

on high-quality habitats throughout the breeding season (e.g., area Z in Fig. 41b) as a result of increased tolerance by breeders given unusually abundant acorns into the summer months.

During the year, floaters search for and fill available breeding vacancies as shown in Figure 41. Although breeding vacancies arise from breeder death throughout suitable habitat, floaters have the greatest probability of gaining a breeding vacancy either in poor quality habitat where breeder turnover may be greater or in high-quality habitat where breeder density has been reduced by an acorn crop failure. Also as shown in Figure 41, there is movement of breeders from one territory to another, often from lower to higher quality habitat. Not illustrated are the relatively rare regional acorn crop failures that may result in breeder density decline and subsequent low reproductive output over a broad area, providing increased opportunity for dispersing offspring and older floaters to gain a territory and breeding status.

These patterns of habitat quality and acorn production, the varied behaviors floaters employ to acquire breeding space and exploit resources, the behavioral interactions between territorial jays and floaters, and the ability of breeders to move and improve the quality of their territories all promote selection for early dispersal and floating in scrub-jays in central coastal California, and selection against cooperative breeding.

ACKNOWLEDGMENTS

Fanny Hastings Arnold, through her continuous generosity, and the Museum of Vertebrate Zoology, provided the exquisite Hastings Natural History Reservation where this research was done. Financial assistance was provided by the Department of Forestry and Resource Conservation (Oliver Lyman Fund), the American Museum of Natural History (Frank M. Chapman Memorial Fund), Sigma Xi, the American Academy of Sciences (O. C. Marsh Fund), and the Museum of Vertebrate Zoology (Kellogg Fund). I was also supported by University Fellowships, Graduate Minority Fellowships, and a Betty S. Davis Memorial Fellowship.

I am especially grateful to Walt Koenig and Ron Mumme for their companionship at Hastings and their ideas concerning cooperative breeding. Frank Pitelka and Dale McCullough continually sent me back to the field with new ideas and rekindled enthusiasm. Numerous field assistants worked on the study: Greg Ashcroft, Bob Beffy, Clay Clifton, Sharon Dougherty, Lenore Feinburg, and Jim Siegel, all of whom braved long hours and certain exposure to poison oak in search of scrub-jay nests.

Frank Pitelka, Walter Koenig, Ron Mumme, Glen Woolfenden, John Fitzpatrick, Peter Stacey, and Dale McCullough made numerous helpful criticisms of earlier drafts. Joseph Jehl and John Rotenberry provided long-term editorial support. Karen J. Nardi provided love and understanding and both the financial and moral support needed to complete the study. To all of these individuals I give my sincere thanks.

LITERATURE CITED

- ALTMANN, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267.
- ARCESE, P. 1987. Age, intrusion pressure, and defense against floaters by territorial male Song Sparrows. *Animal Behaviour* 35:773-784.
- ARCESE, P., AND J. N. M. SMITH. 1985. Phenotypic correlates and ecological consequences of dominance in Song Sparrows. *Journal of Animal Ecology* 54:817-830.
- ARNOLD, K. E., AND I. P. F. OWENS. 1998. Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proceedings of the Royal Society of London, Series B* 265:739-745.
- ARNOLD, K. E., AND I. P. F. OWENS. 1999. Cooperative breeding in birds: the role of ecology. *Behavioral Ecology* 10:465-471.

