

study of Hawaiian stilts on Oahu, and (4) show how dispersal information can be used for mitigation-site selection.

These results can be used not only for Hawaiian stilt management and conservation, but the general principles also are applicable to the other endangered waterbirds in Hawaii (Hawaiian coot *Fulica alai*, common moorhen [Hawaiian gallinule] *Gallinula chloropus sandvicensis*, and Hawaiian duck [koloa] *Anas wyvilliana*). These endangered endemic waterbirds often use habitat that exists in a similar pattern to that of the Hawaiian stilt, although some differences in water depth and salinity preferences exist in foraging and breeding site selection (Walker 1985, Engilis and Reid in press). Koloa and Hawaiian gallinule are more restricted in their habitat use, avoiding saline water (Walker 1985, Engilis and Reid in press). Regardless, the same principles should apply in modelling their population dynamics.

We thank C. Terry and M. Ueoka of the Hawaii Div. of Forest and Wildl., the Commander of the Kaneohe Marine Corps Air Station, J. Beall of the U. S. Fish and Wild. Serv., and F. Kuailani of the National Park Service for access to protected wetlands. This manuscript benefitted from reviews by J. A. R. Alberico, R. A. Coleman, D. J. Delehanty, A. Engilis, Jr., F. A. Reid, and B. Valentine. Research was funded by a National Science Foundation EPSCoR grant to North Dakota. This is Contribution No. 005 of the Nevada Biodiversity Initiative.

DISPERSAL AND PERSISTENCE IN METAPOPOPULATIONS

A central concept of metapopulation theory is that a local population can be maintained even if its intrinsic growth rate (λ) is less than one (Fig. 1) (Brown and Kodric-Brown 1977, Pulliam 1988, Stacey and Taper 1992). However, at least one population in the metapopulation complex must be more than self sustaining ($\lambda > 1.0$) for the metapopulation to persist (Wu et al. 1993). The underlying factor driving the dynamics of metapopulation models is dispersal (Gadgil 1971, Hansson 1991, Harrison 1991, Davis and Howe 1992, Gonzalez-Andujar and Perry 1993, Wu et al. 1993). Specifically, colonization and local population persistence when $\lambda < 1.0$ are products of immigration from other populations (Fig. 2).

There are three critical dispersal questions for metapopulation dynamics: (1) Who leaves?, (2) Where do they go?, and (3) What do they do when they get

there? The importance of the third question is that dispersed animals that do not breed are treated differently in a population model than those that breed. In the following sections, we present information about the second question for Hawaiian stilts; the first and third questions have never been addressed for this species.

HISTORIC DATA ON HAWAIIAN STILT DISPERSAL

Direct and indirect observations indicate that stilts are able to disperse from one population to another. In several studies, Hawaiian stilts (mostly adults) were color-banded or marked with dyes in order to quantify movement. Telfer (1972) marked 20 adult stilts with dye, and noted that one bird moved 32 km before the dye faded. Stilts appeared to move among habitats independently of other stilts, although this was not specifically tested. Eleven other marked birds were recorded as not being seen elsewhere (Telfer 1973). In a subsequent study, Telfer and Burr (1978) marked twenty-three birds on Kauai and Oahu, and noted their subsequent movement. Of the 18 birds subsequently seen, 15 were ≤ 5 km from the release site, two moved 33.8 km, and one moved to another island (from Hanalei, Kauai to Waiawa, Oahu; 186 km, 3 months later). These authors also noted that a bird marked in Kanaha, Maui in 1968 was seen in Kahuku, Oahu (182 km) three months later.

Other records bring the total to four observations of individually-marked individuals moving among islands (not including seasonal movement between Kauai and Niihau). Of 110 birds banded on Oahu during Coleman's (1981) research on the species, one was resighted on Molokai five months later, and one on Maui six months later. Most banded birds stayed at the banding site, but one juvenile moved 35 km within three days of banding (Telfer and Burr 1979).

