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

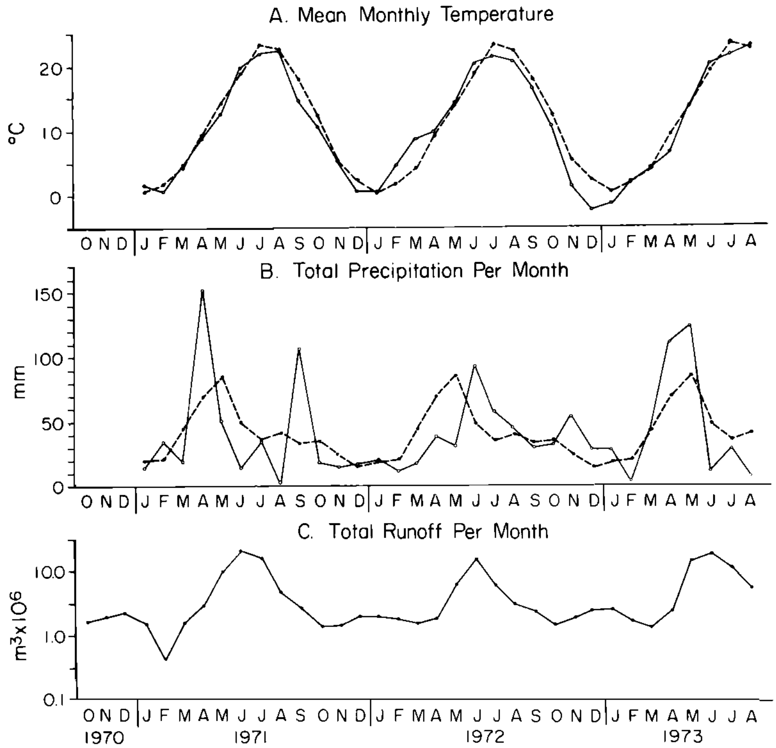

FIGURE 4. Variation of environmental factors in Boulder, Colorado. (Dashed lines show 30-year means, 1930–1960; solid lines, data collected during this study, 1971–1973. Sources: A and B, U.S. Dept. Commerce; C, Colo. Dept. Water Resources.)

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

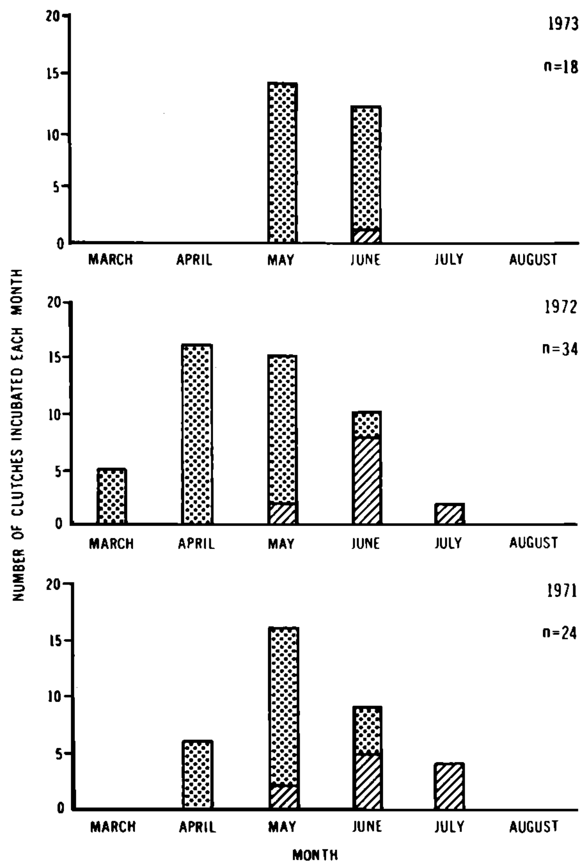

FIGURE 5. Timing and number of clutches being incubated, 1971–1973. (First and replacement clutches are represented by dotted bars; second clutches by bars with diagonal lines.)

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 km^2 and 308 km^2 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.

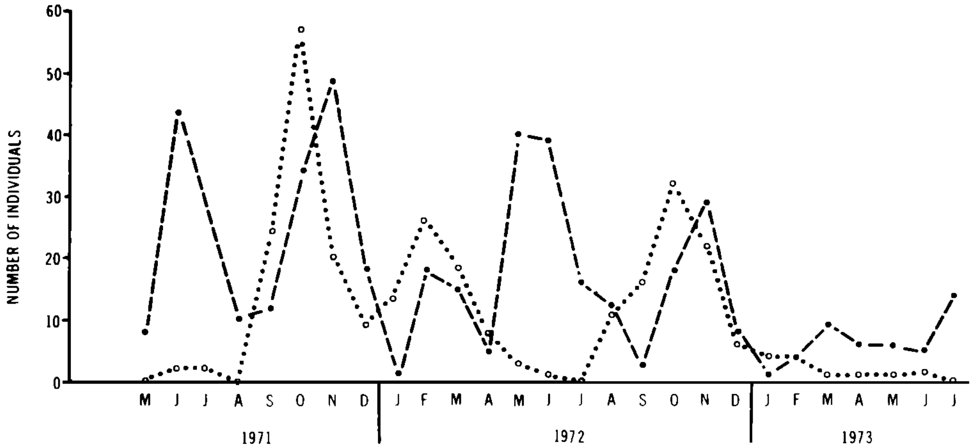

FIGURE 6. Number of banded birds arriving and departing study areas per month. (Dotted line: arrivals, defined as individuals banded in a given month, or previously banded but not seen for at least a month. Dashed line: departures, defined as birds that disappeared and were not observed on the study 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