

Incorporating Effects of Natural Disturbances in Managed Ecosystems

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Abstract — We briefly review the effects of climate (particularly drought and hurricanes), insect outbreaks, and fire on populations of migrant birds. An important feature of all of these natural disturbances is that they occur over a variety of spatial and temporal scales, thus precluding any simple generalization of their effects or of methods for mitigating those effects. We recognize that (1) natural catastrophic phenomena will inevitably occur; (2) an ecosystem will consist of a mosaic of patches that reflects the recurrence time and spatial extent of these disturbances; and (3) after some period a disturbed patch will recover. We therefore recommend that an appropriate goal is to have as a management unit a sufficiently large area (not necessarily contiguous) to contain some minimum number of patches that will be in a recovered state. This "incorporation" of disturbance is facilitated by increasing the size of the management unit or altering the size and/or frequency of disturbance. We suggest that the most pressing research need is to determine the characteristic scale of disturbances that are important and relevant to the species and habitats that we have an interest in preserving.

INTRODUCTION

Populations of migrant birds are affected by natural changes in weather, climate, and habitat, and by unpredictable events like drought, hurricanes, fire, and insect infestations. In this chapter we briefly review the effects of potentially "catastrophic" natural events on bird populations and discuss methods for managing, or at least mitigating, those effects. As natural phenomena, these

events are integral features of every ecosystem (more frequent in some than in others), and coping with their occurrence in any managed ecosystem is not a question of "if" they occur, but of "when." The effects of these events on populations of neotropical migrant birds are discussed in greater detail in Rotenberry et al. (1993).

Although there is obviously a great diversity of potential natural disasters, we restrict our discussion to three major classes - climate (particularly drought and hurricanes), insect outbreaks, and fire. Unfortunately, generalization about these events and their effects is complicated by the strong interrelationships among them. For example, periods of extended drought are often associated with both an increased likelihood of fires and epidemic outbreaks of insects (e.g., Mattson and Haack 1987). Likewise, insect outbreaks contribute to the development of a fuel complex that makes fires more probable (Knight 1987), and, in turn, trees scarred by fire serve as epicenters for outbreaks of insects (Knight and Wallace 1989 and references

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therein). Finally, changes in vegetation cover, particularly the loss of vegetation due to fire or infestation, may affect regional patterns of climate, especially precipitation (e.g., Shukla et al. 1990).

CLIMATE

One of the salient features about climate is that variation in weather can be expressed over a variety of spatial and temporal scales (Michaels and Hayden 1987). Drought, for example, is only manifest over a period of months or even years, whereas a tropical storm may intensify to hurricane strength, make landfall, then dissipate within a week. Likewise, climatic effects on birds can also be observed over extremes of scales. There is ample evidence for the effects of drought on bird populations, and these effects may extend over tens of thousands of square kilometers (e.g., DeSante 1992). Although some individuals die of water stress, in most cases the effects are indirect, mediated through the direct effects of water scarcity on food availability and habitat suitability (Smith 1982, George et al. 1992). During the breeding season, drought effects are particularly manifest in reproductive success (e.g., Marr and Raitt 1983, Petersen et al. 1986, Rotenberry and Wiens 1991, George et al. 1992). In contrast to the large scale effects of drought, a single hailstorm may arise in a few hours on a hot afternoon, and the resulting pounding may destroy all open nests within a few tens of hectares. During the non-breeding season, average annual rainfall influences overall neotropical migrant abundance, particularly in the Caribbean, with relatively drier areas, whether scrub or forest habitat, having consistently lower numbers of individuals (Wunderle and Waide 1992, Terborgh and Faaborg 1980, Askins et al. 1992). The most obvious management strategy to lessen the impact of drought on wintering migrants in the Caribbean is to preserve moist and mesic forests, particularly in drought-prone regions.