Stilts aggregate at freshly flooded fields, apparently because they provide good feeding sites (Telfer 1971, JMR and MS pers. obs.). This type of movement has been observed for shorebirds in other wetlands, such as marbled godwits (*Limosa fedoa*) in the North American prairies (Ryan et al. 1984). Hawaiian stilts frequent roost sites away from feeding areas, and night flight is common (Telfer 1971). The change in stilt numbers noted in repeated censuses of birds at ponds on a single island indicates movement among wetlands (e.g., Bachman et al. 1982, 1983, Paton et al. 1985). Seasonal censuses show that the stilt populations on Niihau and Kauai are related, and birds move between

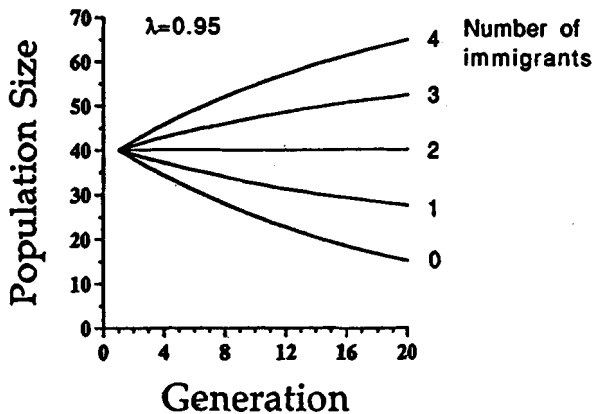


Figure 1. Change in population size over time, given different immigration rates, for a population that is not replacing itself ($\lambda = 0.95$).

these islands in response to seasonal changes in water availability (Telfer 1972, 1974, Engilis and Pratt 1993).

These observations underestimate dispersal because only a subset of dispersers were found. This is partly due to the increased area that needs to be searched for dispersers (Barrowclough 1978), and to the relatively limited time and personnel available for searching.

CURRENT STUDY OF HAWAIIAN STILT DISPERSAL

For the past two years, we have individually marked Hawaiian stilt chicks on several islands, but most work has concentrated on Oahu. Banding was done to examine dispersal. We selected Oahu for concerted effort because its distribution of wetlands and Hawaiian stilt breeding aggregations (Fig. 3) is ideal for metapopulation interactions, and because of the opportunity for regular monitoring. In 1992 and 1993, we banded Hawaiian stilt chicks with a U.S. Fish and Wildlife aluminum band, and three UV-stable plastic (darvic) colored leg bands to allow individual identification. All banding was done above the tibiotarsal-metatarsal ("knee") joint. These birds have been regularly monitored since banding, and here we present preliminary dispersal results. These sightings are cumulative through 10 December, 1993.

We resighted 25 individually marked birds with 134 total observations of marked birds. Most were

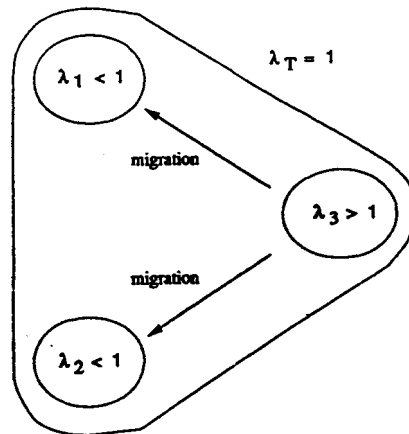


Figure 2. A schematic of a stable metapopulation with two populations that are not replacing themselves (sinks) and one that is overproducing (source), providing immigrants for the other populations.

resighted from June to December, 1993, when a concerted effort was made to survey banded birds. At the Ki'i complex of the James Campbell National Wildlife Refuge, juveniles moved regularly among ponds, including the adjacent shrimp-farm ponds. This is a complex of over 140 ponds, each separated by a dirt road from the next two to eight ponds, depending on location (i.e., terminal versus interior pond). These movements were not normally greater than a few hundred meters, and most (>90%) birds stayed on the same pond on which they were banded.

We resighted few individuals at 10 months or greater after banding. These observations, however, provide some interesting information. Five of seven have been repeatedly resighted in their ponds of origin, even after 16 months for some individuals. Two moved substantial distances on Oahu. One bird moved 12 km within three months of banding and stayed there for the next 7.5 months after which it was not seen. We have no records yet of inter-island movement. The second bird moved 29 km. The fates of these birds is not known with respect to breeding potential because none of our banded birds have reached typical breeding age (≥ 2 years old, although breeding at age one has been observed, JMR pers. obs.).