- ATWOOD, J. L. 1978. The breeding biology of the Santa Cruz Island Scrub Jay, *Aphelocoma coerulescens insularis*. M.A. thesis. California State University, Long Beach, CA.
- ATWOOD, J. L. 1980a. Social interactions in the Santa Cruz Island Scrub Jay. *Condor* 82:440-448.
- ATWOOD, J. L. 1980b. Breeding biology of the Santa Cruz Island Scrub Jay. Pp. 675-688 in D. M. Power (editor). *The California Islands: proceedings of a multidisciplinary symposium*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- ATWOOD, J. L., M. J. ALPERS, AND C. T. COLLINS. 1990. Survival of breeders in Santa Cruz and mainland California Scrub Jay populations. *Condor* 92:783-788.
- AUSTAD, S. N., AND K. N. RABENOLD. 1985. Reproductive enhancement by helpers and an experimental inquiry into its mechanism in the Bicolored Wren. *Behavioral Ecology and Sociobiology* 17:19-27.
- AUSTAD, S. N., AND K. N. RABENOLD. 1987. Demography and the evolution of cooperative breeding in the Bicolored Wren, *Campylorhynchus griseus*. *Behaviour* 97:308-324.
- BAEYENS, G. 1981. Functional aspects of serial monogamy: the magpie pair-bond in relation to its territorial system. *Ardea* 69:145-166.
- BARBER, C. A., AND R. J. ROBERTSON. 1999. Floater males engage in extrapair copulations with resident female Tree Swallows. *Auk* 116:264-269.
- BARBOUR, M. G., AND J. MAJOR. 1977. *Terrestrial vegetation of California*. Wiley-Interscience, New York, NY.
- BEECHER, M. D., AND I. M. BEECHER. 1979. Sociobiology of Bank Swallows: reproductive strategy of the male. *Science* 205:1282-1285.
- BELL, H. L., AND H. A. FORD. 1986. A comparison of the social organization of three syntopic species of Australian thornbill, *Acanthiza*. *Behavioral Ecology and Sociobiology* 19:381-392.
- BOCK, C. E., AND J. H. BOCK. 1974. Geographical ecology of the Acorn Woodpecker: diversity versus abundance of resources. *American Naturalist* 108:694-698.
- BREININGER, D. R., V. L. LARSON, B. W. DUNCAN, R. B. SMITH, D. M. ODDY, AND M. F. GOODCHILD. 1995. Landscape patterns of Florida Scrub Jay use and demographic success. *Conservation Biology* 9:1442-1435.
- BREININGER, D. R., V. L. LARSON, D. M. ODDY, R. B. SMITH, AND M. J. BARKASZI. 1996. Florida Scrub-Jay demography in different landscapes. *Auk* 113:617-625.
- BROWN, J. L. 1963. Social organization and behavior of the Mexican Jay. *Condor* 65:126-153.
- BROWN, J. L. 1969. Territorial behavior and population regulation in birds. *Wilson Bulletin* 81: 293-329.
- BROWN, J. L. 1970. Cooperative breeding and altruistic behavior in the Mexican Jay, *Aphelocoma ultramarina*. *Animal Behaviour* 18:366-378.
- BROWN, J. L. 1974. Alternate routes to sociality in jays - with a theory for the evolution of altruism and communal breeding. *American Zoologist* 14:63-80.
- BROWN, J. L. 1978. Avian communal systems. *Annual Review of Ecology and Systematics* 9: 123-156.
- BROWN, J. L. 1982. Optimal group size in animals. *Journal of Theoretical Biology* 95:793-810.
- BROWN, J. L. 1985. The evolution of helping behavior - an ontogenetic and comparative perspective. Pp. 137-171 in E. Gollin (editor). *The comparative development of adaptive skills: evolutionary implications*. Lawrence Erlbaum Associates, Hillsdale, NJ.
- BROWN, J. L. 1986. Cooperative breeding and the regulation of numbers. *International Ornithological Congress* 18:774-782.
- BROWN, J. L. 1987. *Ecology and evolution of helping and communal breeding in birds*. Princeton University Press, Princeton, NJ.
- BROWN, J. L. 1994. Mexican Jay (*Aphelocoma ultramarina*). In A. Poole and F. Gill (editors). *The Birds of North America*, No. 118. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.
- BROWN, J. L., AND E. S. BROWN. 1981a. Extended family system in a communal bird. *Science* 211: 313-324.

