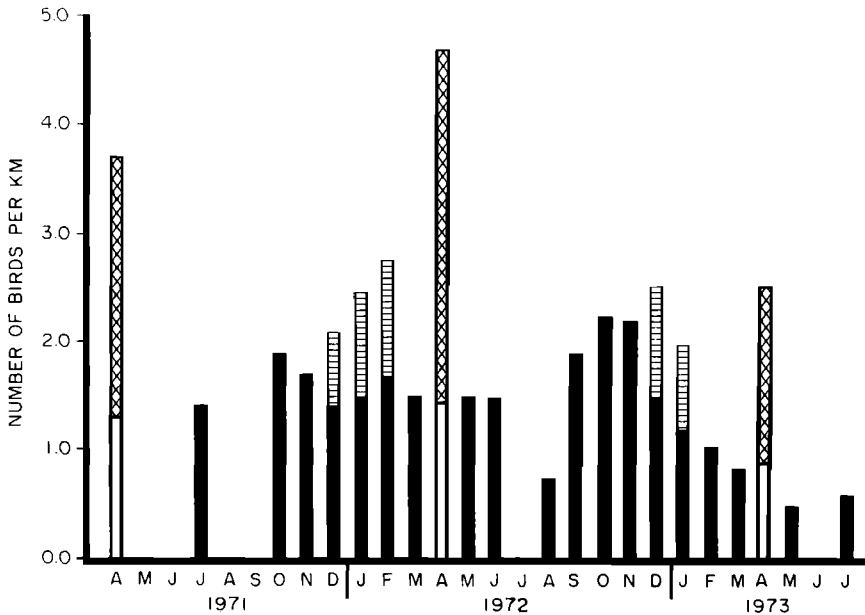
FIGURE 12. Densities observed on Boulder Creek. (Solid black bars indicate number of birds observed on censuses; open white bars indicate density of breeding adults; crosshatched bars indicate nestling density, i.e., total number of nestlings per km in that breeding season; and finely lined bars indicate 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
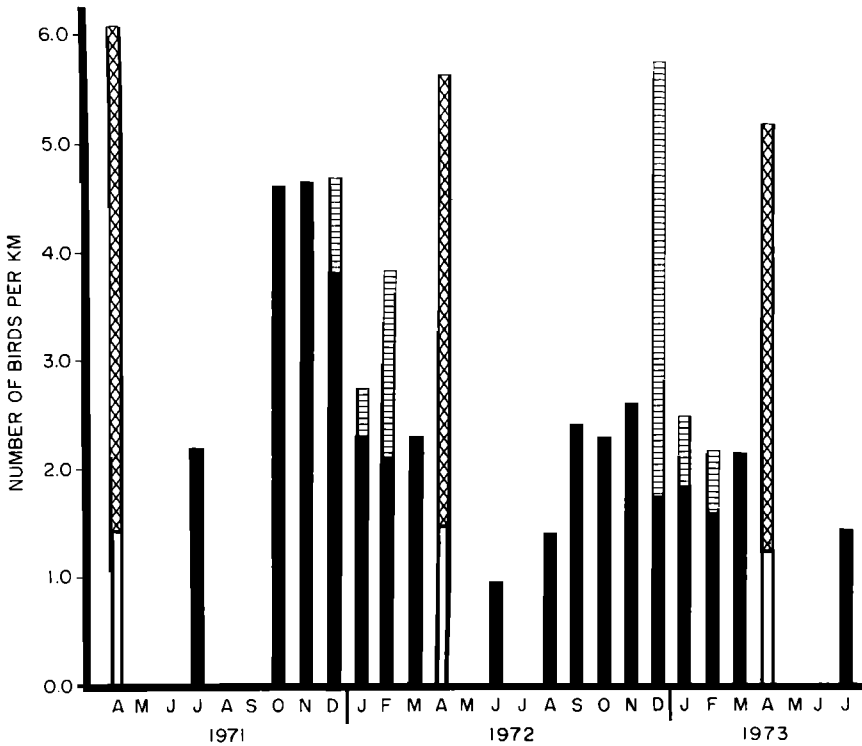
FIGURE 13. Densities observed on South Boulder Creek. (Solid black bars indicate number of birds observed on censuses; open white bars indicate density of breeding adults; crosshatched bars indicate nestling density, i.e., total number of nestlings per km in that breeding season; and finely lined bars 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 fledgings 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]				
	Summer	Fall	Winter	Spring	Breeding
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]	4 (3)	0.17	BOTM	2.0	1	0.16
1971, 1972, 1973			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]	5 (3)	0.27	INTFOOD	1.4	2	0.32
1971, 1972			NSQDIST	2.8		0.18
			BOTM	3.0	1	0.29
			WIDTH	3.6		0.13
			COVR	4.6		0.18
C. Springs[f]	2 (2)	0.17	BOTM	1.0	2	0.33
1972, 1973			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	3 (3)	0.57	ICE	1.7	3	−0.45
1971–1972[g];			INTFOOD	2.0	2	0.46
all segments			WIDTH	3.0	2	0.35
			BOTM	4.3	1	0.24
			NSQDIST	4.3		−0.04
			COVR	5.7		0.15
F. Winter	3 (3)	0.36	ICE	1.3	3	−0.44
1972–1973[h];			NSQDIST	2.3		0.08
all segments			INTFOOD	3.7	1	0.26
			WIDTH	4.0		0.22
			BOTM	4.3		0.16
			COVR	5.3		0.12
G. Winters	6 (6)	0.47	ICE	1.5	6	−0.45
1971–1972[g],			INTFOOD	2.8	3	0.36
1972–1973[h];			NSQDIST	3.3		0.02
all segments			WIDTH	3.5	2	0.29
			BOTM	4.3	1	0.20
			COVR	5.5		0.14
H. Winter	3 (3)	0.34	INTFOOD	2.3	2	0.43
1971–1972[g];			BOTM	2.7	2	0.35
open water[i]			WIDTH	3.0	1	0.41
			NSQDIST	3.0		0.24
			COVR	5.3		0.17
I. Winter	3 (1)	0.25	NSQDIST	1.0	1	0.37
1972–1973[h];			INTFOOD	2.7	1	0.25
open water[i]			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[g], 1972–1973[h]; open water[i]	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[j] 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[k] 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]	3 (2)	0.43	NSQDIST	2.3	1	0.35
1971, 1972, 1973			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]	5 (3)	0.29	BOTM	2.2	2	0.21
1971, 1972			WIDTH	2.2		−0.17
			NSQDIST	2.6	1	−0.00
			INTFOOD	3.4		−0.01
			COVR	4.6		0.11
C. Springs[f]	3 (1)	0.24	COVR	2.0		−0.26
1972, 1973			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	3 (3)	0.75	ICE	1.0	3	−0.76
1971–1972[g];			BOTM	3.0	1	0.37
all segments			NSQDIST	3.3	1	−0.09
			WIDTH	4.0		−0.23
			INTFOOD	4.7		0.03
			COVR	5.0		0.24
F. Winter	3 (3)	0.74	ICE	1.0	3	−0.74
1972–1973[h];			INTFOOD	2.0	1	0.14
all segments			WIDTH	3.7	1	−0.25
			NSQDIST	4.3		−0.15
			BOTM	4.0		0.44
			COVR	5.3		0.18
G. Winters	6 (6)	0.75	ICE	1.0	6	−0.75
1971–1972[g],			INTFOOD	3.3	1	0.09
1972–1973[h];			BOTM	3.8	1	0.41
all segments			NSQDIST	3.8	1	−0.12
			WIDTH	3.8	1	−0.24
			COVR	5.2		0.21
H. Winter	3 (3)	0.80	ICE	1.3	2	−0.77
1971–1972[g]			BOTM	2.7	2	0.49
open water[i]			INTFOOD	4.0		−0.11
			WIDTH	4.0		−0.27
			COVR	4.3		0.32
			NSQDIST	4.7		0.20
I. Winter	3 (3)	0.71	ICE	1.0	3	−0.71
1972–1973[h];			INTFOOD	2.7	1	−0.15
open water[i]			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 1971–1972[g], 1972–1973[h]; open water[i]	6 (6)	0.76	ICE	1.2	5	−0.74
			BOTM	3.2	3	0.44
			INTFOOD	3.3	1	−0.13
			WIDTH	3.7	1	−0.28
			NSQDIST	4.7		0.17
			COVR	4.8		0.26
K. Breeding censuses[j] 1972, 1973	2 (1)	0.34	NSQDIST	1.0	1	0.65
			WIDTH	2.0		−0.36
			INTFOOD	3.0		−0.02
			BOTM	4.0		−0.31
			COVR	5.0		0.09
L. Breeding seasons[k] 1971, 1972, 1973	3 (3)	0.68	INTFOOD	2.0	2	−0.73
			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 [f]).