METAPOPULATION MODELS AND MITIGATION

An important application of metapopulation

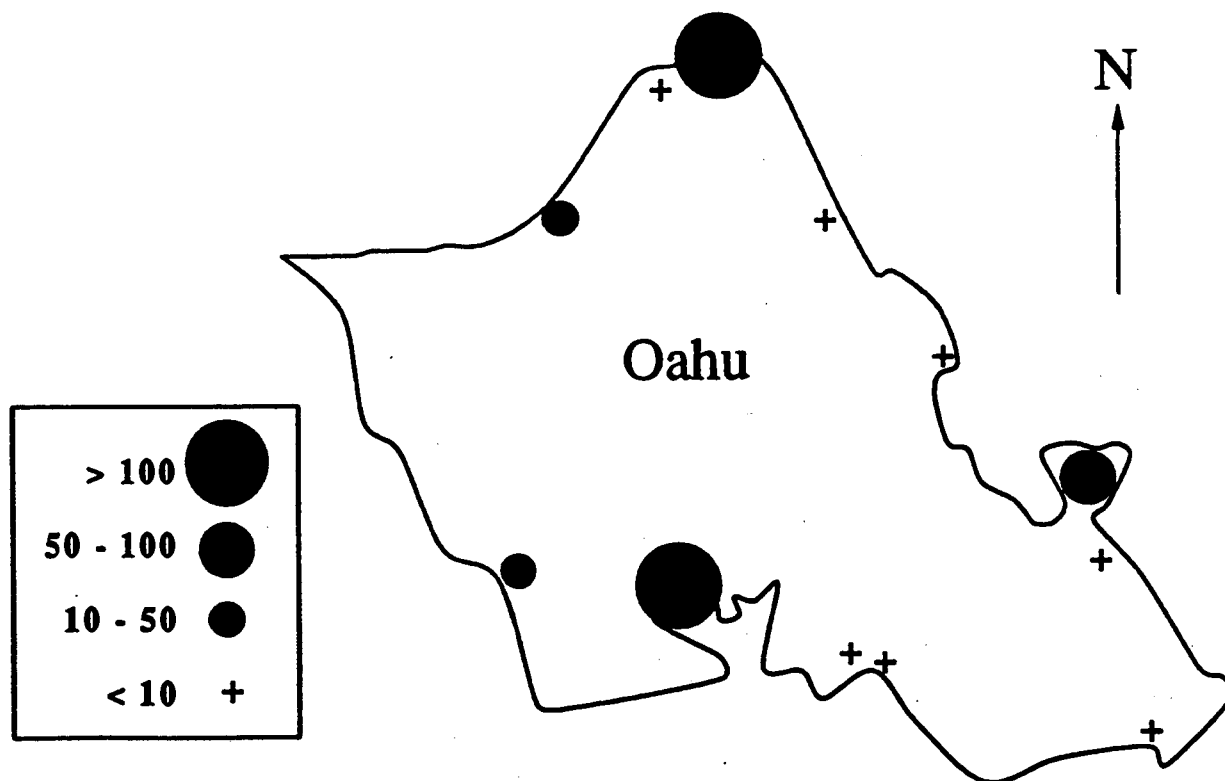


Figure 3. Number of Hawaiian stilts seen at different sites on Oahu during the 1984 Fall census (Buchman et al. 1985).

models to species conservation is in selecting restoration and mitigation sites. In Hawaii, wetlands are being lost rapidly. In the United States, legal mechanisms require that wetlands be built to mitigate natural wetlands loss (Clean Water Act, 33 U.S.C. 466 et seq., Section 404, U.S., Department of Army and Environmental Protection Agency Cooperating, Memorandum of Agreement, February 6, 1990). Restored or replacement wetlands are supposed to perform similar functions to those of destroyed wetlands (Sparrowe et al. 1989). In the following discussions of metapopulation dynamics, we consider only one aspect of mitigation, that of stilt use of habitat. Many other species and environmental issues also are at stake during mitigation.

There are two important concepts that should be kept in mind during discussions of wetland mitigation. (1) Avoidance of wetland loss usually is the best alternative in habitat planning. Mitigation, and the methods discussed below, should not be assumed to be able to make situations better than their current state. (2) Mitigation-site selection in upland sites might be inherently inferior to natural lowland sites currently and historically occupied by stilts. Because of this,

mitigation in the form of restoring overgrown lowland sites is preferable to creating new upland sites. The methods discussed below apply equally well to wetland restoration or creation.