- BROWN, J. L., AND E. S. BROWN. 1981b. Kin selection and individual selection in babblers. Pp. 244–256 in R. D. Alexander and D. W. Tinkle (editors). *Natural selection and social behavior: recent research and new theory*. Chiron Press, New York, NY.
- BROWN, J. L., AND E. S. BROWN. 1984. Parental facilitation: parent–offspring relationships in communally breeding birds. *Behavioral Ecology and Sociobiology* 14:203–209.
- BROWN, J. L., AND E. R. BROWN. 1990. The Mexican Jay: uncooperative breeding. Pp. 267–288 in P. B. Stacey and W. D. Koenig (editors). *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge University Press, New York, NY.
- BROWN, J. L., E. R. BROWN, S. D. BROWN, AND D. D. DOW. 1982. Helpers: effects of experimental removal on reproductive success. *Science* 215:421–422.
- BROWN, J. L., E. R. BROWN, J. SEDRANSK, AND S. RITTER. 1997. Dominance, age, and reproductive success in a complex society: a long-term study of the Mexican Jay. *Auk* 114:279–286.
- BROWN, J. L., AND E. G. HORVATH. 1989. Geographic variation of group size, ontogeny, rattle calls, and body size in *Aphelocoma ultramarina*. *Auk* 106:124–128.
- BROWN, J. L., AND S.-H. LI. 1995. Phylogeny of social behavior in *Aphelocoma* jays: a role for hybridization? *Auk* 112:464–472.
- BURT, D. B. 1996. Habitat-use patterns in cooperative and non-cooperative breeding birds: testing predictions with Western Scrub-Jays. *Wilson Bulletin* 108:712–727.
- BURT, D. B., AND A. T. PETERSON. 1993. Biology of the cooperatively breeding Scrub Jays (*Aphelocoma coerulescens*) of Oaxaca, Mexico. *Auk* 110:207–214.
- CAFFREY, C. 1992. Female-biased delayed dispersal and helping in American Crows. *Auk* 109:609–619.
- CARACO, T. 1979a. Time budgeting and group size: a test of theory. *Ecology* 60:618–627.
- CARACO, T. 1979b. Time budgeting and group size: a theory. *Ecology* 60:611–617.
- CARMEN, W. J., W. D. KOENIG, AND R. L. MUMME. 1987. Acorn production by five species of oaks over a seven year period at the Hastings Reservation, Carmel Valley, CA. Pp. 429–434 in T. R. Plumb and N. H. Pillsbury (editors). *Proceedings of the symposium on multiple-use management of California hardwood resources*. USDA Forest Service Technical Bulletin PSW-100. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Albany, CA.
- CARRICK, R. 1963. Ecological significance of territory in the Australian Magpie, *Gymnorhina tibicen*. *International Ornithological Congress* 13:740–753.
- CARRICK, R. 1972. Population ecology of the Australian Black-backed Magpie, Royal Penguin, and Silver Gull. Pp. 41–99 in *Population ecology of migratory birds: a symposium*. U.S. Department of the Interior Wildlife Research Report 2. USDI, Washington, D.C.
- CAUGHLEY, G. 1977. *Analysis of vertebrate populations*. John Wiley, New York, NY.
- CHARLES, J. K. 1972. Territorial behavior and the limitation of population size in crows, *Corvus corone* and *C. cornix*. Ph.D. dissertation. University of Aberdeen, Aberdeen, Scotland.
- CRAIG, J. L., AND I. G. JAMIESON. 1990. Pukeko: different approaches and some different answers. Pp. 385–412 in P. B. Stacey and W. D. Koenig (editors). *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge University Press, New York, NY.
- CUSTER, T. W., AND F. A. PITELKA. 1977. Demographic features of a Lapland Longspur population near Barrow, Alaska. *Auk* 94:505–525.
- DEGANGE, A. R. 1976. The daily and annual time budget of the Florida Scrub Jay. M.A. thesis. University of South Florida, Tampa, FL.
- DEGANGE, A. R., J. W. FITZPATRICK, J. W. LAYNE, AND G. E. WOOLFENDEN. 1989. Acorn harvesting by Florida Scrub Jays. *Ecology* 70:348–356.
- EDEN, S. F. 1987. Dispersal and competitive ability in the magpie: an experimental study. *Animal Behaviour* 35:764–772.
- EDWARDS, T. C., JR. 1986. Ecological distribution of the Gray-breasted Jay: the role of habitat. *Condor* 88:456–460.
- EDWARDS, S. V., AND S. NAEEM. 1993. The phylogenetic component of cooperative breeding in perching birds. *American Naturalist* 141:754–789.

