

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.

ACKNOWLEDGMENTS

Financial support for the field work on which this report is based was provided by NSF Grant GB-30917 to Bock, and by grants from the Maude Gardiner O'Dell Fund of the University of Colorado and from the Society of the Sigma Xi to Price. Additional funds for computer services were provided by the University of Colorado, Oberlin College and Hamilton College, and for publication costs, by the Committee on University Scholarly Publications, University of Colorado.

In addition, personal support was provided by a number of individuals, only a few of whom we can mention here. We especially wish to thank some of those who helped make field observations, often under trying conditions: Tom Light, Linda Waltz, Peter Stacey, Chris Porter, Larry Leptien, Laura Hendrie, Janice Centa, Rob McKnight, and many of the graduate students in the Department of Environmental, Population and Organismic Biology. Larry Leptien also provided much help with computer analysis. Sue Ann Miller and staff in the Audiovisual Services of the Department of Molecular, Cellular and Developmental Biology executed many of the figures.

LITERATURE CITED

- ALDER, J. 1963. Behaviour of Dippers at the nest during a flood. *Brit. Birds* 56:73-76.
- ANDERSSON, J. S., AND S. A. L. WESTER. 1971. Length of wing, bill, and tarsus as a character of sex in the Dipper *Cinclus cinclus*. *Ornis Scand.* 2:75-79.
- ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. *The Distribution and abundance of animals*. Univ. of Chicago Press, Chicago.
- BAKUS, G. J. 1957. The life history of the Dipper on Rattlesnake Creek, Missoula County, Montana. M.A. Thesis. Montana St. Univ., Missoula.
- BAKUS, G. J. 1959a. Observations on the life history of the Dipper in Montana. *Auk* 76:190-207.
- BAKUS, G. J. 1959b. Territoriality, movements, and population density of the Dipper in Montana. *Condor* 61:410-425.
- BALÁT, F. 1960. Studie o pelichání skorce vodního, *Cinclus cinclus* (L.). [A study on moulting in the Dipper, *Cinclus cinclus* (L.).] *Zool. Listy* 9:257-264. [English summ.]
- BALÁT, F. 1962. Rozmístění a presuny skorce vodního na potoce v závislosti na stáří, roční dobe a prostředí. [Distribution and movements of the Dippers, *Cinclus cinclus aquaticus* Bechst. on a creek and their changes during a year.] *Zool. Listy* 11:131-144. [English summ.]
- BALÁT, F. 1964. Breeding biology and population dynamics in the Dipper. *Zool. Listy* 13:305-320.
- BARRY, R. B., AND R. J. CHORLEY. 1970. *Atmosphere, weather and climate*. Holt, Rinehart and Winston, New York.
- BENT, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds and their allies. U.S. Natl. Mus., Bull. 176:111-130.
- BENT, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. Natl. Mus., Bull. 195:96-113.

