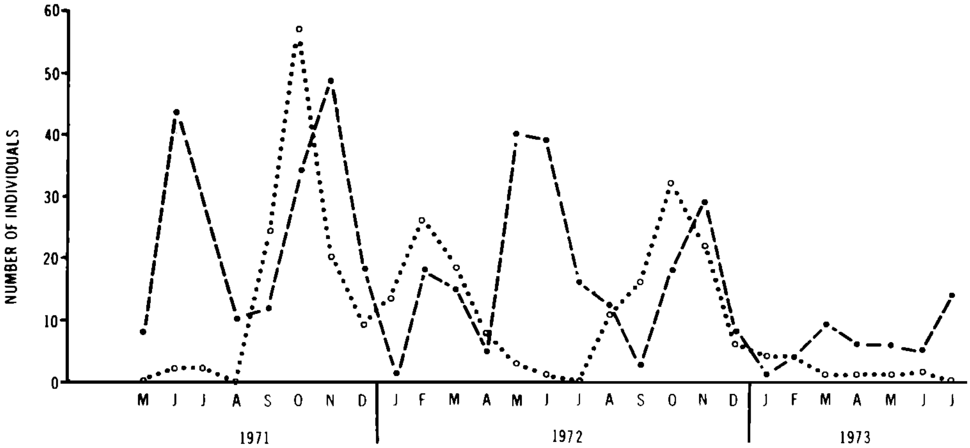

FIGURE 6. Number of banded birds arriving and departing study areas per month. (Dotted line: arrivals, defined as individuals banded in a given month, or previously banded but not seen for at least a month. Dashed line: departures, defined as birds that disappeared and were not observed on the study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

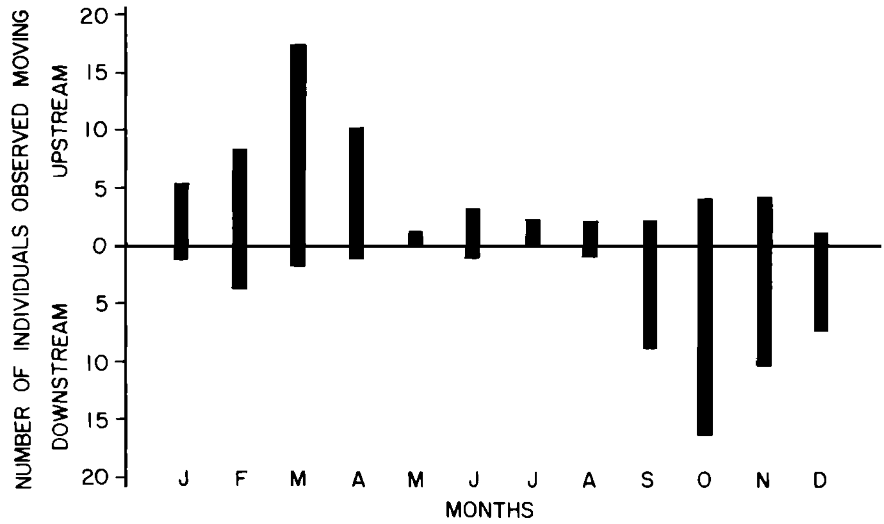

FIGURE 7. Mean number of banded Dippers moving more than 1.6 km on study areas per month (April 1971 through March 1973.)

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 Czechoslovakia, 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