Hurricanes also cause declines in wintering or passage migrants in the southeastern U.S. and Caribbean (e.g., Walkinshaw 1983, Hamel 1986). Since most hurricanes occur early in the migratory period, migrant birds are not likely to suffer directly from hurricanes, but are more likely to suffer from secondary effects, which often involve massive habitat alteration (Wunderle et al. 1992). Furthermore, this alteration has a disproportionate impact on certain foraging guilds, especially frugivores and nectar feeders. The most effective mitigation strategies involve habitat corridors between montane forest reserves, which are especially susceptible to storm damage, and lowland forest reserves to which montane forest inhabitants can migrate after hurricanes (Wunderle 1990, Waide 1991). Lowland vegetation, because of its rapid growth rate, can recover faster than montane vegetation, and thus can serve as refugia for montane species in a storm's aftermath.

INSECT OUTBREAKS

Whereas the effect of the habitat destruction wrought by a hurricane can from most perspectives be viewed as a catastrophe, the effects of other forms of potential disturbance on birds may be much more equivocal. For example, most neotropical migratory birds inhabiting eastern forests are insectivorous during the breeding season. It is, therefore, not surprising that many species of neotropical migrants increase in both density and productivity in response to outbreaks of defoliating caterpillars (e.g., Morris et al. 1958, Zach and Falls 1975, Morse 1978, Sealy 1979, Holmes et al. 1986, Crawford and Jennings 1989). Fluctuations in abundance of caterpillars accounted for some major fluctuations in bird populations observed by Holmes and his colleagues in New Hampshire (Holmes et al. 1986). Low caterpillar densities apparently caused poor reproductive success and low survival of several species, and led Holmes and his colleagues to suggest that birds at their site were normally food limited except during caterpillar outbreaks, when release from food limitation occurred. Insect outbreaks may also affect birds negatively, however, in that excessive tree mortality caused by an insect outbreak may decrease overall habitat suitability for some species, and further contribute to increasing edge habitat in temperate forests. Also, the primary method of managing outbreaks of serious forest pests is pesticide application, which has deleterious effects on birds, especially when applied over thousands of hectares. In general, the question of how management of forest insect pests affects populations of neotropical migratory birds has hardly been addressed. Of particular concern is the gypsy moth (*Lymantria dispar*), an introduced species still expanding its range into the Southeast and Midwest. It can have a serious impact on habitat quality (e.g., Thurber 1992), and is not a major prey item for many bird species (Smith 1985). Fortunately, there are silvicultural alternatives to pesticides that are effective in simultaneously managing for forest birds and insect pests.

FIRE

Historically, fires were common on the prairies of North America and in the coniferous forests of the Southeast. In many ecosystems fire normally occurs with sufficient frequency that both plants and animals are well-adapted to its passage; indeed, some species may require fire-maintained vegetation or habitat for their continued existence (Van Lear and Waldrop 1989). Fires may maintain openings within forests that may be important to birds (Taylor and Taylor 1979). Fire suppression activities can retard the natural frequency of burns in such systems, which may in turn adversely affect those species whose persistence depends on its periodic occurrence (e.g., Mayfield 1960, Remsen 1986).

Fire can have many impacts upon an ecosystem, including changes in local climate and microclimatic conditions, composition and structure of the vegetation, and animal

abundances and distributions (Bendell 1974). Fires may vary in intensity, duration, frequency, location, shape, and extent, and effects may differ with season, nature of fuel, and properties of the site and soil. Because of the wide variation that occurs in fires and their effects, it has been difficult to generalize about the relationship between fire and birds (Bendell 1974, Sousa 1984). However, Wright and Bailey (1982) summarized results of several studies and presented a list of birds, many of which are neotropical migrants, that are favored by open plant communities caused by fires and those that are more common in unburned areas. More recently, regional reviews and computer simulations of impacts of fire on bird communities have appeared (e.g., Landers 1987, Kerpez and Stauffer 1989, McMahon and Calestra 1990). The results of these studies are described more fully in Rotenberry et al. (1993).