- BERGER, M., AND J. S. HART. 1974. Physiology and energetics of flight. Pp. 416-477 in D. S. Farner and J. R. King (eds.), Avian biology. Vol. 4. Academic Press, New York.
- BERNDT, R., AND H. STERNBERG. 1968. Terms, studies and experiments on the problems of bird dispersion. *Ibis* 110:256-269.
- BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76:160-169.
- BROWN, J. L. 1969a. The buffer effect and productivity in tit populations. *Amer. Natur.* 103:347-354.
- BROWN, J. L. 1969b. Territorial behavior and population regulation in birds. *Wilson Bull.* 81:293-329.
- BROWN, J. L., AND G. H. ORIANS. 1970. Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst.* 1:239-262.
- BURT, W. H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24:346-352.
- CARLANDER, K. D. 1969. Handbook of freshwater fishery biology. Vol. 1. Iowa St. Univ. Press, Ames.
- CHITTY, D. 1967. What regulates bird populations? *Ecology* 48:698-701.
- CODY, M. L. 1966. A general theory of clutch size. *Evolution* 20:174-184.
- CODY, M. L. 1971. Ecological aspects of reproduction. Pp. 461-512 in D. S. Farner and J. R. King (eds.), Avian biology. Vol. 1. Academic Press, New York.
- CONDÉR, P. J. 1949. Individual distance. *Ibis* 91:649-655.
- CONNELL, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710-723.
- CONNELL, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecol. Monogr.* 40:49-78.
- CROW, J., AND M. KIMURA. 1970. An introduction to population genetics theory. Harper and Row, New York.
- DEMENT'EV, G. P., AND N. A. GLADOV. (EDS.). 1954. Birds of the Soviet Union. 6:773-790. Trans. by A. Birron and Z. S. Cole. U.S. Dept. Commerce, Springfield, Virginia.
- DEMPSTER, J. P. 1975. Animal population ecology. Academic Press, New York.
- DIXON, W. J. (ED.). 1971. BMD biomedical computer programs. Univ. of California Press, Berkeley.
- DOBZHANSKY, T. 1973. Active dispersal and passive transport in *Drosophila*. *Evolution* 27:535-575.
- DOW, D. D., AND D. M. SCOTT. 1971. Dispersal and range expansion by the Cardinal: an analysis of banding records. *Can. J. Zool.* 49:185-198.
- EHRLICH, P. R., R. R. WHITE, M. C. SINGER, S. W. McKECHNIE, AND L. E. GILBERT. 1975. Checkerspot butterflies: A historical perspective. *Science* 188:221-228.
- EL-WAILLY, A. J. 1966. Energy requirements for egg-laying and incubation in the Zebra Finch, *Taeniopygia castanotis*. *Condor* 68:582-594.
- FARNER, D. S. 1955. Bird banding in the study of population dynamics. Pp. 397-449 in A. Wolfson (ed.), Recent studies in avian biology. Univ. Illinois Press, Urbana.
- FERGUSON, G. A. 1971. Statistical analysis in psychology and education. McGraw-Hill Book Co., New York.
- FRANK, P. W. 1965. The biodemography of an intertidal snail population. *Ecology* 46:831-844.
- FRETWELL, S. D. 1970. On territorial behavior and other factors influencing habitat distribution in birds. III. Breeding success in a local population of Field Sparrows (*Spizella pusilla* Gmel.). *Acta Biotheor.* 19:45-52.
- FRETWELL, S. D., AND H. L. LUCAS, JR. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* 19:16-36.
- FUCHS, E. 1970. Zur Biologie der Wasseramsel *Cinclus cinclus*. [On the biology of the Dipper *Cinclus cinclus*.] *Ornithol. Beob.* 67:3-14. [English summ.]
- GADGIL, M. 1971. Dispersal: population consequences and evolution. *Ecology* 52:253-261.
- GALBRAITH, H. 1979. Polygamy in the Dipper. *Scottish Birds* 10:180-181.
- GOODGE, W. R. 1959. Locomotion and other behavior of the Dipper. *Condor* 61:4-17.
- GOODGE, W. R. 1960. Adaptations for amphibious vision in the Dipper (*Cinclus mexicanus*). *J. Morphol.* 107:79-91.
- GREEN, J. C. 1970. Additional Dipper sightings in 1970. *Loon* 42:137.