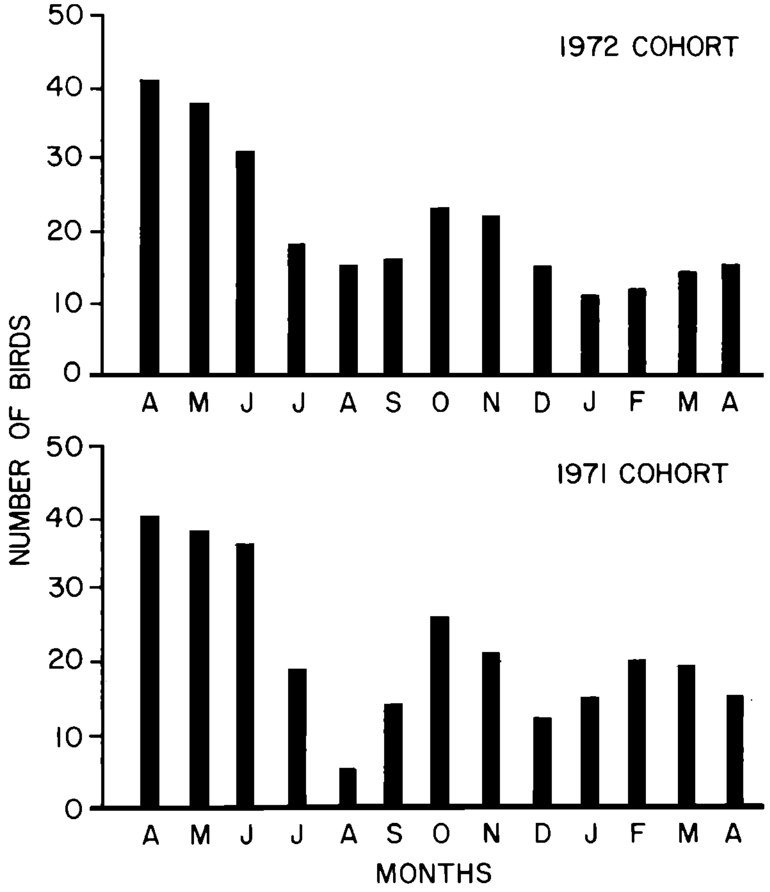

FIGURE 8. Numbers of 1971 and 1972 breeding birds present on study areas in each month after breeding.

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

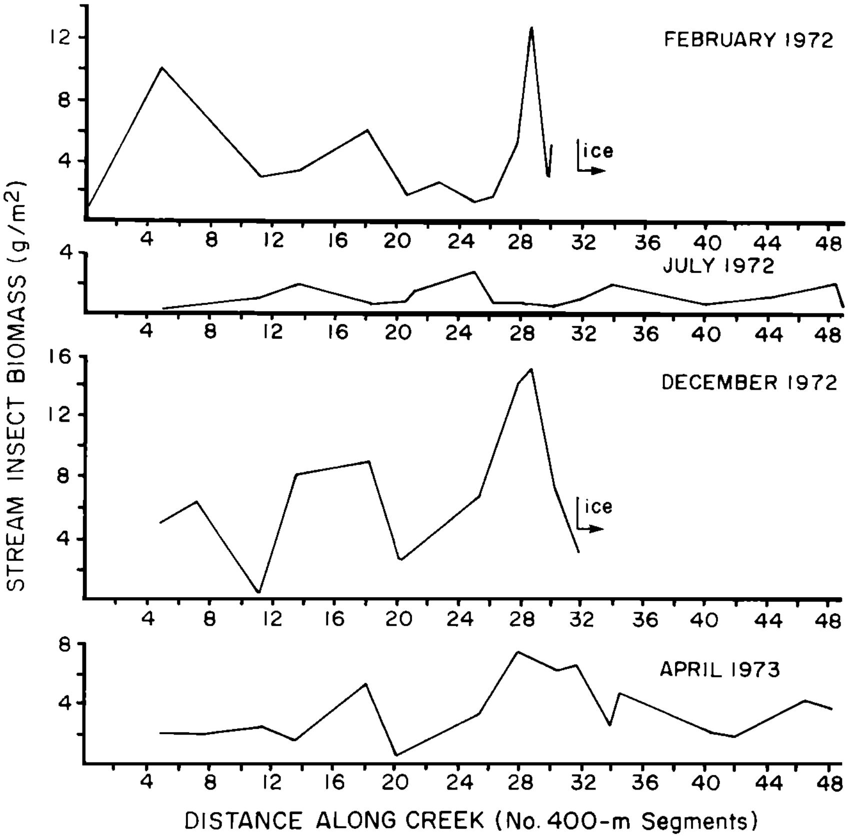

FIGURE 9. Boulder Creek food samples.

insect biomass. Collections in December, February, and April averaged 10.0–15.2 g/m^2 on South Boulder Creek and 3.5–7.0 g/m^2 on Boulder Creek. The samples taken in summer averaged only 3.1 and 1.1 g/m^2, 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