- EKMAN, J., AND C. ASKENMO. 1984. Social rank and habitat use in Willow Tit groups. *Animal Behaviour* 32:508-514.
- EKMAN, J., AND C. ASKENMO. 1986. Reproductive cost, age-specific survival, and comparison of the reproductive strategy in two European tits (genus *Parus*). *Evolution* 40:159-168.
- ELKIN, R. G., W. R. FEATHERSTON, AND J. C. ROGLER. 1978. Investigations of leg abnormalities in chicks consuming high tannin sorghum grain diets. *Poultry Science* 57:757-762.
- EMLEN, S. T. 1982. The evolution of helping. I. An ecological constraints model. *American Naturalist* 119:29-39.
- FITZPATRICK, J. W., AND G. E. WOOLFENDEN. 1986. Demographic routes to cooperative breeding in some New World jays. Pp. 137-160 in M. H. Nitecki and J. A. Kitchell (editors). *Evolution of animal behavior*. Oxford University Press, Oxford, UK.
- FITZPATRICK, J. W., AND G. E. WOOLFENDEN. 1988. Components of lifetime reproductive success in the Florida Scrub Jay. Pp. 305-320 in T. H. Clutton-Brock (editor). *Reproductive success*. University of Chicago Press, Chicago, IL.
- FITZPATRICK, J. W., G. E. WOOLFENDEN, AND K. J. MCGOWAN. 1989. Sources of variance in lifetime fitness of Florida Scrub Jays. *International Ornithological Congress* 19:876-91.
- FREED, L. A. 1986. Territory takeover and sexually selected infanticide in tropical House Wrens. *Behavioral Ecology and Sociobiology* 19:197-206.
- FRETWELL, S. 1969. Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*). *Bird-Banding* 40:1-25.
- GAYOU, D. C. 1986. The social system of the Texas Green Jay. *Auk* 103:540-547.
- GIBBS, H. L., AND P. R. GRANT. 1987. Adult survivorship in Darwin's Ground Finch (*Geospiza*) populations in a variable environment. *Journal of Animal Ecology* 56:797-813.
- GLASE, J. C. 1973. Ecology of social organization in the Black-capped Chickadee. *Living Bird* 12: 235-267.
- GOLDMAN, P. 1980. Flocking as a possible predator defense in Dark-eyed Juncos. *Wilson Bulletin* 92:88-95.
- GOWATY, P. A. 1985. Multiple parentage and apparent monogamy in birds. *Ornithological Monographs* 37:11-21.
- GRIMES, L. G. 1980. Observations of group behavior and breeding biology of the Yellow-billed Shrike *Corvinella corvina*. *Ibis* 122:166-192.
- HANNON, S. J., R. L. MUMME, W. D. KOENIG, AND F. A. PITELKA. 1985. Acorn crop failure, dominance, and a decline in numbers in the cooperatively breeding Acorn Woodpecker. *Journal of Animal Ecology* 56:197-207.
- HARVEY, P. H., P. J. GREENWOOD, C. M. PERRINS, AND A. R. MARTIN. 1979. Breeding success of Great Tits *Parus major* in relation to age of male and female parent. *Ibis* 121:216-219.
- HATCHWELL, B. J., A. F. RUSSELL, M. K. FOWLIE, AND D. J. ROSS. 1999. Reproductive success and nest-site selection in a cooperative breeder: effect of experience and a direct benefit of helping. *Auk*:355-363.
- HEINSOHN, R. G. 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding White-winged Choughs. *American Naturalist* 137:864-881.
- HEINSOHN, R. G., A. COCKBURN, AND R. B. CUNNINGHAM. 1988. Foraging, delayed maturation, and advantages of cooperative breeding in White-winged Choughs, *Corcorax melanorhamptus*. *Ethology* 77:177-186.
- HEINSOHN, R. G., A. COCKBURN, AND R. A. MULDER. 1990. Avian cooperative breeding: old hypotheses and new directions. *Trends in Ecology and Evolution* 5:403-407.
- HUNTER, L. A. 1987. Acquisition of territories by floaters in cooperatively breeding Purple Gallinules. *Animal Behaviour* 35:402-410.
- HURLY, T. A., AND R. J. ROBERTSON. 1984. Aggression and territorial behavior in female Red-winged Blackbirds. *Canadian Journal of Zoology* 62:148-153.
- HÖGSTEDT, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. *Science* 210:1148-1150.