Metapopulation models can be used to anticipate the relative benefits to endangered waterbirds of the restoration or development of different sites, in order to evaluate which site would best fulfill this directive. The converse question also can be addressed: What are the consequences of wetland loss to an island's population? With increased fragmentation and insularization, local extinction will increase (Whitcomb et al. 1981, Wilcove 1985, Wilcox and Murphy 1985, Wilcove et al. 1986, Quinn and Hastings 1987, Burkey 1989, Newmark 1991, Saunders et al. 1991). Therefore, these models can be used to predict the potential results of changes in management practices that disrupt local metapopulation structure.

Aside from the intrinsic ability of a potential mitigation site to support stilts, which is determined by size, habitat quality, food base, presence of predators, etc., other factors may be important in site selection. These factors include proximity to other wetlands

(location), physical orientation, and the behavior of dispersing birds. Location is the most obvious of these. Mitigation sites that might connect larger breeding populations would be preferred to sites with low connectedness (Fig. 4). One tool for site selection would be to use metapopulation dynamic modelling to compare the expected effects of different mitigation sites. A potential mitigation site can be treated in a model as an "empty patch" that becomes colonized, or as a conduit between larger patches. We hypothesize dispersal routes for stilts among wetlands on Oahu (Fig. 5). If accurate, mitigation sites along these routes should facilitate dispersal. This hypothesis is easily tested by monitoring their effectiveness (Murphy and Noon 1992, Wiens et al. 1993).

If stilts disperse without knowing the location of the next wetland, the orientation of new wetlands can be important (Gutzwiller and Anderson 1992). For example, wetlands that present their broad side to dispersing birds might be encountered more often than sites that do not. The behavior of dispersing birds also will affect dispersal. Birds often wander, doing reconnaissance for potential breeding sites (e.g., Zicus and Hennes 1989, Reed and Oring 1992, Reed and Dobson 1993, and references therein). Naive birds might follow experienced birds to other wetlands, or they might follow geographic cues. Knowing the mechanism(s) regulating dispersal can aid in selecting mitigation sites.

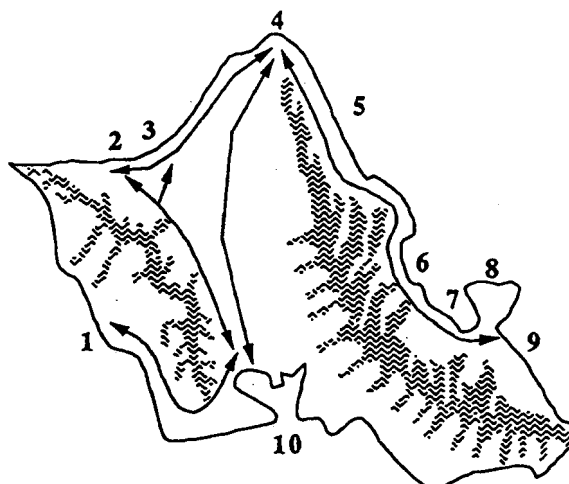


Figure 5. Hypothetical dispersal routes among the major wetland sites on Oahu. Numbers correspond to those in Engilis and Reid (in press); hatched marks indicate mountains.

DISCUSSION

Hawaiian stilts appear to exist as a metapopulation, or set of metapopulations among islands, but how much sub-populations affect their neighbor's population dynamics is unknown. The picture arising from the research presented here is that Hawaiian stilts are capable of long-distance movements, but they usually do not move except to take advantage of sudden resource availability. Even then, the moves can be temporary. Therefore, the potential for affecting the dynamics of other populations exists, but might be infrequently realized. Early studies of Hawaiian stilt dispersal used temporary marking, or lacked individual marking so movements later in life and the permanence of observed movements was not discernable. In addition, the fates of the dispersers was not known. Individuals that enter the breeding pool can have a strong impact on local populations, unlike those that merely move and do not breed.