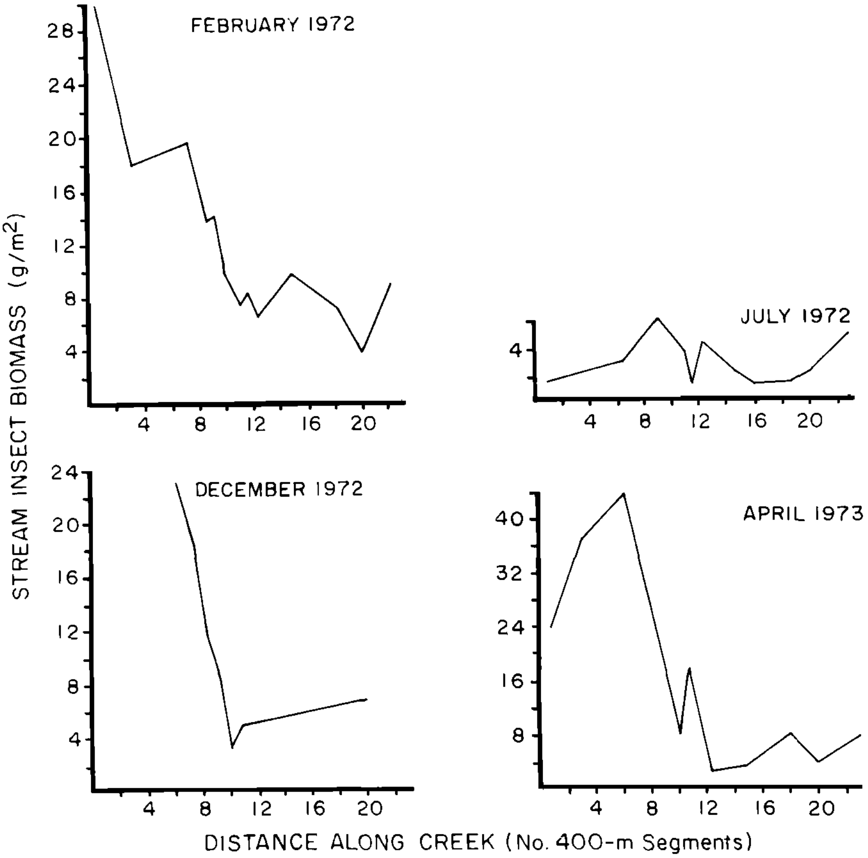

FIGURE 10. South Boulder Creek food samples.

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

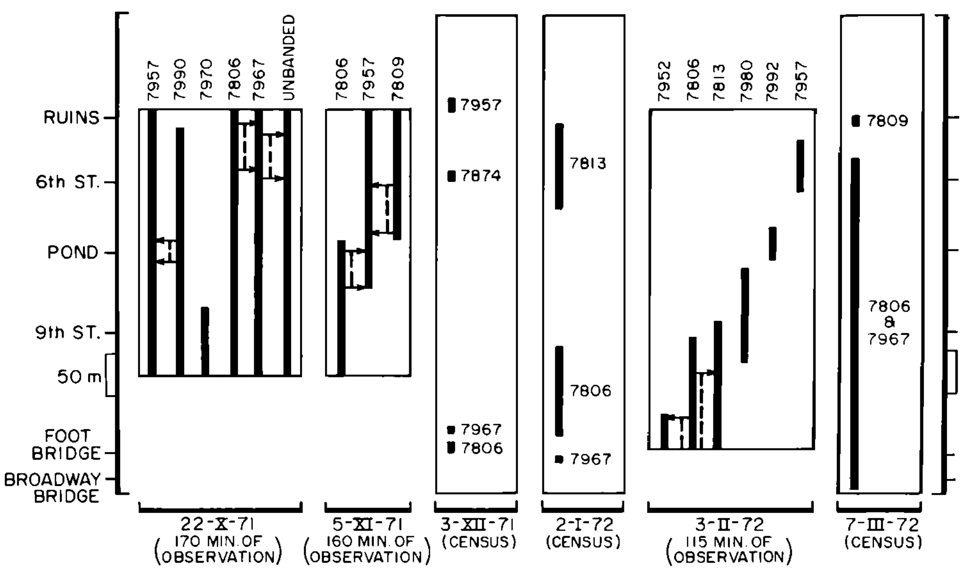

FIGURE 11. Home ranges and observed interactions of wintering Dippers on six days in the winter of 1971–1972. (Areas under observation are enclosed by rectangles; observed ranges of individual birds are shown by heavy vertical bars; areas of stream where aggressive interactions occurred are shown by 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