[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. NUMBIRDS 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	1	0.17***	INTFOOD	0.41***
($n = 710$)	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	1	0.06***	ICE	−0.25***
($n = 422$)	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 (FEM-AGE), male age (MALEAGE), mean food density within territory (MEANFOOD), nest site quality (SITEQUAL), presence of open ends without neighbors (OPE-NENDS), 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[a] added	r of variable	R^2 of step	F ratio of step	F ratio of variable in last step
A. Boulder Creek	1	MEANFOOD	-0.70***	0.49	26.53***	24.96***
1972, 1973	2	FEMAGE	0.09	0.55	16.58***	4.65**
($n = 30$)	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	1	FEMAGE	0.47*	0.22	7.06*	8.42***
1971, 1972,	2	POLYGYNY	0.44*	0.40	8.08**	0.63
1973	3	MALEAGE	-0.15	0.43	5.80**	3.06+
($n = 27$)	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

[a] 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.
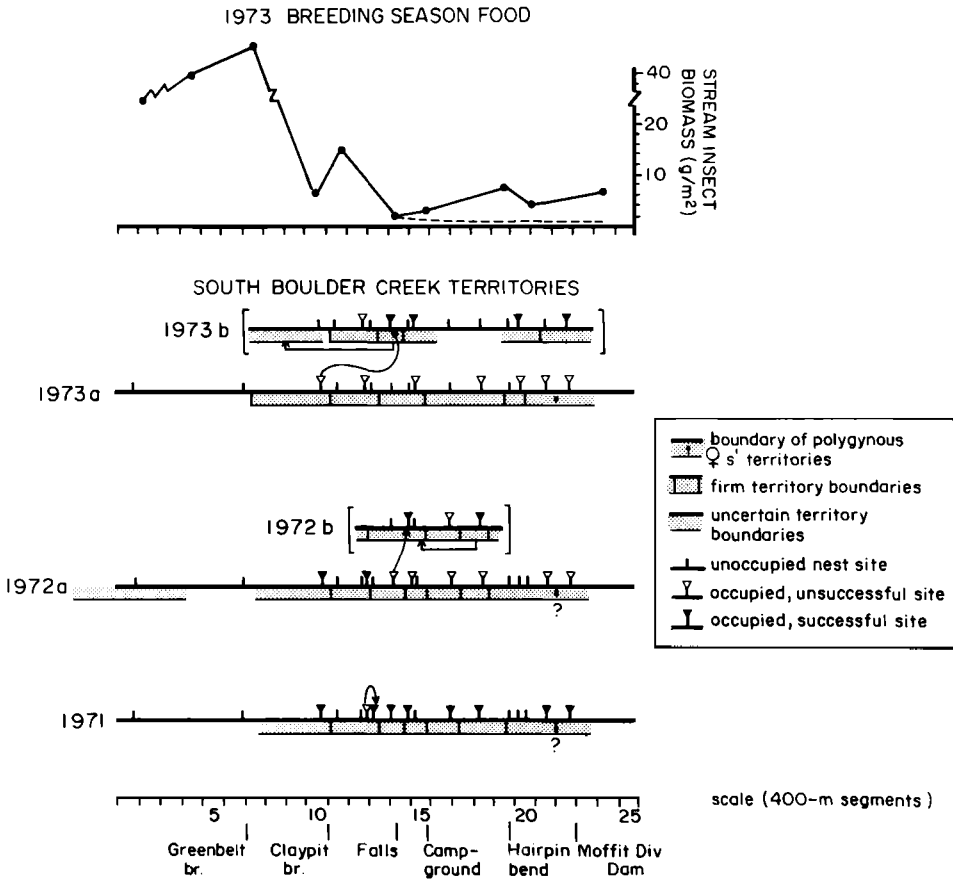
FIGURE 14. Breeding territories, 1971–1973, and 1973 breeding season food on South Boulder Creek. (Horizontal axes of both graphs indicate 400-m segments with upstream to the right. Short segments labeled 1972b and 1973b show changes that occurred after territories were established; arrows show movements 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,
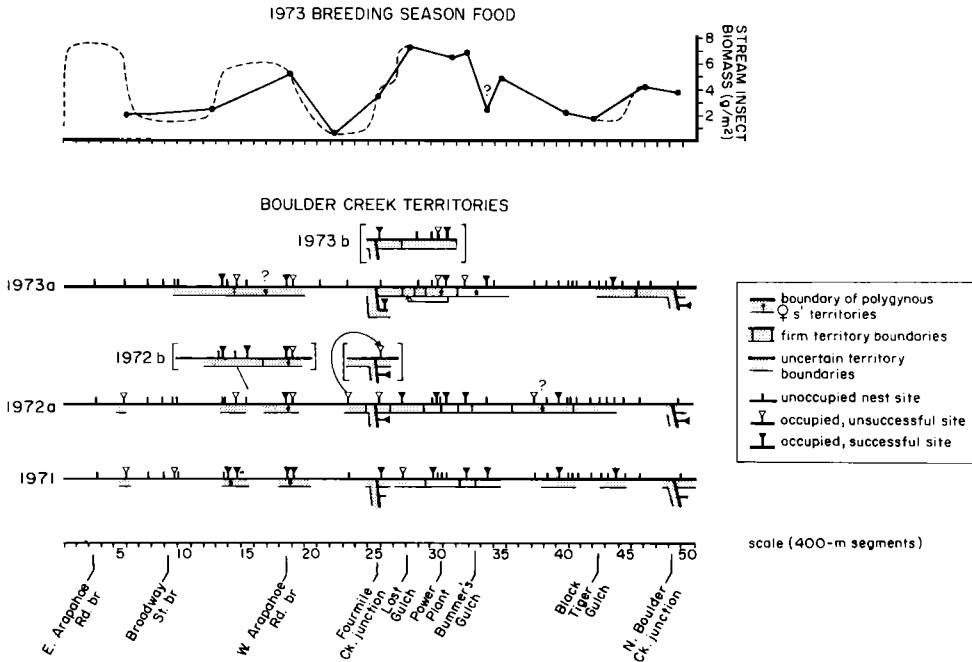
FIGURE 15. Breeding territories, 1971–1973, and 1973 breeding season food on Boulder Creek. (Horizontal axes of both graphs indicate 400-m segments with upstream to the right. Short segments labeled 1972b and 1973b show changes that occurred after territories were established; arrows show movements by 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
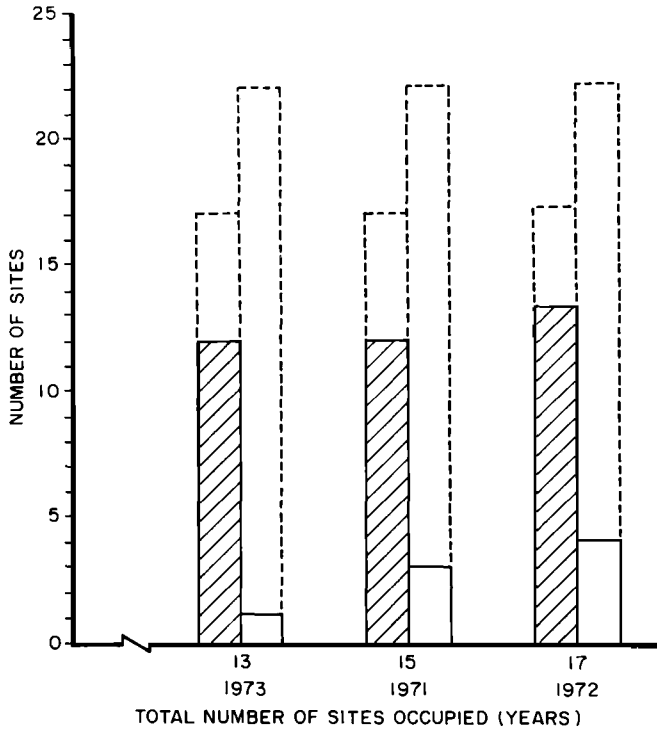
FIGURE 16.   Total number of optimal and suboptimal nest sites occupied at differing population densities on Boulder Creek. (The crosshatched bar indicates the number of occupied optimal sites, SITEQUAL = 3; the open bar the number of occupied suboptimal sites, SITEQUAL = 2 or 1; and dotted lines the 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 renested 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 ± SD	1971	1972	1973	Mean ± SD
A. No. adults seen on study area	44	55	30	43.0 ± 12.5	27	34	32	31.0 ± 3.6
B. No. observed attempting to breed[a]	29	40	23	30.7 ± 8.6	19	22	21	20.7 ± 1.5
C. No. failing to breed[b]	8	12	5	8.3 ± 3.5	4	7	10	7.0 ± 3.0
D. No. failing and replaced at observed site	4	11	3	6.0 ± 4.4	3	5	6	4.7 ± 1.5
E. % observed attempting to breed[c]	65.9	72.7	76.7	71.8 ± 5.5	70.4	64.7	65.6	66.9 ± 3.1
F. % failing and replaced (estimated surplus)[d]	13.8	27.5	13.0	18.1 ± 8.2	15.8	22.5	28.6	22.3 ± 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) × 100.
[d] (Row D/Row B) × 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 Tinbergan 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,

TABLE 12

ESTIMATED SURVIVAL RATES OF ADULT AND JUVENILE DIPPERS

	1971	1972	1973
A. No. breeding birds	40	44	32
B. No. surviving from previous breeding season	nd[a]	21	17
(% survival of adults)[b]	(nd)	(52.5)	(38.6)
C. No. new breeders[c]	nd	23	15
D. No. fledglings banded	70	66	00
E. Estimated no. fledglings alive next spring[d]	nd	23	15
(estimated % survival of first-year birds)[e]	(nd)	(32.9)	(22.7)
F. Estimated total population[f]	110	110	nd
G. Estimated no. alive in next spring[g]	nd	44	32
(estimated % survival of population)[h]	(nd)	(40.0)	(29.1)

[a] nd = data not available.
[b] (Row B/row A) × 100.
[c] Row A − row B.
[d] Assumed = row C.
[e] (Row E/row D) × 100.
[f] Row A + row D.
[g] Row B + row E.
[h] (Row G/row F) × 100.

and 2) that the study areas were similar to other Front Range habitats in reproductive rate, mortality rates of adults and juveniles, and rates of immigration and emigration. These are the same assumptions used in the discussion of juvenile dispersal. While these are bold assumptions, they permit a rough estimate of survivorship. Annual adult survival rates from 1971–1972 and 1972–1973 were estimated at 52.5 and 38.6%. Juvenile survival rates were estimated at 32.9 and 22.7% in the same periods. Estimated annual survival rates for the population as a whole in the two years were 40.1 and 29.1%. We do not feel the quantity of data justifies estimates of survival by sex or study area.