- GREENWAY, J. C., AND C. VAURIE. 1958. Remarks on some forms of *Cinclus* (Aves). *Breviora* 89: 1-10.
- GREGG, R. E. 1963. The ants of Colorado. Univ. Colorado Press, Boulder.
- GRIFFITH, J. S. 1974. Utilization of invertebrate drift by Brook Trout (*Salvelinus fontinalis*) and Cutthroat Trout (*Salmo clarki*) in small streams in Idaho. *Trans. Amer. Fish. Soc.* 103:440-447.
- HAILMAN, J. P. 1978. [Review of] On the adaptive significance of territoriality. *Bird-Banding* 49:84.
- HANEDA, K., AND S. KOSHIHARA. 1969. [Life history of the Pallas's Dipper *Cinclus pallasi hondoensis*.] *Bull. Inst. Nat. Educ. Shiga Heights* 8:49-57. [In Japanese, English summ.]
- HANN, H. W. 1950. Nesting behavior of the American Dipper in Colorado. *Condor* 52:49-62.
- HELLMAYR, C. E. 1934. Catalogue of the birds of the Americas. Part VII. Corvidae-Sylviidae. *Field Mus. Nat. Hist. Zool. Series* 13:106-110.
- HENDERSON, J. 1908. The American Dipper in Colorado. *Bird Lore* 10:1-7.
- HEWSON, R. 1967. Territory, behaviour and breeding of the Dipper in Banffshire. *Brit. Birds* 60: 244-252.
- HEWSON, R. 1969. Roosts and roosting habits of the Dipper. *Bird Study* 16:89-100.
- HINDE, R. A. 1956. The biological significance of the territories of birds. *Ibis* 98:340-369.
- HOLMBRING, J., AND H. KJEDEMAR. 1968. Strömvärten (*Cinclus cinclus*) i Östergötland. *Vår Fågelvärld* 27:97-121. [In Swedish, English summ.]
- HUXLEY, J. 1934. A natural experiment on the territorial instinct. *Brit. Birds* 26:270-277.
- HYNES, H. B. N. 1970. The ecology of running waters. Univ. Toronto Press, Toronto.
- JENKINS, T. M. 1969. Night feeding of brown and rainbow trout in an experimental stream channel. *J. Fish. Res. Bd. Canada* 26:3275-3278.
- JENKINS, T. M., C. R. FELDMUTH, AND G. V. ELLIOT. 1970. Feeding of rainbow trout (*Salmo gairdneri*) in relation to abundance of drifting invertebrates in a mountain stream. *J. Fish. Res. Bd. Canada* 27:2356-2361.
- JOHNSON, N. K. 1953. Dipper eaten by Brook Trout. *Condor* 55:158.
- JOHNSTON, J. S., AND W. B. HEED. 1976. Dispersal of desert-adapted *Drosophila*: The saguaro-breeding *D. nigrospiracula*. *Amer. Natur.* 110:629-651.
- JOHNSTON, R. F. 1961. Population movements of birds. *Condor* 63:386-389.
- JOST, O. 1969. Über die bedeutung der wasserscheiden beim ortswchsel der Wasseramsel (*Cinclus cinclus aquaticus*). [On the significance of water sheds in the movements of the Dipper (*Cinclus cinclus aquaticus*).] *J. Ornithol.* 110:71-78 [English summ.]
- JOURDAIN, F. C. R. 1938. Share of the sexes in incubation of the Dipper. *Brit. Birds* 31:380-381.
- KENDEIGH, S. C. 1963. Thermodynamics of incubation in the House Wren, *Troglodytes aedon*. *Proc. XIII Int. Ornithol. Congr.*, Ithaca (1962), pp. 884-904.
- KING, J. A. 1973. The ecology of aggressive behavior. *Ann. Rev. Ecol. Syst.* 4:117-138.
- KLUYVER, H. N., AND L. TINBERGEN. 1953. Territory and regulation of density in Titmice. *Arch. Neerl. Zool.* 10:265-289.
- LACK, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, Oxford.
- LACK, D. 1966. Population studies of birds. Oxford Univ. Press, Oxford.
- LEWIS, S. L. 1969. Physical factors influencing fish populations in pools of a trout stream. *Trans. Amer. Fish. Soc.* 98:14-19.
- LIDICKER, W. Z. 1973. Regulation of numbers in an island population of the California Vole, a problem in community dynamics. *Ecol. Monogr.* 43:271-302.
- MARLER, P. 1956. Territory and individual distance in the Chaffinch *Fringilla coelebs*. *Ibis* 98:496-501.
- MARR, J. W. 1967. Ecosystems of the East Slope of the Front Range in Colorado. Univ. Colorado Studies, Ser. Biol. 8. Univ. Colorado Press, Boulder.
- MAYNARD SMITH, J. 1974. Models in ecology. Cambridge Univ. Press, Cambridge.
- MAYR, E. 1970. Populations, species and evolution. Harvard Univ. Press, Cambridge, Mass.
- MCLAREN, I. A. 1972. Polygyny as the adaptive function of breeding territory in birds. *Trans. Conn. Acad. Arts Sci.* 44:191-210.
- MCLAY, C. 1970. A theory concerning the distance travelled by animals entering the drift of a stream. *J. Fish. Res. Bd. Canada* 27:359-370.
- MECOM, J. O. 1969. Productivity and feeding habits of trichoptera larvae in a Colorado mountain stream. Ph. D. Dissertation, Univ. Colorado, Boulder.

