INTRODUCTION

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

Background

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

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

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

Ecology of Dippers

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

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

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

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

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

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

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

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

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

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

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

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

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

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