These estimates of overall mortality are in general agreement with other studies. Farner (1955) estimated annual mortality in passerines at 40–70%; Lack (1954) estimated annual mortality rates of 40–60% for adult passerines and 82–92% from egg to breeding adult. Of an estimated 283 eggs laid on both of our study areas in 1971 and 1972, 38 were estimated to have reached breeding age, (Table 12E), an estimated 86.6% mortality. Robson (1956) estimated annual mortality of his Dipper population at 64.4%.

Little can be said about the timing or the causes of mortality. We suspect that predation was not an important cause of adult death. In 472 days in the field we witnessed only one attempt at predation on a Dipper, an unsuccessful attempt by a Sharp-shinned Hawk (*Accipiter striatus*). Recently fledged juveniles appeared to be less wary and probably were taken more often by predators. Johnson (1953) identified the remains of a fledgling Dipper in the stomach of a 25-cm brook trout (*Salvelinus fontanalis*). One juvenile banded in this study was found dead a month after fledging. Its remains were intact and dessicated, suggesting that death was caused by starvation, disease, or both.

Winter appears to have been the period of major loss for the population as a whole. Table 13 gives our data on population turnover from spring to subsequent fall (i.e., March to September) and from fall to spring (September to March). Losses over the two winters were significantly higher than those over the spring·

TABLE 13
RELATIVE LOSS OF DIPPERS FROM STUDY AREAS, SUMMER VS. WINTER

	1971	1972	Total
No. banded birds[a] in spring	65	63	128
No. spring birds seen in following fall	41	34	75
% birds lost over summer	36.9	46.0	41.4
No. banded birds in fall	99	80	179
No. fall birds seen in following spring	38	28	66
% birds lost over winter	61.6	65.0	63.1

[a] Only birds observed on study areas are included in this table.

summer periods ($P < 0.001$, both years' data; $0.025 > P > 0.001$, individual years, Chi-square test). Most of this loss was among juveniles and birds of unknown age, so there was a large emigration component to this "mortality" estimate. The fact that turnover was higher during the 1972 breeding season and summer (46.0% vs. 36.9% in 1971) when density was high (see Figs. 12, 13) suggests that losses were density-dependent. Without many more data it would be presumptuous to attempt a more detailed analysis of the rates and causes of losses from our population.

PRODUCTIVITY AND RECRUITMENT

The production of young to fledging was more easily observed than mortality. Table 14 presents data collected on several parameters of reproduction. There were surprisingly few differences between study areas and years for most of the parameters, and none of the logical comparisons was statistically significant. However, a few points are worth noting. Considering the population as a whole, 1972 was the year of highest population size and of poorest average reproduction. Only 50% of broods successfully fledged any young and the mean number of fledglings per brood was only 1.8. On South Boulder Creek the most likely cause of the poor performance was the silting and food decline in the upper three territories. On the Boulder Creek study area the number of breeding adults increased by 27% from 1971 to 1972, yet the number of fledglings per brood declined by 27%.

The total productivity (mean number of fledglings per brood times total number of broods) on both streams was estimated to have been 70 fledglings in both 1971 and 1972. However, the total breeding population increased 19% in the same period. In 1973 the total productivity declined to an estimated 42 fledglings, although the number of fledglings per brood rose 22% from the low of 1.8 in 1972. Because of the cold winter and delayed start of breeding, the number of second broods in 1973 was significantly lower than in 1972 and 1971 ($P = 0.008$, Fisher's exact test; Table 14 and Fig. 6), and the mean number of fledglings per adult female was also lower in 1973.

Table 15 lists data from this study along with data reported in the literature on reproduction in the family Cinclidae. The data from Dipper populations in the Boulder area appeared to be comparable to data from other studies in clutch size, percent of eggs fledging, and percent of broods fledging at least one young.

Factors affecting productivity

Lack (1954) and Cody (1966, 1971) have formulated a general theory of the selective forces operating on clutch size in birds, but the proximate determinants

TABLE 14

PRODUCTIVITY OF THE BOULDER AREA DIPPER POPULATION

Study area, data	1971	1972	1973	All years
A. Boulder Creek				
No. breeding adults[a]				
Males	9	13	8	30
Females	13	15	10	38
No. 1st broods	12	14	12	38
No. 2nd broods[b]	4	11	1	16
Total broods	16	25	13	54
Eggs/brood, mean $\pm$ SD	4.6 $\pm$ 0.5	4.3 $\pm$ 0.8	4.2 $\pm$ 0.9	4.4 $\pm$ 0.8
(no. broods)[c]	(13)	(24)	(10)	(47)
Nestlings/brood, mean $\pm$ SD	2.9 $\pm$ 1.8	2.4 $\pm$ 2.0	2.5 $\pm$ 2.1	2.6 $\pm$ 1.9
(no. broods)[c]	(15)	(24)	(10)	(49)
Fledglings/brood, mean $\pm$ SD	2.6 $\pm$ 1.7	1.9 $\pm$ 2.1	2.0 $\pm$ 1.9	2.1 $\pm$ 1.9
(no. broods)[c]	(15)	(24)	(12)	(51)
Fledglings/adult female[d]	3.2	3.1	2.6	3.0
% Broods successful[e]	80.0	50.0	66.7	62.7
B. South Boulder Creek				
No. breeding adults[a]				
Males	7	7	6	20
Females	8	9	7	24
No. 1st broods	8	9	6	23
No. 2nd broods[b]	3	5	0	8
Total broods	11	14	6	31
Eggs/brood, mean $\pm$ SD	3.7 $\pm$ 0.8	4.4 $\pm$ 0.7	4.6 $\pm$ 0.6	4.2 $\pm$ 0.8
(no. broods)[c]	(6)	(10)	(5)	(21)
Nestlings/brood, mean $\pm$ SD	3.4 $\pm$ 1.0	2.5 $\pm$ 1.9	2.5 $\pm$ 1.6	2.9 $\pm$ 1.5
(no. broods)[c]	(10)	(10)	(6)	(26)
Fledglings/brood, mean $\pm$ SD	2.6 $\pm$ 1.4	1.7 $\pm$ 2.0	2.5 $\pm$ 1.6	2.2 $\pm$ 1.7
(no. broods)[c]	(10)	(10)	(6)	(26)
Fledglings/adult female[d]	3.6	2.7	2.1	2.9
% Broods successful[e]	90.0	50.0	83.3	73.1
C. Both study areas				
No. breeding adults[a]				
Males	16	20	14	50
Females	21	24	17	62
No. 1st broods	20	23	18	61
No. 2nd broods[b]	7	16	1	24
Total broods	27	39	19	85
Eggs/brood, mean $\pm$ SD	4.3 $\pm$ 0.8	4.3 $\pm$ 0.8	4.3 $\pm$ 0.8	4.3 $\pm$ 0.8
(no. broods)[c]	(14)	(34)	(15)	(68)
Nestlings/brood, mean $\pm$ SD	3.1 $\pm$ 1.5	2.4 $\pm$ 1.9	2.5 $\pm$ 1.9	2.7 $\pm$ 1.8
(no. broods)[c]	(25)	(34)	(16)	(75)
Fledglings/brood, mean $\pm$ SD	2.6 $\pm$ 1.6	1.8 $\pm$ 2.0	2.2 $\pm$ 1.8	2.2 $\pm$ 1.9
(no. broods)[c]	(25)	(34)	(18)	(77)
Fledglings/adult female[d]	3.3	3.0	2.4	3.0
% Broods successful[e]	84.0	50.0	72.2	61.8

[a] Includes only pairs laying eggs.
[b] Includes replacement broods.
[c] no. broods = no. of broods used to calculate means and standard deviations.
[d] [(mean no. fledglings/brood)× (no. broods)]/no. adult females.
[e] Success defined as fledging at least one young.