- INNES, K. E., AND R. E. JOHNSTON. 1996. Cooperative breeding in the White-throated Magpie-Jay. How do auxiliaries influence nesting success? *Animal Behaviour* 51:519-533.
- JAMES, F. C., AND H. H. SHUGART, JR. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727-736.
- JAMES, P. C., AND N. A. M. VERBEEK. 1984. Temporal and energetic aspects of food storage in Northwestern Crows. *Ardea* 72:207-215.
- KLOMP, H. 1970. The determination of clutch size in birds: a review. *Ardea* 58:1-124.
- KOENIG, W. D. 1981. Space competition in the Acorn Woodpecker: power struggles in a cooperative breeder. *Animal Behaviour* 29:396-427.
- KOENIG, W. D., W. J. CARMEN, R. L. MUMME, AND M. STANBACK. 1994b. Acorn production by oaks in central coastal California: variation within and among years. *Ecology* 75:99-109.
- KOENIG, W. D., J. M. H. KNOPS, W. J. CARMEN, M. STANBACK, AND R. L. MUMME. 1994a. Estimating acorn crops using visual surveys. *Canadian Journal of Forest Research* 24:2105-2112.
- KOENIG, W. D., AND R. L. MUMME. 1987. Population ecology of the Acorn Woodpecker. Princeton University Press, Princeton, NJ.
- KOENIG, W. D., AND F. A. PITELKA. 1981. Ecological factors and kin selection in the evolution of cooperative breeding in birds. Pp. 261-280 in R. D. Alexander and D. W. Tinkle (editors). *Natural selection and social behavior: recent research and new theory*. Chiron Press, New York, NY.
- KOENIG, W. D., F. A. PITELKA, W. J. CARMEN, R. L. MUMME, AND M. STANBACH. 1992. The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology* 67:111-150.
- KOFORD, R. R., B. S. BOWEN, AND S. L. VEHCAMP. 1990. Groove-billed Anis: joint-nesting in a tropical cuckoo. Pp. 289-332 in P. B. Stacey and W. D. Koenig (editors). *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge University Press, New York, NY.
- KOMDEUR, J. 1991. Influence of territory quality and habitat saturation on dispersal options in the Seychelles Warbler: an experimental test of the habitat saturation hypothesis for cooperative breeding. *International Ornithological Congress* 20:1325-1332.
- KOMDEUR, J. 1996. Influence of helping and breeding experience on reproductive performance in the Seychelles Warbler: a translocation experiment. *Behavioral Ecology* 7:326-333.
- KREBS, J. R. 1971. Territory and breeding density in the Great Tit *Parus major* L. *Ecology* 52: 2-22.
- LACK, D. 1966. Population studies of birds. Clarendon Press, Oxford, UK.
- LANGEN, T. A. 1996a. Skill acquisition and the timing of natal dispersal in the White-throated Magpie-Jay (*Calocitta formosa*). *Animal Behaviour* 51:575-588.
- LANGEN, T. A. 1996b. The mating system of the White-throated Magpie-Jay *Calocitta formosa* and Greenwood's hypothesis for sex-biased dispersal. *Ibis* 138:506-513.
- LANGEN, T. A. 1996c. Social learning of a novel foraging skill by White-throated Magpie-Jays (*Calocitta formosa*, Corvidae): a field experiment. *Ethology* 102:157-166.
- LANGEN, T. A. AND S. L. VEHCAMP. 1999. Ecological factors affecting group and territory size in White-throated Magpie-Jays. *Auk* 115:327-339.
- LAWTON, M. F., AND R. O. LAWTON. 1986. Heterochrony, deferred breeding, and avian sociality. *Current Ornithology* 3:187-222.
- LEIGHTON, M. 1986. Hornbill social dispersion: variations on a monogamous theme. Pp. 108-130 in D. I. Rubenstein and R. W. Wrangham (editors). *Ecological aspects of social evolution*. Princeton University Press, Princeton, NJ.
- LIGON, J. D. 1981. Demographic patterns and communal breeding in the Green Woodhoopoe, *Phoeniculus purpureus*. Pp. 231-243 in R. D. Alexander and D. W. Tinkle (editors). *Natural selection and social behavior: recent research and new theory*. Chiron Press, New York, NY.
- LIGON, J. D. 1988. Cavity roosting, philopatry, and cooperative breeding in the Green Woodhoopoe may reflect a physiological trait. *Auk* 105: 123-127.
- LIGON, J. D., AND S. H. LIGON. 1978. Communal breeding in Green Woodhoopoes as a case for reciprocity. *Nature* 280:174.