- MENGE, J. L., AND B. A. MENGE. 1974. Role of resource allocation and spatial heterogeneity in coexistence of two competing intertidal starfish. *Ecol. Monogr.* 44:189-209.
- MITCHELL, P. A. 1968. The food of the Dipper (*Cinclus mexicanus* Swainson) on two western Montana streams. M.A. Thesis, Univ. Montana, Missoula.
- MOON, H. J. 1923. Dipper nesting away from water. *Brit. Birds* 17:59.
- MUELHAUSEN, M. H. 1970. First Dipper record for Minnesota. *Loon* 42:136.
- MUIR, J. 1894. The mountains of California. The Century Co., New York.
- MURRISH, D. E. 1970a. Responses to diving in the Dipper, *Cinclus mexicanus*. *Comp. Biochem., Physiol.* 34:853-858.
- MURRISH, D. E. 1970b. Responses to temperature in the Dipper, *Cinclus mexicanus*. *Comp. Biochem., Physiol.* 34:859-869.
- NICE, M. M. 1941. The role of territory in bird life. *Amer. Midl. Natur.* 26:441-487.
- NIE, H. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. SPSS statistical package for the social sciences. McGraw-Hill, New York.
- ODUM, E. P. 1971. Fundamentals of ecology. W. B. Saunders, Philadelphia.
- PADDOCK, M. W. 1964. The climate and topography of the Boulder region. Pp. 25-33 in H. Rodeck (ed.), Natural history of the Boulder area. Univ. Colorado Mus. Leaflet No. 13, Boulder.
- PAYNE, R. B. 1972. Mechanism and control of molt. Pp. 104-155 in D. S. Farner and J. R. King (eds.). Avian biology. Vol. 2. Academic Press, New York.
- PENNAK, R. W., AND E. D. VAN GERPEN. 1947. Bottom fauna production and physical nature of the substrate in a northern Colorado trout stream. *Ecology* 28:42-48.
- PENOT, J. 1948. Notes biologique sur le Cincle Plongeur *Cinclus cinclus* (L.). *Oiseau* 18:141-151.
- PIANKA, E. R. 1974. Evolutionary ecology. Harper and Row, New York.
- PIELOU, E. C. 1969. An introduction to mathematical ecology. Wiley and Sons, New York.
- PRICE, F. E., AND C. E. BOCK. 1973. Polygyny in the Dipper. *Condor* 75:457-459.
- RICHTER, C. J. J. 1970. Aerial dispersal in relation to habitat in eight wolf spider species (*Pardosa*, Araneae, Lycosidae). *Oecologia* 5:200-214.
- RICKLEFS, R. E. 1979. Ecology. Second ed. Chiron Press, Newton, Mass.
- ROBSON, R. W. 1956. The breeding of the Dipper in north Westmorland. *Bird Study* 3:170-180.
- SCHWERDTFEGER, F. 1958. Is the density of animal populations regulated by mechanisms or by chance? *Proc. 10th Int. Congr. Entomol.* 4:115-122.
- SHOOTER, P. 1970. The Dipper population of Derbyshire, 1958-1968. *Brit. Birds* 63:158-163.
- SKINNER, M. P. 1922. Notes on the Dipper in Yellowstone National Park. *Condor* 24:18-21.
- SMITH, R. L. 1966. Ecology and field biology. Harper and Row, New York.
- SOLOMON, M. E. 1958. Meaning of density-dependence and related terms in population dynamics. *Nature* 181:1778-1780.
- SOUTHWOOD, T. R. E. 1968. The abundance of animals. Inaug. Lect. Imp. Coll. Sci. Technol. 8:1-16.
- SOUTHWOOD, T. R. E. 1975. The dynamics of insect populations. Pp. 151-199 in D. Pimentel (ed.), Insects, science and society. Academic Press, New York.
- STEIGER, J. A. 1940. Dipper, wilderness dweller. *Bird Lore* 43:10-14.
- SULLIVAN, J. O. 1965. "Flightlessness" in the Dipper. *Condor* 67:535-536.
- SULLIVAN, J. O. 1966. A Dipper nest away from water. *Condor* 68:107.
- SULLIVAN, J. O. 1973. Ecology and behavior of the Dipper, adaptations of a passerine to an aquatic environment. Ph.D. Dissertation, Univ. Montana, Missoula.
- SUNQUIST, M. E. 1976. Territory size and nesting habits of Brown Dippers *Cinclus pallasi*. *Ibis* 118: 577-578.
- TAMARIN, R. H. (ED.). 1978. Population regulation. Benchmark Papers in Ecology, Vol. 7. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.
- THUT, R. N. 1970. Feeding habits of the Dipper in Southwestern Washington. *Condor* 72:234-235.
- TROCHET, B. 1967. Un nid de cincle sur un arbre. *Jean le Blanc* 6:100-101.
- U.S. DEPARTMENT OF COMMERCE. 1964. Climatography of the United States No. 86-5, Colorado. Washington, D.C.
- U.S. DEPARTMENT OF COMMERCE. 1965. Climatography of the United States No. 86-20, Montana. Washington, D.C.
- U.S. DEPARTMENT OF COMMERCE. 1971-1973. Climatological data for Colorado. Vols. 76-78. Washington, D.C.