TABLE 15
REPORTED CLUTCH SIZES AND FLEDGING SUCCESSES FOR THE FAMILY CINCLIDAE

Cinclus species	Clutch size Mean	(n)	Eggs fledged %	(n)	Broods successful[a] %	(n)	Location	Reference
mexicanus	4.3	(68)	56.5	(315)	61.8	(73)	Colorado, USA	This study
mexicanus	4.8	(4)	68.4	(19)	57.1	(7)	Montana, USA	Bakus (1959a)
mexicanus	4.1	(51)	68.8	(208)	66.7	(51)	Montana, USA	Sullivan (1973)
cinclus	4.7	(46)	50.6	(218)	61.4	(57)	Czechoslovakia	Balát (1964)
cinclus	4.1	(92)	75.0	(377)	nd[b]		Great Britain	Robson (1956)
cinclus								
Above 800′	3.7	(>100)	61.6	(12)	nd		Great Britain	Shooter (1970)
Below 800′	4.3							
cinclus	3.4[c]	(9)	nd		nd		Great Britain	Hewson (1967)
pallasii	4[d]	(nd)	nd		nd		Japan	Haneda and Koshihara (1967)

[a] Success defined as fledging at least one young.
[b] nd = data not available.
[c] Biased by small sample and one female with unusually small clutches.
[d] Modal clutch size, not mean.

of actual numbers laid are not understood (Cody 1971). In our study areas mean clutch size did not vary significantly (Table 14). The fact that productivity per adult declined when the total breeding population rose in 1972 suggests that resources might have been more limiting than in 1971. We expected a closer correlation between productivity and environmental parameters when population size was close to carrying capacity. Recall that there was a closer correlation between dispersion of birds and resources during periods of resource shortage (Tables 7, 8).

To analyze factors affecting productivity, the following variables were tabulated and punched onto Hollerith cards for each clutch (see Methods and Table 2 for methods of calculating indices and brief definitions of abbreviations): 1) clutch number (CLCHNUM), 2) elevation (ELEV), 3) age of male parent (MALEAGE), 4) age of female parent (FEMAGE), 5) sum of male and female ages (TOTA-GEPR = MALEAGE + FEMAGE), 6) nest site quality (SITEQUAL), 7) height of nest site above water (SITEHITE), 8) date nest construction started (D8START), 9) date nest dome was completed (D8DOME), 10) date inner nest cup was completed (D8CUP), 11) date of first egg (D8EGGS), 12) clutch size (NOEGGS), 13) date incubation started (D8INCUB), 14) date eggs hatched (D8HATCH), 15) number of nestlings (NONESTL), 16) date of fledging (D8FLEDG), 17) number of fledglings (NOFLEDG), 18) size of female's territory (FEMTRSIZ), 19) mean food index of female's territory (MEANFOOD), 20) total food in territory (TOT-FOOD = MEANFOOD × FEMTRSIZ), 21) presence or absence of at least one open end in territory (OPNENDS), 22) presence or absence of polygny (POLYG-YNY), 23) mean stream flow in week before D8START (FLOB4CON), 24) mean stream flow during nestling period (FLONSTL), 25) mean minimum daily temperature during incubation (XMNTINC), 26) mean minimum daily temperature during nestling period (XMNTNSTL), 27) total precipitation during incubation (TPTNINC), 28) mean precipitation per storm during incubation (XPTNINC), 29) total precipitation during nestling period (TPTNNSTL), and 30) mean pre-

TABLE 16

STEPWISE CORRELATION OF EIGHT VARIABLES WITH NUMBER OF FLEDGLINGS PER BROOD (1971–1973)[a]

Step	Variable[b]	r of variable	R^2 of step	F ratio of step	F ratio in final step
1	XPTNNSTL	−0.28*	0.08	3.30	11.55***
2	TOTAGEPR	0.22+	0.22	5.64*	3.34*
3	NOEGGS	0.25+	0.28	4.92*	5.59***
4	FEMTRSIZ	0.06	0.34	4.76**	3.61**
5	XMNTINC	−0.20+	0.38	4.34**	1.16
6	POLYGYNY	−0.14	0.39	3.70*	1.82
7	MEANFOOD	0.11	0.41	3.32*	4.51**
8	SITEQUAL	0.09	0.47	3.64**	3.78**

[a] $n = 42$ (listwise deletion used).
[b] FEMTRSIZ, size of female's territory; MEANFOOD, mean of interpolated food at 100-m intervals in territory; NOEGGS, clutch size; POLYGYNY, presence or absence of polygyny; SITEQUAL, nest site quality index; TOTAGEPR, sum of ages of male and female; XMNTINC, mean minimum daily temperature during incubation; XPTNNSTL, mean precipitation per storm during nestling period.
+ $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

cipitation per storm during nestling period (XPTNNSTL). The data were submitted to a Pearson product-moment correlation program to obtain a correlation matrix. Point biserial coefficients were calculated as the best estimates of correlations between dichotomous variables (OPNENDS, POLYGYNY) and continuous variables; a phi coefficient was calculated and inserted as the best estimate of the correlation between the dichotomous variables (Ferguson 1971). These were inserted into appropriate rows and columns of the matrix. Preliminary analysis indicated that the best variables for predicting NOFLEDG were: SITEQUAL, TOTAGEPR, NOEGGS, FEMTRSIZ, MEANFOOD, POLYGYNY, XPTNNSTL and XMNTINC. These eight variables were used in stepwise correlations to determine their relationship with number of fledglings.

Table 16 summarizes the results of the first stepwise regression using data from both study areas and all three years (1971 Boulder Creek data were deleted because of inadequate data on territory size). Taken together, the eight variables accounted for 47% of the variance in number of fledglings per brood, and the overall correlation coefficient was significant at the 0.01 level.

XPTNNSTL was the most powerful single predictor variable and accounted for 8% of the variation in NOFLEDG. Storms with large amounts of precipitation flooded some nests and hindered adult foraging by raising water levels and increasing turbidity.

With the effect of the first predictor removed, TOTAGEPR was the strongest variable and added 14% to the multiple R^2 (Table 16). Older, more experienced pairs tended to have better fledging success than younger pairs. Age of female may be more important ($r = 0.15$, $P > 0.30$) than male age ($r = 0.06$, $P > 0.60$). However, this cannot be confirmed from our data, for the two coefficients do not differ significantly ($P > 0.50$). Interestingly, MALEAGE was negatively correlated with females' territory sizes ($r = −0.14$, $P > 0.30$) and food density ($r = −0.27$, $0.10 > P > 0.05$), but positively correlated with nest site quality ($r = 0.35$, $0.05 > P > 0.01$). It is not surprising that older males occupied better sites than younger males, but one might expect older males to have larger territories and more food. High-quality sites occurred most often in steep portions of canyons with many cliffs and bridges, and low food densities. The negative correlation of mean food

and site quality was especially strong ($r = -0.67$, $P < 0.001$). It is likely that there was strong competition for sites in these areas despite low food densities. Older males appear to have been better able to compete for these sites and thus their territories tended to be small because of the presence of adjacent males' territories. These data suggest that, on our study areas, good nest sites were more important than food to birds choosing territories.

NOEGGS and FEMTRSIZ, the third and fourth predictors entered, were both positively correlated with number of fledglings and increased the amount of variance explained to 28 and 34%, respectively. Whereas FEMTRSIZ alone was not significantly correlated with number of fledglings, removing the effects of XPTNNSTL, TOTAGEPR and NOEGGS resulted in a significant partial correlation of FEMTRSIZ with number of fledglings ($r_p = 0.29$, $0.10 > P > 0.05$).

Unexpectedly, XMNTINC was negatively correlated with number of fledglings ($r = -0.20$, $P < 0.10$). Low temperatures during incubation would increase the females' energy expenditures and require them to spend more time foraging during a period when eggs would cool rapidly. This would be more important for Dippers than for species where males assist in incubation. Low fledging success associated with low temperatures should produce a positive correlation coefficient. We believe this relatively high negative correlation was due to a combination of other variables and is probably an artifact. The computer program which produced the results shown in Table 16 used a "listwise deletion" option which omitted any case with incomplete data (i.e., clutches lacking data for any of the nine variables). This resulted in elimination of 33 cases from the calculations. When all data were used ("pairwise deletion"), the correlation between these two variables dropped to -0.09 ($n = 66$, $P > 0.20$). This difference of 0.11 between the listwise and pairwise correlation coefficients was unusual. The correlation coefficients of the other seven variables with number of fledglings were more stable; they changed an average of only 0.06 when list- and pairwise correlation coefficients were compared.

Another complication arose from the fact that minimum temperature was highly correlated with time of breeding ($r = 0.90$, $n = 68$, $P < 0.001$), while number of eggs was significantly and negatively correlated with date of the first egg ($r = -0.21$, $n = 75$, $0.05 > P > 0.02$). The first-order partial correlation of XMNTINC with number of fledglings (controlling for NOEGGS) was -0.07 ($n = 63$, $P > 0.25$), indicating that part of the negative correlation of minimum temperature with number of fledglings may have been due to the decline in clutch size as the breeding season progressed. The temperatures during our study may have had an effect, but it cannot be discerned from this analysis because of difficulties with the particular sample and with confounding variables. Dippers have a low minimum critical temperature (Murrish 1970b) and we expect temperatures to have relatively less effect than on many other species.