- LOERY, G., K. H. POLLOCK, J. D. NICHOLS, AND J. E. HINES. 1987. Age-specificity of Black-capped Chickadee survival rates: analysis of capture-recapture data. *Ecology* 68:1038-1044.
- MACROBERTS, M. H., AND B. R. MACROBERTS. 1976. Social organization and behavior of the Acorn Woodpecker in central coastal California. *Ornithological Monographs* 21:1-115.
- MARQUARDT, R. R., AND A. T. WARD. 1979. Chick performance as affected by autoclave treatment of tannin-containing and tannin-free cultivars of favabeans. *Canadian Journal of Animal Science* 59:781-789.
- MARSHALL, J. T., JR. 1957. Birds of the pine-oak woodland in southern Arizona and adjacent Mexico. *Pacific Coast Avifauna* 32:1-125.
- MATTHYSEN, E. 1987. Territory establishment of juvenile nuthatches after fledging. *Ardea* 75:53-58.
- MCGOWAN, K. J. 1987. Social development in young Florida Scrub Jays. Ph.D. dissertation. University of South Florida, Tampa, FL.
- MCGOWAN, K. J., AND G. E. WOOLFENDEN. 1989. A sentinel system in the Florida Scrub Jay. *Animal Behaviour* 37:1000-1006.
- MUGAAS, J. N., AND J. R. KING. 1981. Annual variation of daily energy expenditure by the Black-billed Magpie: a study of thermal and behavioral energetics. *Studies in Avian Biology* 5: 1-78.
- MUMME, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida Scrub Jay. *Behavioral Ecology and Sociobiology* 31:319-328.
- MURRAY, B. G., JR. 1984. A demographic theory on the evolution of mating systems as exemplified by birds. *Evolutionary Biology* 18:71-140.
- MURTON, R. K., AND N. J. WESTWOOD. 1977. *Avian breeding cycles*. Clarendon Press, Oxford, UK.
- NOBLE, G. K. 1939. The role of dominance in the social life of birds. *Auk* 56:263-273.
- OFARCIC, R. P., AND E. E. BURNS. 1971. Chemical and physical properties of selected acorns. *Journal of Food Science* 36:576-578.
- PATTERSON, I. J. 1980. Territorial behavior and the limitation of population density. *Ardea* 68: 53-62.
- PERRINS, C. M. 1970. The timing of birds' breeding season. *Ibis* 112:242-255.
- PERRINS, C. M. 1976. Possible effects of qualitative changes in the insect diet of avian predators. *Ibis* 118:580-584.
- PETERSON, A. T., AND D. B. BURT. 1992. Phylogenetic history of social evolution and habitat use in the *Aphelocoma* jays. *Animal Behaviour* 44:859-866.
- PETERSON, A. T., AND D. VARGAS. 1992. Ecological diversity in Scrub Jays (*Aphelocoma coerulescens*). Pp. 66-84 in T. P. Ramamoorthy, R. Bye, A. Lot and J. Fa (editors). *Biological diversity of Mexico: origins and distribution*. Oxford University Press, New York, NY.
- PITELKA, F. A. 1945. Pterylography, molt, and age determination of American jays of the genus *Aphelocoma*. *Condor* 47:229-260.
- PITELKA, F. A. 1951. Speciation and ecological distribution in American jays of the genus *Aphelocoma*. *University of California Publications in Zoology* 50:195-464.
- PITELKA, F. A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. *Condor* 61:233-264.
- PITELKA, F. A. 1986. A first in the literature on avian cooperative breeding. *Ecology* 67:1434-1435.
- POWELL, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Animal Behaviour* 22:501-505.
- POWELL, R. A. 1989. Effects of resource productivity, patchiness and predictability on mating systems and dispersal strategies. Pp. 101-123 in V. Standen and R. A. Foley (editors). *Comparative socioecology*. Clarendon Press, Oxford, UK.
- PRUETT-JONES, S. G., AND M. J. LEWIS. 1990. Sex ratio and habitat limitation promote delayed dispersal in Superb Fairy-wrens. *Nature* 348:541-542.
- PULLIAM, H. R. 1976. The principle of optimal behavior and the theory of communities. Pp. 311-332 in P. P. G. Bateson and P. H. Klopfer (editors). *Perspectives in ethology*, Vol. 2. Plenum Press, New York, NY.