Also unknown for Hawaiian stilts are the sex ratios of dispersers, the conditions under which birds disperse or settle, and the differences in juvenile and adult dispersal patterns. Most dispersal studies on Hawaiian stilts to date have concentrated on adult dispersal; juvenile dispersal typically exceeds adult dispersal in

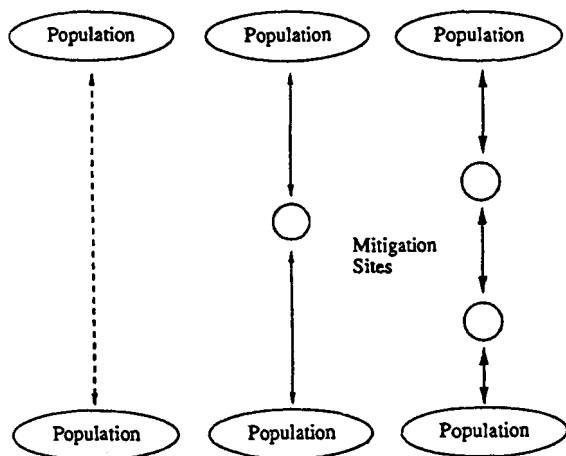


Figure 4. A schematic of the potential effect of mitigation sites between two populations. Double-arrow intensity is correlated with the rate of individual exchange.

other avian species (Rockwell and Barrowclough 1987). All of these factors affect population dynamics (e.g., Smith and Peacock 1990, Reed and Dobson 1993), and therefore management options. As a consequence, gathering data on Hawaiian stilt dispersal has a high priority.

A priori experiments (Wiens et al. 1993) on wetland selection for restoration and mitigation are difficult. Because of this, the methods discussed here can be used to make educated decisions on site selection. It is important to reiterate that avoiding wetland loss usually is the best alternative in habitat planning, and that mitigation in the form of restoring overgrown lowland sites probably is preferable to creating new upland sites. These are the sites historically used by stilts and they probably still retain some basic wetland attributes that might be difficult or impossible to duplicate. In addition, restored or created wetlands for conservation or mitigation should be monitored to determine if they are functioning as intended for the target species. Monitoring these wetlands should involve more than simple censuses - knowing reproductive success and recruitment are critical for site evaluation.

It is possible that the limited dispersal observed for stilts is due to wetland availability. Most research on Hawaiian stilts has occurred, and continues to occur, in artificially managed wetlands. Because these wetlands are managed for water depth (Walker 1985, Engilis and Reid in press) they are available for longer periods of time than would natural wetlands. Because of this, dispersal data might be biased towards managed wetlands. However, because adequate wetlands are in short supply, managed wetlands will probably always exist in Hawaii. This means our results should accurately reflect at least the short-term future for Hawaii.

Our work on Hawaiian stilts might be directly applicable as a preliminary model for the other three endangered Hawaiian waterbirds. These endangered endemics often use the same wetland complexes as Hawaiian stilts, but even less is known about their biology (Walker 1985, Chang 1990). In addition, the metapopulation models could be applicable to insular birds worldwide, particularly waterbirds, such as the endangered black stilt (*Himantopus novaezealandiae*) of New Zealand.