POLYGYNY was also negatively correlated with number of fledglings. In an earlier analysis of two years' data on polygyny in the Dipper, we suggested that reproductive success of polygynous birds was higher than the success of monogamous ones (Price and Bock 1973). In the three years of this study, polygynous males fledged significantly more young than monogamous males (polygynous mean = 6.11, monogamous mean = 3.31; $0.01 > P > 0.005$; t test). Polygynous females fledged insignificantly fewer young than monogamous females (polygy-

TABLE 17

MULTIPLE AND STEPWISE CORRELATIONS OF GROUPED VARIABLES WITH NUMBER OF
FLEDGLINGS PER BROOD (1971–1973)[a]

	Total R^2 of group alone	R^2 of groups in steps (increment)
A. Territory quality variables[b]		
SITEQUAL		
FEMTRSIZ		
MEANFOOD		
POLYGYNY	0.13	0.13 (0.13)
B. Weather variables		
XPTNNSTL		
XMNTINC	0.13	0.26 (0.13)
C. Other variables		
TOTAGEPR		
NOEGGS	0.09	0.47** (0.21)

[a] $n = 42$.
[b] FEMTRSIZ, size of female territory; MEANFOOD, mean interpolated food at 100-m intervals in territory; NOEGGS, clutch size; POLYGYNY, presence or absence of polygyny; SITEQUAL, nest site quality index; TOTAGEPR, sum of male and female ages; XMNTINC, mean minimum daily temperature during incubation; XPTNNSTL, mean precipitation per storm in nestling period.
** $P < 0.01$.

nous mean = 3.06, monogamous mean = 3.22; $P > 0.50$). For our three years' data, the point biserial correlation coefficient of polygyny with number of fledglings was −0.14 ($n = 75$; $P > 0.50$).

MEANFOOD and SITEQUAL were positively associated with number of fledglings. Nests in high-quality sites were less likely to fall off a ledge or to be destroyed by predators or high water. High food density enabled parents to keep up a high feeding rate because food could easily be found. We should note again that the food data used in this analysis were taken in the spring of 1973, so this probably is an underestimate of the importance of food.

It is perhaps surprising that the two factors we believe were most important in the choice of breeding site (food and site quality) entered the correlations late. Evidently Dippers rarely chose to breed at poor sites in areas seriously deficient in food. This is an example of the difficulty of analyzing complex feedback loops which affect reproduction and population size. Below a threshold of food density and/or nest site quality, it is unlikely that Dippers will attempt to breed. Resource levels just above the threshold, such as barely adequate food availability, may be compensated for by other factors, such as a larger territory. Abundant resources may allow for much reduced territory sizes. Once a territory is established, stochastic factors, such as weather, may be of major importance.

The computer programs used in this analysis allowed us to group variables together. Table 17 shows the eight variables placed into three groups for analysis. The first cluster (Table 17A) includes four variables which could be said to characterize territory quality. The second group (Table 17B) includes measures of the effects of two weather variables on breeding success. Finally, clutch size and parental age are placed separately (Table 17C) because they are, to some extent, intrinsic to the birds themselves. These three groups are, of course, not completely independent. The quality of a bird's territory is determined in part by intrinsic factors such as the bird's aggressiveness and its skill in assessing the environment. The components of territory quality and weather accounted for equal and inde-

TABLE 18

MULTIPLE AND STEPWISE CORRELATIONS OF GROUPED VARIABLES WITH NUMBER OF FLEDGLINGS PER BROOD FOR SUBSETS OF DATA

Data subset (n)	Variable group	Variable[a]	r of variable	Total R^2 group alone[b]	R^2 of step in stepwise correlation[b]
A. Both study areas, 1972, 1973 (33)	Territory quality			0.17	0.17
		SITEQUAL	0.07		
		FEMTRSIZ	0.07		
		MEANFOOD	0.17		
		POLYGYNY	−0.17		
	Weather			0.19+	0.34
		XPTNNSTL	−0.34+		
		XMNTINC	−0.25		
	Other			0.13	0.65***
		TOTAGEPR	0.23		
		NOEGGS	0.31		
B. Both study areas, 1972 (20)	Territory quality			0.63**	0.63**
		SITEQUAL	0.23		
		FEMTRSIZ	0.19		
		MEANFOOD	0.16		
		POLYGYNY	−0.31		
	Weather			0.21	0.74**
		XPTNNSTL	−0.39+		
		XMNTINC	−0.26		
	Other			0.31+	0.88***
		TOTAGEPR	0.20		
		NOEGGS	0.47*		
C. Both study areas, 1973 (13)	Territory quality			0.12	0.12
		SITEQUAL	−0.19		
		FEMTRSIZ	−0.17		
		MEANFOOD	0.18		
		POLYGYNY	0.12		
	Weather			0.17	0.34
		XPTNNSTL	−0.38		
		XMNTINC	0.07		
	Other			0.13	0.81
		TOTAGEPR	0.29		
		NOEGGS	0.29		
D. Boulder Creek 1972, 1973 (21)	Territory quality			0.34	0.34
		SITEQUAL	0.46*		
		FEMTRSIZ	0.11		
		MEANFOOD	0.13		
		POLYGYNY	−0.15		
	Weather			0.15	0.55+
		XPTNNSTL	−0.31		
		XMNTINC	−0.21		
	Other			0.20	0.91***
		TOTAGEPR	0.42+		
		NOEGGS	0.33		
E. Boulder Creek 1972 (13)	Territory quality			0.61	0.61
		SITEQUAL	0.58		
		FEMTRSIZ	0.32		

TABLE 18
CONTINUED

Data subset (n)	Variable group	Variableᵃ	r of variable	Total R² group aloneᵇ	R² of step in stepwise correlationᵇ
		MEANFOOD	0.09		
		POLYGYNY	−0.29		
	Weather			0.17	0.80
		XPTNNSTL	−0.24		
		XMNTINC	−0.20		
	Other			0.34	0.93⁺
		TOTAGEPR	0.39		
		NOEGGS	0.38		

ᵃ FEMTRSIZ, size of female's territory; MEANFOOD, mean of interpolated food at 100-m intervals in territory; NOEGGS, clutch size; POLYGYNY, presence or absence of polygyny; SITEQUAL, nest-site quality index; TOTAGEPR, sum of ages of male and female; XMNTINC, mean minimum daily temperature during incubation; XPTNNSTL, mean precipitation per storm during nestling period.
ᵇ Significance levels based on F ratios.
⁺ P < 0.10, * P < 0.05, ** P < 0.01, and *** P < 0.001.

pendent amounts of the variation in fledging success. By themselves, number of eggs and age of parents accounted for only 9% of the variance in number of fledglings per brood (Table 17C). However, NOEGGS and TOTAGEPR almost doubled the amount of variance explained by the other two groups when all three groups were used together.

This analysis demonstrates that territory quality and weather, along with birds' physiological condition and genotype (i.e., age, clutch size) were important factors in determining the number of young fledged per brood. However, the amount of variation in fledging success explained by these variables was only 47% (Tables 16, 17). In our discussion of factors affecting population density and dispersion we predicted a high correlation between density and environmental resources during the reproductive season. Multiple R^2's of various environmental factors with dispersion of breeding adults were greater than 0.47 in four of the five analyses performed. A number of factors contributed to the low overall correlation with NOFLEDG. If each of the years and study areas was different from the others in some systematic way (e.g., stream flow, population density, temperatures), we might expect the differences to even out when years were analyzed together. Also, in the absence of better data, the food measured in 1973 was used for 1971 and 1972.

To avoid some of these problems we performed analyses on several subsets of the data (Table 18). Stepwise correlations are shown for data from both study areas in 1972 and 1973 together, 1972 and 1973 separately, Boulder Creek in 1972 and 1973 together, and Boulder Creek in 1972 alone. Other subsets of data were too small for meaningful analysis.

The results support our hypothesis that the previous correlations were done on data that were not comparable. With all 1971 data removed, the multiple coefficient of determination was 0.65, whereas R^2 for the 1972 data was 0.88 and 0.81 for the 1973 data (Table 18A, B, C). When analysis was restricted to a single study area (Boulder Creek), the resulting correlations were even higher for 1972 and 1973 together, and for 1972 alone (Table 18D, E). These results support our contention that the factors "regulating" the productivity of our populations differed from year to year and from one study area to the other. Combining data

from the Boulder and South Boulder study areas obscured processes which operated independently on each area.

Our samples are too small for rigorous tests, but some general comments are worthwhile. For example, 1973 was wetter in April and May than 1972 (Fig. 4). The correlation of XPTNNSTL with NOFLEDG was higher than that of any other variable in 1973, but was less outstanding in 1972 (Table 18B, C). On the other hand, the population densities on our study areas were higher in 1972 than in 1973 (Figs. 12, 13) and we believe that competition for territories, food, nest sites, and mates was higher in 1972 (Fig. 16, Table 11). Correlations of territory-quality variables with number of fledglings were generally higher in 1972 than in 1973 (Table 18B, C). MEANFOOD was the only exception. This is not surprising, considering that food data from 1973 were used for all correlations. The multiple correlation for the four territory-quality variables was much higher in 1972 ($0.10 > P > 0.05$, Fisher's z transform and t test). Comparisons of the Boulder Creek study area with the South Boulder Creek study area would be most interesting; however, as mentioned in the section on dispersion, our South Boulder Creek sample was small and there were several unusual problems on the study area (silting, polygyny).