- RABENOLD, K. N. 1984. Cooperative enhancement of reproductive success in tropical wren societies. *Ecology* 65:871-885.
- RABENOLD, K. N. 1985. Cooperation in breeding by nonreproductive wrens: kinship, reciprocity, and demography. *Behavioral Ecology and Sociobiology* 17:1-17.
- ROOT, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. *Ecological Monographs* 37:317-350.
- ROWLEY, I. 1965. The life history of the Superb Blue Wren, *Malurus cyaneus*. *Emu* 64:251-297.
- RUTBERG, A. T., AND S. ROHWER. 1980. Breeding strategies of male Yellow-headed Blackbirds: results of a removal experiment. *Auk* 97:619-622.
- SABINE, W. S. 1959. The winter society of the Oregon Junco: intolerance, dominance, and the pecking order. *Condor* 61:110-135.
- SÆTHER, B.-E. 1990. Age specific variation in reproductive performance in birds. *Current Ornithology* 7:251-283.
- SÆTHER, T. R., AND G. E. FONSTAD 1981. A removal experiment showing unmated females in a breeding population of Chaffinches. *Animal Behaviour* 29:637-639.
- SCHAUB, R., R. L. MUMME, AND G. E. WOOLFENDEN. 1992. Predation on the eggs and nestlings of Florida Scrub Jays. *Auk* 109:585-593.
- SCHODDE, R. 1982. Origin, adaptation and evolution of birds in Australia. Pp. 191-224 in W. R. Barker and P. J. M. Greenslade (editors). *Evolution of the flora and fauna of arid Australia*. Peacock, Frewville, Australia.
- SCHOECH, S. J. 1996. The effect of supplemental food on body condition and the timing of reproduction in a cooperative breeder, the Florida Scrub-Jay. *Condor* 98:234-244.
- SELANDER, R. K. 1964. Speciation in wrens of the genus *Campylorhynchus*. University of California Publications in Zoology 74:1-224.
- SHERMAN, P. W., AND M. L. MORTON. 1984. Demography of Belding's ground squirrel. *Ecology* 65:1617-1628.
- SKUTCH, A. F. 1961. Helpers among birds. *Condor* 63:198-226.
- SMITH, C. C., AND O. J. REICHMAN. 1984. The evolution of food caching by birds and mammals. *Annual Review of Ecology and Systematics* 15:329-352.
- SMITH, J. N. M., AND P. ARCESE. 1989. How fit are floaters? Consequences of alternative territorial behavior in a nonmigratory sparrow. *American Naturalist* 133:830-845.
- SMITH, S. M. 1978. The underworld in a territorial sparrow: adaptive strategy for floaters. *American Naturalist* 112:571-582.
- SMITH, S. M. 1984. Flock switching in chickadees: why be a winter floater? *American Naturalist* 123:81-98.
- SOUTHWOOD, T. R. E. 1978. *Ecological methods*. 2nd ed. Chapman and Hall, London, UK.
- STACEY, P. B., AND C. E. BOCK. 1978. Social plasticity in the Acorn Woodpecker. *Science* 202:1298-1302.
- STACEY, P. B., AND J. D. LIGON. 1987. Territory quality and dispersal options in the Acorn Woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. *American Naturalist* 130:654-676.
- STACEY, P. B., AND J. D. LIGON. 1991. The benefits of philopatry hypothesis for the evolution of cooperative breeding: variance in territory quality and group size effects. *American Naturalist* 137:831-846.
- STALLCUP, J. A., AND G. E. WOOLFENDEN. 1978. Family status and contribution to breeding by Florida Scrub Jays. *Animal Behaviour* 26:1144-56.
- STEARNS, S. C., AND R. E. CRANDALL. 1981. Quantitative predictions of delayed maturity. *Evolution* 35:455-463.
- STRAHL, S. D., AND J. L. BROWN. 1987. Geographic variation in social structure and behavior of *Aphelocoma ultramarina*. *Condor* 89:422-424.
- STRAHL, S. D., AND A. SCHMITZ. 1990. Hoatzins: cooperative breeding in a folivorous neotropical bird. Pp 131-156 in P. B. Stacey and W. D. Koenig (editors). *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge University Press, New York, NY.

