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

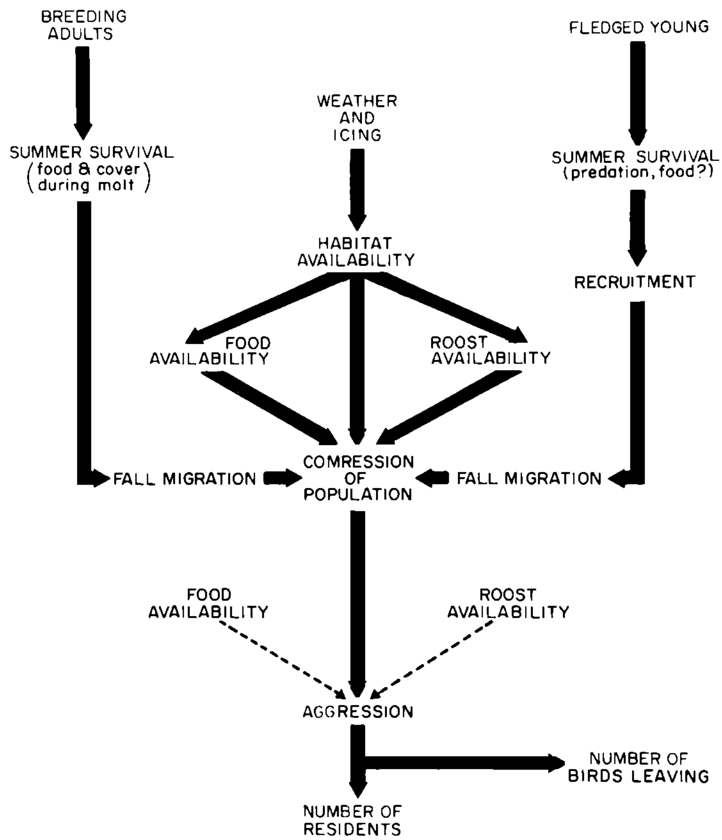

FIGURE 18. Suggested relationships among major factors affecting size of winter Dipper population. (Solid lines indicate corroborated relationships; dotted lines, uncertain relationships.)

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

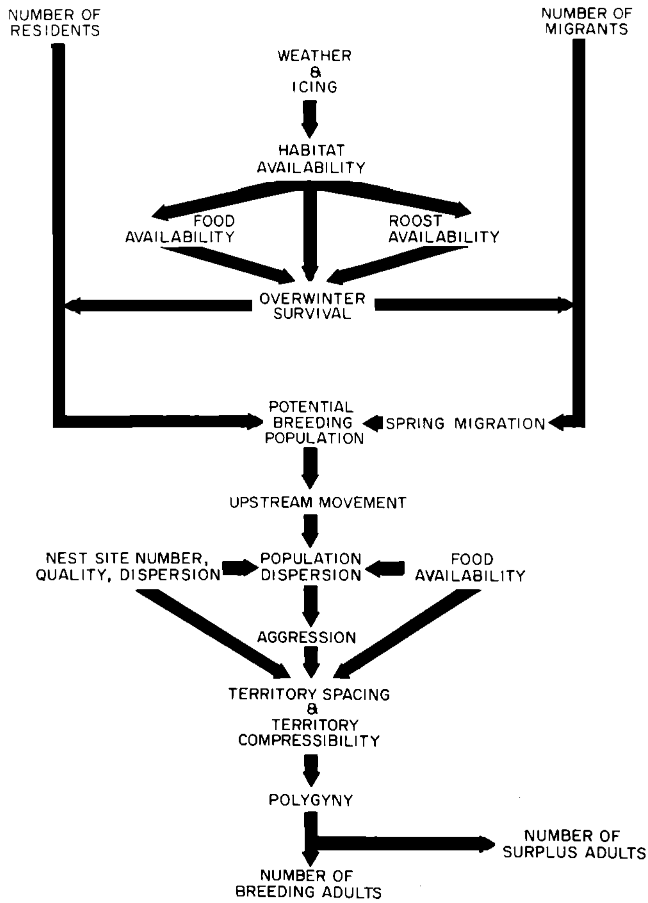

FIGURE 19. Suggested relationships among major factors affecting size of breeding Dipper population.

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

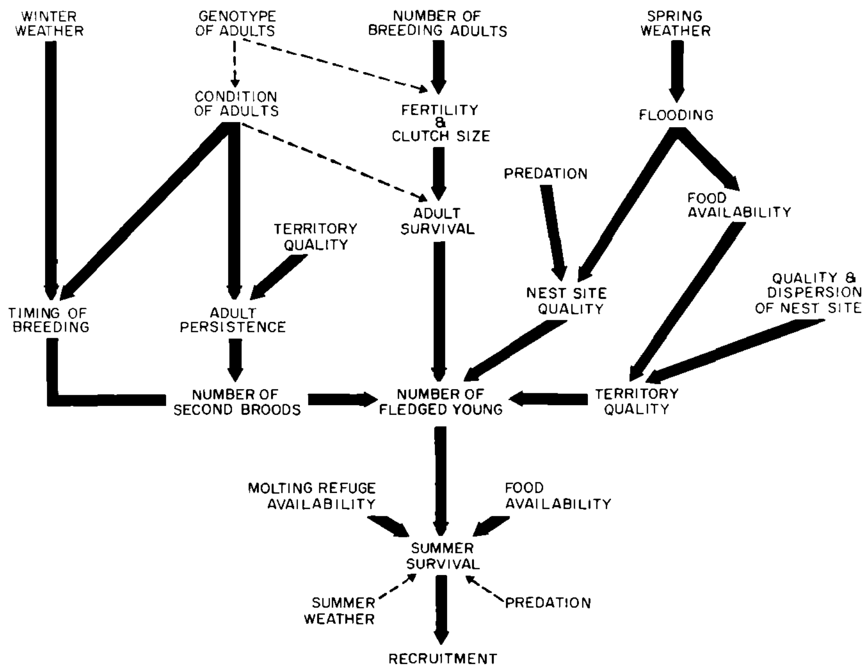

FIGURE 20. Suggested relationships among major factors affecting recruitment of Dippers. (Solid lines indicate well corroborated relationships; dotted lines, less certain relationships.)

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.

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