Proximate causes of nesting failure

The immediate causes of nesting failure usually were difficult to pinpoint, but we do have data from 31 closely-watched broods. Eight (26%) were abandoned (one female is known to have died and two broods were abandoned by adults that later bred elsewhere). Eleven (36%) were destroyed, seven (23%) by flooding and three (10%) probably by humans. One brood (3%) probably starved, for the nest was in the area of South Boulder Creek where silting occurred in 1972. Disease cannot be ruled out, however. Several dead broods off the main study areas were autopsied by personnel of the Denver Zoological Garden and diagnosed as having died of aspergillosis. Four broods on the study areas were heavily infested with feather lice (Mallophaga) but all fledged apparently normal young. Three broods failed because the female may have been sterile. She laid three clutches over two years; all either failed to hatch or died soon after hatching. (Those that hatched did so only after abnormally long incubation periods.) The two males involved were polygynous and sired other broods successfully. Finally, a pair of Dippers flew into an adjacent territory after the male abandoned it and were observed pecking into the abandoned female's nest and pulling it apart. No fledglings were seen from this nest and it is likely that the nestlings were killed. The remaining seven broods (23%) failed for unknown reasons.

EFFECT OF STOCHASTIC EVENTS IN SURVIVAL AND PRODUCTIVITY

There has been considerable debate in the literature over the role played by "density-independent," random factors in the dynamics of natural populations (Andrewartha and Birch 1954, Lack 1966). Theoretical models of population processes have shown that stochastic processes may have considerable impact (e.g., Crow and Kimura 1970, Gadgil 1971). Of particular importance are catastrophic events that decimate populations or their habitat. Although no major disasters occurred during our study, there are data to indicate that Front Range Dipper populations are subject to occasional catastrophes.
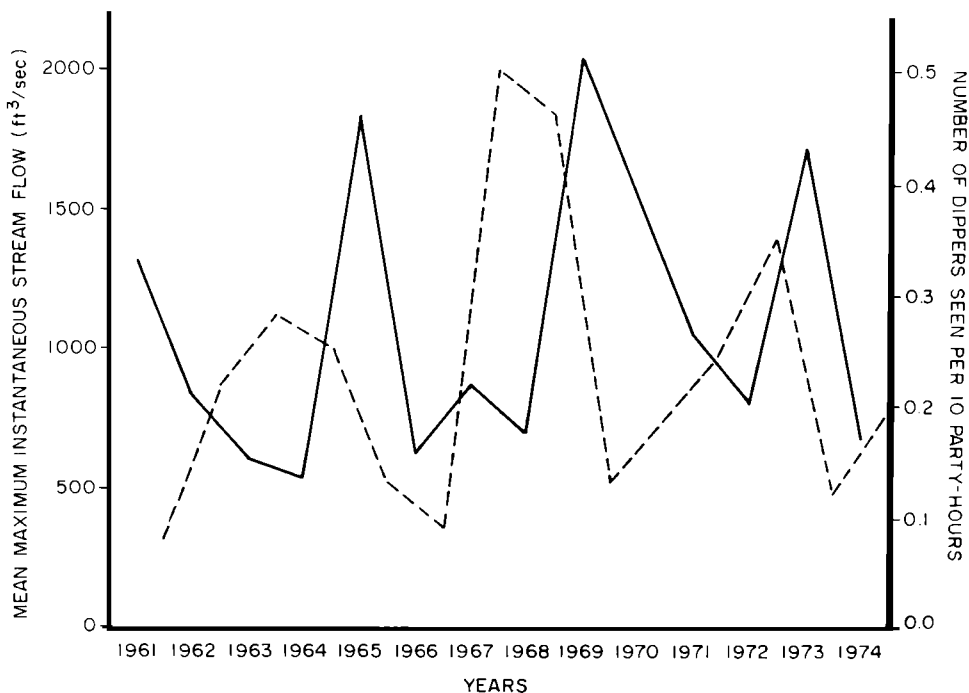
FIGURE 17. Relationship of winter densities to stream flow in spring. (The dashed line indicates mean number of Dippers seen in Boulder area Audubon Christmas Counts, 1961–1974, Audubon Field Notes, vols. 17–24, and American Birds, vols. 25–28; the solid line indicates the mean maximum instantaneous flow of six Boulder area streams in the previous spring, Colo. Dept. Water Resources, pers. comm.)

Because flooding was a major cause of nesting failure, we studied the relationship of flooding to population size. We tabulated the number of Dippers seen in 14 consecutive winters and correlated them with previous springs' runoff of local streams. Population sizes were based on six Audubon Society Christmas Bird Counts from 1961 to 1974 (Fort Collins, Rocky Mountain Park near Estes Park, Longmont, Boulder, Idaho Springs, and Denver); the runoffs were of six local streams (St. Vrain, Boulder, South Boulder, and Clear Creeks, and Big Thompson and South Platte Rivers). The results of this analysis are shown in Fig. 17.

There was a clear tendency for the number of Dippers seen in winter to decline following springs with high runoff ($r = -0.58$, $n = 14$, $0.05 > P > 0.02$). Maximum stream flow almost invariably occurred during the nesting season and is probably the best predictor of impact of stream flow on Dipper populations, for none of our streams dried up.

It is worth noting that the various rivers did not fluctuate synchronously. Not surprisingly, closely adjacent streams tended to be most closely correlated ($r > 0.70$), with lower correlations ($0.50 > r > 0.10$) between more widely separated streams. The South Platte did not correlate closely with other streams. Although the South Platte receives the others, the gauging station from which these data were taken was located at Kassler (Fig. 1), far upstream of the junction of the South Platte with the other drainages.

In 1965 the South Platte River flooded and caused millions of dollars damage, but Boulder Creek and the Big Thompson did not flood. The reverse occurred in 1969 when the streams north of Clear Creek flooded, but not the South Platte upstream of Denver (Colo. Dept. of Water Resources, pers. comm.). The Whitneys (1972, pers. comm.) noted that the 1969 flood drastically reduced Dipper fledging success in the St. Vrain drainage. In late July 1976 the Big Thompson River had a record flood, but none of the other streams flooded significantly.

Floods affect Dippers in several ways. They wash away poorly placed nests. High, turbid water kills many stream organisms (Mecom 1969) and makes the remainder harder to find. Poor nutrition of adults and nestlings would reduce the growth rate of young and increase the susceptibility of adults and young to mortality from many causes.

Although the occurrence and severity of floods are not related to population density, their effect on the population would, in part, depend on population density. At high densities a greater proportion of the breeding birds occupied poor territories and nest sites (Fig. 16) and thus larger numbers would be affected by flooding. Severe floods could reduce the local carrying capacity for several years until the bed stabilized and stream fauna recovered.

The silting on South Boulder Creek in 1972 and the short 1973 breeding season also illustrate effects of stochastic events on breeding. Heavy silting significantly reduced Dipper productivity on the South Boulder study area. In the upper 4 km of the study area only four young were fledged in 1972, compared with 21 in 1971 ($P < 0.01$, t test of mean fledging success). It is worth noting that Dippers normally persist with a breeding attempt even under adverse circumstances (see Alder, 1963, for an example). Of 12 females that lost first broods elsewhere in our study areas, nine renested; none of the four females in the silted area did so ($P = 0.01$, Fisher's exact test).

Unusual temperatures may also affect Dipper populations, although data comparable to those on streamflow and winter densities are difficult to find. Temperatures in the breeding season affect melting of snow and thus stream flow, as well as the thermal physiology of the birds. We cannot measure these effects, however. Winter temperatures would influence the extent of ice formation and Dippers' metabolic rates, and thus winter mortality and population density. An example may have been the winter of 1972–1973, which was unusually early and cold (Fig. 4). The 1973 breeding population was smaller than in 1971 or 1972 (32 vs. 40 and 44) and had a lower percentage of birds surviving from previous years than in 1972 (29.1% vs. 40.0%). We believe that much of the high mortality was due to the low temperatures that winter. After the hard winter of 1972–1973, the 1973 breeding season was much shorter (from first egg laid to last brood fledged, 88 days vs. 131 days in 1971 and 134 in 1972) and there were significantly fewer second broods than in other years (Fig. 6; Table 14; $P < 0.005$, Chi-square test).

From these data it is clear not only that spring floods and winter weather can seriously affect survival and productivity, but that in the Colorado Front Range such catastrophes may be quite local. Dipper habitats in the Front Range may be characterized as patchy, with asynchronously fluctuating carrying capacities. The birds themselves use the environment in a more coarse-grained manner (Pianka

1974) than other Dipper populations reported in the literature. The fact that our population was more mobile than others confirms Gadgil's (1971) hypothesis that these conditions should lead to high dispersal rates.

DISCUSSION OF SURVIVAL AND PRODUCTIVITY

We conclude that survival and reproduction of Dipper populations are heavily dependent on a number of factors that are both intrinsic and extrinsic to the birds themselves, and that may or may not be responsive to density.

Adult mortality was highest in winter and probably was due to the severity of winter weather, to the extent of ice formation, and to winter population density. Adults had higher survival rates than first-year birds. While adults did not appear to be vulnerable to predation, this may not have been true of juveniles, which appeared to be less wary. Although the freezing of streams was not affected by Dipper density, the resulting population density in winter was in part determined by survival and productivity in the previous spring. It appears that at high densities more individuals were forced by aggression to move to other streams, and hence to be more vulnerable to death from many causes. Thus, the proportion of the population which died because of severe weather may well have been a function of population density.