- STUTCHBURY, B. J., AND R. J. ROBERTSON. 1986. Behavioral tactics of subadult female floaters in the Tree Swallow. *Behavioral Ecology and Sociobiology* 20:413-419.
- TRAIL, P. W., S. D. STRAHL, AND J. L. BROWN. 1981. Infanticide in relation to individual and flock histories in a communally breeding bird, the Mexican Jay (*Aphelocoma ultramarina*). *American Naturalist* 118:72-82.
- VAN BALEN, J. H. 1980. Population fluctuations of the Great Tit and feeding conditions in winter. *Ardea* 68:143-164.
- VAN BALEN, J. H., A. J. VAN NOORDWIJK, AND J. VISSER. 1987. Lifetime reproductive success and recruitment in two Great Tit populations. *Ardea* 75:1-10.
- VANDER WALL, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, IL.
- VANDER WALL, S. B., AND R. P. BALDA. 1977. Coadaptations of the Clark's Nutcracker and the piñon pine for efficient seed harvest and dispersal. *Ecological Monographs* 47:89-111.
- VARLEY, G. C., AND G. R. GRADWELL. 1960. Key factor analysis in population studies. *Journal of Animal Ecology* 29:399-401.
- VELTMAN, C. J. 1989. Flock, pair and group living lifestyles without cooperative breeding by Australian Magpies, *Gymnorhina tibicen*. *Ibis* 131:601-608.
- VERBEEK, N. A. M. 1970. The exploitation system of the Yellow-billed Magpie. Ph.D. dissertation. University of California, Berkeley, CA.
- VERBEEK, N. A. M. 1973. The exploitation system of the Yellow-billed Magpie. University of California Publications in Zoology 99:1-58.
- WAITE, T. A., AND D. STRICKLAND. 1997. Cooperative breeding in Gray Jays: philopatric offspring provision juvenile siblings. *Condor* 99:523-525.
- WAINIO, W. W., AND E. B. FORBES. 1941. The chemical composition of forest fruits and nuts from Pennsylvania. *Journal of Agricultural Research* 62:627-635.
- WALTERS, J. R. 1990. Red-cockaded Woodpeckers: a "primitive" cooperative breeder. Pp. 67-102 in P. B. Stacey and W. D. Koenig (editors). *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge University Press, New York, NY.
- WALTERS, J. R., C. K. COPEYON, AND J. H. CARTER, III. 1992b. A test of the ecological basis of cooperative breeding in Red-cockaded Woodpeckers. *Auk* 109:90-97.
- WALTERS, J. R., P. D. DOERR, AND J. H. CARTER, III. 1992a. Delayed dispersal and reproduction as a life-history tactic in cooperative breeders: fitness calculations from Red-cockaded Woodpeckers. *American Naturalist* 139:623-643.
- WASER, P. M. 1981. Sociality or territorial defense: the influence of resource renewal. *Behavioral Ecology and Sociobiology* 8:231-237.
- WASER, P. M. 1988. Resources, philopatry, and social interactions among mammals. Pp. 109-130 in C. Slobodchikoff (editor). *The ecology of social behavior*. Academic Press, New York, NY.
- WATSON, A. 1985. Social class, socially-induced loss, recruitment and breeding of Red Grouse. *Oecologia* 67:493-498.
- WATSON, A., AND R. MOSS. 1970. Dominance, spacing behavior and aggression in relation to population limitation in vertebrates. Pp. 167-218 in A. Watson (editor). *Animal populations in relation to their food resources*. Blackwell, Oxford, UK.
- WEBBER, T., AND J. L. BROWN. 1994. Natural history of the Unicolor Jay in Chiapas, Mexico. *Proceedings of the Western Foundation of Vertebrate Zoology* 5:135-160.
- WILLIAMS, P. L., AND W. D. KOENIG. 1980. Water dependence of birds in a temperate oak woodland. *Auk* 97:339-350.
- WOLGAST, L. J., AND B. B. STOUT. 1977. Effects of age, stand density, and fertilizer application on bear oak reproduction. *Journal of Wildlife Management* 41:685-691.
- WOOLFENDEN, G. E. 1974. Nesting and survival in a population of Florida Scrub Jays. *Living Bird* 12:25-49.
- WOOLFENDEN, G. E. 1975. Florida Scrub Jay helpers at the nest. *Auk* 92:1-15.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1977. Dominance in the Florida Scrub Jay. *Condor* 79:1-12.

- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1978. The inheritance of territory in group-breeding birds. *BioScience* 28:104-108.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. The Florida Scrub Jay: demography of a cooperative-breeding bird. Princeton University Press, Princeton, NJ.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1986. Sexual asymmetries in the life history of the Florida Scrub Jay. Pp. 87-107 in D. I. Rubenstein and R. W. Wrangham (editors). *Ecological aspects of social evolution*. Princeton University Press, Princeton, NJ.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1990. The Florida Scrub Jay: a synopsis after 18 years of study. Pp. 239-266 in P. B. Stacey and W. D. Koenig (editors). *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge University Press, New York, NY.
- ZACK, S. 1990. Coupling delayed breeding with short-distance dispersal in cooperatively breeding birds. *Ethology* 86:265-286.
- ZACK, S., AND J. D. LIGON. 1985a. Cooperative breeding in *Lanius* shrikes. I. Habitat and demography of two sympatric species. *Auk* 102:754-765.
- ZACK, S., AND J. D. LIGON. 1985b. Cooperative breeding in *Lanius* shrikes. II. Maintenance of group living in a nonsaturated habitat. *Auk* 102:766-773.
- ZACK, S., AND K. N. RABENOLD. 1989. Assessment, age and proximity in dispersal contests among cooperative wrens: field experiments. *Animal Behaviour* 38:235-247.

