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 10× 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 m^2; 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 m^2 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