Reproduction in Dipper populations was heavily dependent on environmental factors and on the quality of the adults' territories. Probably the major factors affecting productivity were those relating to stream flow (precipitation, temperature), food availability (stream flow, food density, territory size, bottom structure), nest security (probability of flooding, accessibility to predators), and timing of breeding (weather). Winter and early spring weather were important and unpredictable determinants of timing of breeding, and hence the number of second broods. Weather during spring affected water levels, and hence accessibility of food and probability of nests being flooded. Local flooding increased the difficulty of foraging as well as the amount of food available. Cold, wet weather increased food and shelter requirements of both adults and young, and made those resources more difficult to obtain. The quality of the birds' nest sites and territories had much to do with how severely high water and weather affected their reproductive output. Population density and territorial behavior affected reproduction at high densities by forcing more individuals to move off the study areas or to accept poor-quality nest sites and territories.

GENERAL DISCUSSION AND CONCLUSIONS

After individual analyses of the major parameters of the Front Range Dipper population, we are in a position to discuss what "regulates" that population and to assess the general significance of our study. Ecologists have proposed a number of hypotheses to explain the dynamics of animal populations. It is not our intention to comprehensively review the enormous literature on this subject; for this the reader should consult such works as Watson (1973), Dempster (1975), Southwood (1975), or a recent ecology text such as Ricklefs (1979). Tamarin (1978) provides an excellent anthology on this topic. We will briefly review our findings regarding the major influences on our population, then discuss their relevance to the study of population dynamics.

TABLE 19
SUMMARY OF MAJOR FACTORS AFFECTING THE BOULDER AREA DIPPER POPULATION

Season	Important factors
A. Winter	1. Weather and ice
	2. Number of adults and juveniles surviving from breeding season
	3. Food availability
	4. Aggression
	5. Roost availability
B. Breeding	1. Number of survivors from previous year
	2. Nest site quality
	3. Nest site dispersion
	4. Food availability
	5. Territoriality
	6. Weather, especially precipitation
C. Summer	1. Food
	2. Refuges for molt
D. Unstudied factors of possible importance	1. Disease
	2. Competition from trout
	3. Predation on juveniles
	4. Genetic composition of population

FRONT RANGE DIPPER POPULATIONS

Table 19 lists the major factors and Figures 18–20 diagram suggested relationships among the factors affecting our population in each season. Figure 18 summarizes relationships among factors that we believe affected wintering populations of Dippers in our study areas. In the fall, adults and juveniles moved downstream from higher elevations. Whether this fall migration was initiated by cooler temperatures, shortened day length, or actual loss of habitat from freezing is not clear. During September, October, and November the population was in a state of flux (Fig. 7). There appeared to be little correlation between resources and population density (Table 5), probably because of the movement of birds unfamiliar with the habitat. In December, as the population approached maximum compression, aggression increased and many birds were forced to leave in search of less crowded habitat. It is not clear whether the level of aggression was determined by resource availability or by population density, or both. Winter weather, survival over the previous year, and recruitment from the previous spring determined how dense the population became, how many were forced to emigrate, and the number that ultimately survived the winter. In areas such as the Boulder Creek study area where there were large stretches of open water, population dispersion patterns were strongly correlated with resource availability, especially food and shelter (Table 7). Ice, where it covered a significant portion of the stream's surface, was the major factor in determining distribution of the population (Tables 7, 8). Weather and ice formation combined with movements in the fall to determine how compressed the population became. Although temperature and ice were stochastic factors, we believe that their effects on the population were mediated by availability of resources and the aggressive behavior of the Dippers themselves.

Thus winter was a critical period for our population because availability of
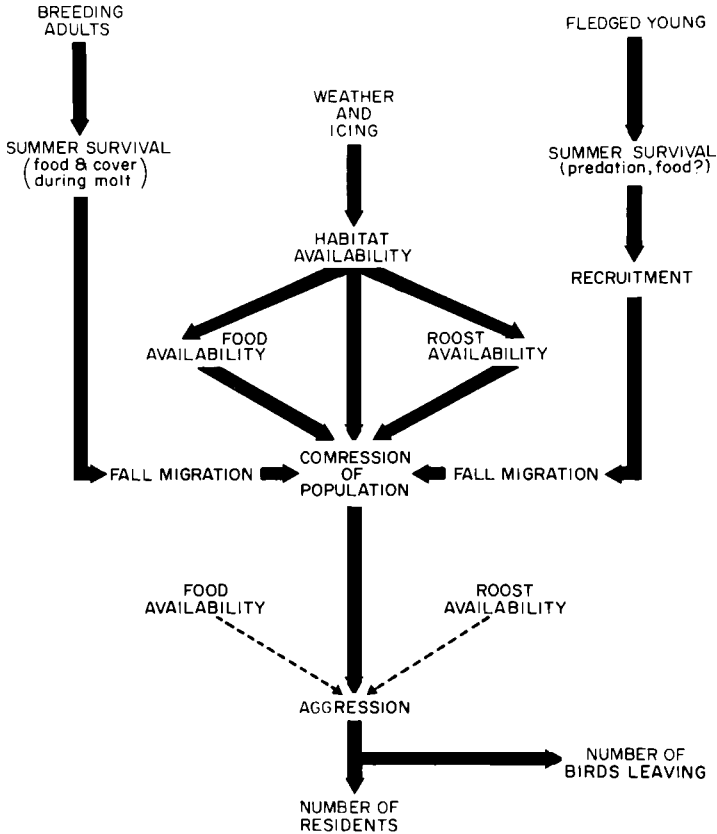
FIGURE 18. Suggested relationships among major factors affecting size of winter Dipper population. (Solid lines indicate corroborated relationships; dotted lines, uncertain relationships.)

critical resources (food, roosts) was reduced by freezing at a time when population density and energy costs were high. Competition and aggression played a role in spacing individuals and, along with weather, influenced over-winter survival (Table 19).

Figure 19 summarizes the factors we believe affected breeding population size and dispersion. The number of residents surviving the winter, the number of returning winter migrants, and the number of new arrivals made up the potential breeding population. As these birds moved upstream and competed for breeding sites, a number of variables came into play. The quality and distribution of nest sites (determined by geology and human activity) clearly were of major importance, as were the distribution and availability of food (Tables 7, 8). Territoriality was a key factor in determining breeding density, for if a pair established a territory that encompassed several suitable sites, they effectively prevented others from using those sites. When over-winter survival was high, more birds were forced by competition to emigrate or to use poor sites.

Breeding success of our population was the result of interactions summarized in Figure 20. Winter weather, in addition to its role in determining size of breeding
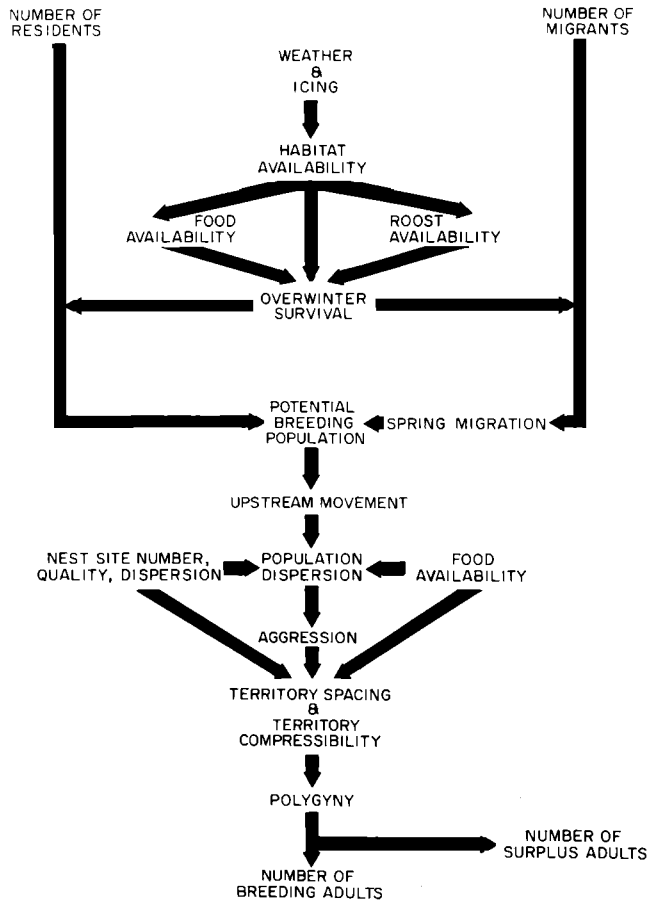
FIGURE 19.   Suggested relationships among major factors affecting size of breeding Dipper population.