LITERATURE CITED

- Bachman, R.E., M.L. Ueoka, R.S. Saito, and T.C. Telfer. 1982. Surveys and inventories of waterbirds and their habitats in the state of Hawaii. Prog. Rep., Job No. R-III-A, Proj. No. W-18-R-6. Div. Forest. Wildl., Honolulu. 30 pp.
- Bachman, R.E., M.L. Ueoka, R.S. Saito, T.C. Telfer, M.P. Morin, T. Sutterfield, R.L. Walker, and L.K. Lankgraf. 1985. Surveys and inventories of waterbirds in the state of Hawaii. Prog. Rep., Job No. R-III-A, Proj. No. W-18-R-9. Div. Forest. Wildl., Honolulu. 66 pp.
- Barrowclough, G.F. 1978. Sampling bias in dispersal studies based on finite area. *Bird-Banding* 49:333-341.
- Brown, J.H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445-449.
- Burkey, T.V. 1989. Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments. *Oikos* 55:75-81.
- Chang, P.R. 1990. Strategies for managing endangered waterbirds on Hawaiian national wildlife refuges. M.S. Thesis. Univ. of Massachusetts.
- Coleman, R.A. 1981. The reproductive biology of the Hawaiian subspecies of the black-necked stilt, *Himantopus mexicanus knudseni*. Unpubl. Ph.D. Dissert., Pennsylvania State Univ., State College. 106 pp.
- Davis, G.J., and R.W. Howe. 1992. Juvenile dispersal, limited breeding sites, and the dynamics of metapopulations. *Theor. Pop. Biol.* 41:184-207.
- den Boer, P.J. 1990. The survival value of dispersal in terrestrial arthropods. *Biol. Conserv.* 54:175-192.
- Engilis, A., Jr., and F.A. Reid. 1994. Hawaiian waterbirds recovery plan, 3rd ed. U.S. Fish and Wildl. Serv., Portland, OR. In press.
- Engilis, A., Jr., and T.K. Pratt. 1993. Status and population trends of Hawaii's native waterbirds, 1977-1987. *Wilson Bull.* 105:142-158.
- Gadgil, M. 1971. Dispersal: population consequences and evolution. *Ecology* 52:253-261.
- Gonzalez-Andujar, J.L., and J.N. Perry. 1993. Chaos, metapopulations and dispersal. *Ecol. Modelling* 65:255-263.
- Goodman, D. 1987. The demography of chance extinction. Pages 11-34 *In* M. Soulé, ed. *Viable Populations for Conservation*. Cambridge Univ. Press, Cambridge, U.K.

- Waterfowl in North America. Texas Tech. Univ. Press, Lubbock, Texas. 560 pp.
- Stacey, P.B., and M. Taper. 1992. Environmental variation and the persistence of small populations. *Ecol. Appl.* 2:18-29.
- Telfer, T.C. 1971. Field investigation of native Hawaiian waterbirds on the island of Kauai (S.I.). Progress Report, Job No. VIII-C (1), Project No. W-15-1. Div. Forest. Wildl., Honolulu. 9 pp.
- _____. 1972. Field investigation of native Hawaiian waterbirds on the island of Kauai (S.I.). Progress Report, Job No. VIII-C (2), Project No. W-15-2. Div. Forest. Wildl., Honolulu. 11 pp.
- _____. 1973. Field investigation of native Hawaiian waterbirds on the island of Kauai (S.I.). Progress Report, Job No. VIII-C (2), Project No. W-15-3. Div. Forest. Wildl., Honolulu. 8 pp.
- _____. 1974. Field investigation of native Hawaiian waterbirds on the island of Kauai (S.I.). Progress Report, Job No. VIII-C (4), Project No. W-15-4. Div. Forest. Wildl., Honolulu. 8 pp.
- Telfer, T.C., and T.A. Burr. 1979. Description of waterbird habitats as related to food availability and feeding behavior of endangered waterbird species on the islands of Kauai and Oahu. Progress Report, Job No. R-III-D, Project No. W-18-R-4. Div. Forest. Wildl., Honolulu. 22 pp.
- _____. 1978. Description of waterbird habitats as related to food availability and feeding behavior of endangered waterbird species on the islands of Kauai and Oahu. Progress Report, Job No. R-III-D, Project No. W-18-R-3. Div. Forest. Wildl., Honolulu. 35 pp.
- Walker, R. L. 1985. Hawaiian waterbirds recovery plan, 2nd ed. U. S. Fish and Wildl. Serv., Portland, OR. 99 pp.
- Whitcomb, R.F., C.S. Robbins, J.F. Lynch, B.L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-205, *In* R.L. Burgess and D.M. Sharpe, eds. *Forest Island Dynamics in Man-dominated Landscapes*. Springer-Verlag, New York.
- Wiens, J.A., N.Chr. Stenseth, B. Van Horne, and R.A. Ims. 1993. Ecological mechanisms and landscape ecology. *Oikos* 66:369-380.
- Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.
- Wilcove, D.S., C.H. McLellan, and A.P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237-246 *In* M. Soulé, ed. *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Assoc., Sunderland, Mass.
- Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *Amer. Natur.* 125:879-887.
- Wu, J., J.L. Vankat, and Y. Barlas. 1993. Effects of patch connectivity and arrangement on animal metapopulation dynamics: a simulation study. *Ecol. Modelling* 65:221-254.
- Zicus, M.C., and S.K. Hennes. 1989. Nest prospecting by common goldeneyes. *Condor* 91:807-812.