- VADER, W. 1971. Dippers feeding on marine invertebrates. *Brit. Birds* 64:456-458.
- VAN TYNE, J., AND A. J. BERGER. 1959. Fundamentals of ornithology. John Wiley and Sons, New York.
- VAN VALEN, L. 1971. Group selection and the evolution of dispersal. *Evolution* 25:591-598.
- VERNER, J. 1977. On the adaptive significance of territoriality. *Amer. Natur.* 111:769-775.
- VOGT, W. 1944. Über die territorien der Wasseramsel, *Cinclus cinclus* (L.), in Winter 1943/44 an der Aare bei Bern. *Ornithol. Beob.* 41:36-43.
- WATERS, T. F. 1962. Diurnal periodicity in the drift of stream invertebrates. *Ecology* 43:316-320.
- WATSON, A. 1973. A review of population dynamics in birds. *Brit. Birds* 66:417-437.
- WATSON, A., AND G. R. MILLER. 1971. Territory size and aggression in a fluctuating Red Grouse population. *J. Anim. Ecol.* 40:367-383.
- WATSON, A., AND R. MOSS. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. Pp. 167-218 in A. Watson (ed.), *Animal populations in relation to their food resources*. Blackwell, Oxford.
- WATSON, A., AND R. MOSS. 1972. A current model of population dynamics in Red Grouse. *Proc. XV Int. Ornithol. Congr.*, The Hague (1970), pp. 134-149.
- WEST, G. C. 1960. Seasonal variation in the energy balance of the Tree Sparrow in relation to migration. *Auk* 77:306-329.
- WHITNEY, M., AND G. WHITNEY. 1972. A study of the Dippers on the St. Vrain Creek, Colorado. *Western Bird Bander* 47:3-9.
- WILSON, E. O. 1975. *Sociobiology: the modern synthesis*. Harvard Univ. Press, Cambridge, Mass.
- WYNNE-EDWARDS, V. C. 1962. Animal dispersion in relation to social behaviour. Oliver and Boyd, Edinburgh.
- ZAR, J. H. 1974. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, N.J.
- ZIMMERMAN, J. L. 1965. Bioenergetics of the Dickcissel, *Spiza americana*. *Physiol. Zool.* 38:370-389.