population, also appeared to influence the birds' physical condition and the date birds laid their first eggs, hence the number of second broods (Fig. 6). Food availability, quality and spacing of nest sites, and population size appeared to influence the actual spacing of breeding pairs. Spring weather determined the amount of flooding, but nests and foraging areas of high-quality did much to mediate the impact of flooding and of predation, two major causes of nest failure. Overall quality of the birds' territories, especially food availability and nest site quality, had much to do with fledging success (Tables 16, 17, 18). Thus the ability of individual birds to select and defend high-quality territories contributed significantly to their reproductive success. Although the total population increased under favorable conditions, reproduction per adult declined at high population densities because of lower average quality of nest sites and territories. Clearly, density-related factors, such as competition for good nest sites and feeding areas, affected our populations. Because the period between the end of the breeding season and the start of fall migration was poorly documented, we have noted the presumed major factors with dotted lines in Figure 20. Both adults and juveniles
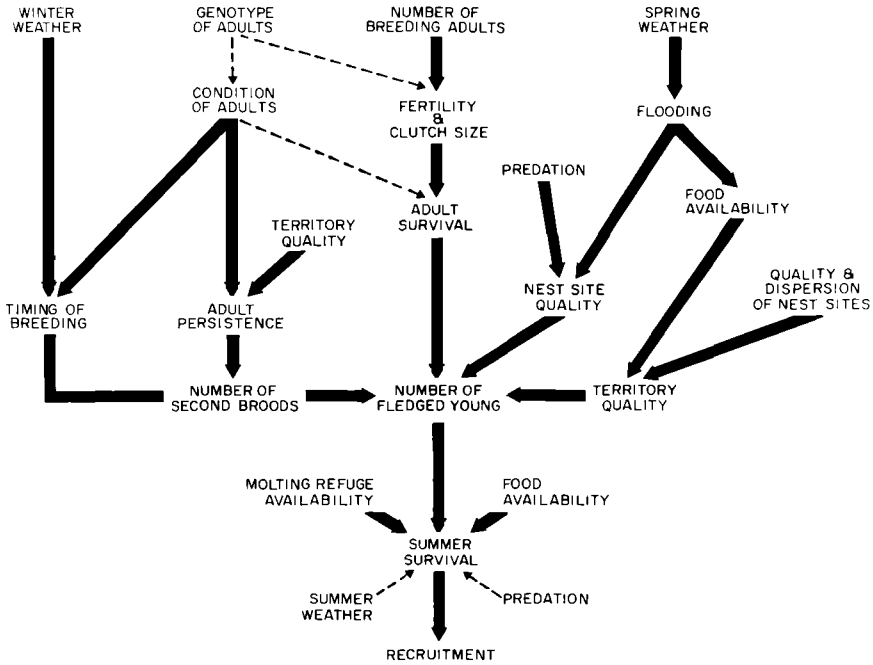
FIGURE 20. Suggested relationships among major factors affecting recruitment of Dippers. (Solid lines indicate well corroborated relationships; dotted lines, less certain relationships.)

moved to high elevations after the breeding season. Poor food availability at low elevations forced adults and juveniles to move upstream after breeding. This was probably the period of highest juvenile mortality, when inexperienced young were exposed to predation and low food levels. Upstream movements by adults also were necessitated by their synchronous molt of flight feathers, which prevented them from flying during a period when food was least available at low elevations. We have included "genotype of adults" in Figure 20 because of the one female that appeared to be sterile. This entry should, in theory, appear several times on each of our summaries, but we have no real data on this.

From our data we could not determine how important disease and competition with trout were to our Dippers. Studies of the relationship between trout and Dippers may prove fruitful. We would expect disease to be most important when adults and juveniles are in poor condition due to severe weather or high population density.

In addition to these more or less predictable factors, the Front Range is subject to random catastrophes that reduce survival and reproductive success of the birds as well as the carrying capacity of their environment. Such catastrophes may be regional, such as severe winters or droughts, or local, such as the severe thunderstorms that cause many floods.

POPULATION REGULATION

Based on the preceding summary of the major variables and interactions affecting the Dipper population in the Boulder area, certain generalizations can be

drawn regarding population regulation. We found a multitude of causes both responsive and unresponsive to density (i.e., "density-dependent" and "density-independent"). These factors encompassed virtually the entire range of variables influencing the ecosystem of which the Dipper was one component. The stochastic fluctuations of weather played a major role, as did the chance placement of nest sites. Such complex interactions have led some authors (e.g., Andrewartha and Birch 1954, Schwerdtfeger 1958) to suggest that populations may be regulated by the chance interaction of innumerable randomly fluctuating factors. Lack (1966) and others have pointed out that we would expect natural selection to reduce the influence of such variables, and result in density-dependent regulation. Nevertheless, insistence on the logical necessity of density-dependent regulation is not particularly useful, because some variables cannot be categorized as clearly dependent or independent of density (Solomon 1958).

A major point which emerges from our study is that the importance of any environmental factor in "limiting" Dipper populations depends not only on the severity of that factor, but also on the intensity of other factors and on the size of the population. If breeding success is poor (due to shortage of food or nest sites, or to flooding), then food or open water may not be in short supply in the following winter. If over-winter survival is low (due to low food or to excessively severe weather and ice), then territoriality may have little or no effect on breeding density or productivity in the following spring because there may be sufficient resources for all birds attempting to breed. Even in the brief period of our study it became obvious that there is no simple way to classify the processes that regulated our Dipper population, for their interactions were diverse, and varied over space and time.

It should be clear by now that one or two factors cannot be extracted and proudly displayed as those that "determine" population size or density of the Dipper. Instead, there are many interacting variables that operate with differing intensities to influence the major population processes of reproduction, mortality, emigration, and immigration. A reasonably complete picture of population regulation in our populations would require combining Figures 18, 19 and 20 into one. To illustrate fully the feedback loops, the bottom arrows of Figure 18 would have to be joined with the corresponding ones of Figure 19. The bottom arrow of Figure 19 would be joined with the corresponding one of Figure 20, and with the top left-hand arrow of Figure 18. The bottom arrow of Figure 20 would connect with the upper right-hand arrow of Figure 18.

Given such feedback loops, classification of population-regulating factors into hard-and-fast categories is not practical. Depending on the point of view of the investigator and on the local situation, a given phenomenon might be viewed in different ways. For example, starvation is commonly regarded as a density-dependent phenomenon. It probably is only rarely the proximate cause of death for adult Dippers. However, the nutritional status of the population would mediate the effects of temperature, precipitation, disease, etc. Availability of food is affected by the terrestrial ecosystem (which contributes detritus for stream insects), by stream flow (a result of topography, temperature, and precipitation), by Dipper population density (a result of the previous history of the population), and by social behavior.

Variables may not fit unambiguously into only one category. The effect of

weather, classically a density-independent factor, on mortality rates is in part determined by how much food and shelter are available in relation to the demands of the population, demands that are in part determined by population density, by breeding status, and by metabolic needs affected by temperature itself. The situation becomes still more complex when we consider that the intensity of variables changes in time and space with varying degrees of predictability.

A number of studies on other organisms have reached essentially the same conclusion: that populations are regulated by complex interactions among many variables and that their clarification may require broader investigations than are customary. Jenkins, Moss, Watson, and their co-workers have shown this clearly in their excellent series of reports on the Red Grouse (*Lagopus lagopus scoticus*) in Scotland. In a summary of 15 years' work, Watson and Moss (1972) emphasized the role of interactions among nutrition (related to geological substrate and successional status of vegetation), the physical structure of the environment (especially as it affected visibility), population structure, inheritance, agonistic and territorial behavior, and possibly interspecific competition. Comparison of our results (Table 19) with theirs shows some differences. They evidently believed that weather was not significant for their population. We were not able to gather such detailed, long-term data on population structure, inheritance, or competition as they did. We suspect, although we have no proof, that food quality will prove to be of less importance to secondary consumers such as Dippers than to herbivores such as Red Grouse. This and other factors remain to be studied in Dippers. Despite the difference in duration, our study corroborates the Red Grouse work in that population regulation in these two species is the result of at least five or six major variables.

Lidicker's (1973) study of an island population of voles (*Microtus californicus*) is also pertinent. Seasonal changes in the physical environment were of paramount importance to his population. The onset of the dry season caused grasses to dry up and stopped vole reproduction. The population density at which this suppression occurred varied widely, so cessation of reproduction was not dependent on density. As the dry season continued, the population became too dense for the food available, resulting in stunted growth, aggression, physiological damage, and increased mortality. The magnitude of these effects did increase disproportionately with increasing population density. Lidicker concluded that interactions among a minimum of six factors were necessary to account for the observed changes in his population. The main conclusion from his research (p. 272) was that:

> "we need to view a natural population of microtines in a community context, rather than simply as a population of organisms being variously suppressed or stimulated by one or a few environmental factors. A community perspective implies . . . realization that most organisms live in complex environments in which not only can a variety of physical and biological factors affect their numbers, but such factors may interact with each other to produce important and predictable effects."

This also is the major conclusion emerging from our work.

A number of interesting parallels between our study, the grouse work, and Lidicker's study are important. All three of these studies dealt with populations of marked individuals living in spatially simple and (for Dippers and voles)

restricted habitats. Populations were censused and observed throughout the year. Interspecific competition and predation probably either were not significant or (for the grouse) could be only roughly estimated. Social behavior could be observed or at least inferred. Finally, important resources could be roughly quantified. Thus each of these three studies satisfied most of the requirements for a simplified natural system suggested in our introduction. Despite the simplicity of these systems, a large number of processes were shown to be clearly important.

It is reasonable to conclude that in order to make progress in the study of population regulation, researchers must study a wide range of factors affecting their populations. Given the state of our knowledge, studies on relatively simple systems are much more likely to yield results that are valid, and more easily interpreted. Much about the dynamics of Dipper populations remains to be clarified, but because of their simple habitat and other characteristics mentioned earlier, this species is unusually well suited to studies of population regulation. Further work on this fascinating group of birds should be well rewarded.

ACKNOWLEDGMENTS

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