After humans arrived in North America, the use of fire, both purposefully and carelessly (Smith and Petit 1988) greatly intensified its effects and frequency, particularly in grasslands (Wright and Bailey 1982) and coniferous forests (Van Lear and Waldrop 1989, Baker 1992). Currently, both prescribed burning and suppression of natural fires are important management tools (Wade and Lundsford 1990). In some instances, prescribed burning may mimic the effects of naturally occurring fires, while in others, effects of wildfires may be quite different from prescribed burning (Baker 1992). When wildfires do occur after a long period of fire suppression, as a result of extra fuel buildup they may escape to burn a larger area and at a greater intensity than they would otherwise, transforming a normal ecological event into a catastrophe. For example, high intensity canopy fires probably occurred less frequently before settlement of the western United States (Baker 1992), but those kinds of fires can have a great impact on the structure of the post-fire bird community (R. Hutto, unpubl. data).

Even under a normal fire regime, local habitat conditions are altered, and may become temporarily unsuitable for some species (Wright and Bailey 1982). Additionally, fire may enhance the invasion of exotic plant species, such as cheatgrass (*Bromus tectorum*) in Great Basin shrubsteppe, which may in turn prevent the normal post-fire successional pathway or recovery process (e.g., West 1979). Unfortunately, our review (Rotenberry et al. 1993) indicates a lack of many long term controlled studies of the effects on passerine birds of fire frequency, habitat type, timing, and weather conditions, all important considerations in developing a burn prescription (Stoddard 1962).

MANAGEMENT ISSUES

Each of these phenomena has the ability to alter the number of individuals present in a local or regional population of birds, either through direct effects on survivorship, or indirectly by modifying the abundance of prey and/or suitable habitat. While these phenomena are often viewed from a human perspective as catastrophes, their effects on birds may be either positive or

negative. It is difficult to determine, however, the degree to which this represents a natural "regulation" of population size (Sherry and Holmes 1992). In the case of large scale climatic patterns (as opposed to localized "disasters"), the answer is almost trivially "yes" - species do not occur where the climate is routinely unfavorable for their particular life history and physiology, or creates a habitat type to which they are not adapted. To the extent that a species is dependent upon a fire-maintained habitat type or any "sub-climax" or early successional habitat, then its distribution, if not its actual population size, is regulated by fire or disturbance.

Perhaps more important from the perspective of a land manager charged with the responsibility of preserving a particular species or habitat type is not whether a population's abundance is "regulated" by some particular disturbance, but whether such a disturbance could cause the extinction of that population. Such can clearly be the case, for the local extinction of several species of terrestrial island birds in the Caribbean due to the passage of hurricanes has been documented (Raffaele 1977, Hamel 1986, Wauer and Wunderle 1992). Indeed, we may have just lost 5-6 species of Hawaiian Islands endemics, whose last known populations (most less than 50 individuals; Scott et al. 1986) occurred in the Alakai Swamp on Kauai, just devastated by Hurricane Iniki on 11 September 1992.

Apart from the shop-worn observation that smaller populations are more at risk than larger ones, theoretical predictions of the effects of disturbances on populations are few. We would like to provide a more general model of managing for disturbance based on emerging theory from landscape ecology (e.g., Forman and Godron 1985, Turner 1986, Urban et al. 1987), part of the "new paradigm" in ecology described by Maurer (Maurer et al., this volume). We recognize that certain natural phenomena that adversely affect bird populations will inevitably occur even in the most intensively managed ecosystem, and that these phenomena tend to occur over characteristic spatial and temporal scales (e.g., Michaels and Hayden 1987). We further recognize that these ecosystems will (or should) consist of a mosaic of patch types (of an average size reflecting the characteristic spatial scale of the disturbance), and that these patch types will vary depending on the time since last disturbance - after some period of time, depending on the type of disturbance, a patch will "recover," or be returned to its pre-disturbance state (assuming it is possible to do so). The goal is to have as a managed ecosystem a sufficiently large area (not necessarily contiguous) to contain some minimum number of patches (i.e., some minimum area, which will depend on the life history of the species of management interest) that will be in a recovered state. In other words, the disturbance is "incorporated" as a natural part of the managed ecosystem (Urban et al. 1987). Not only should this provide protection for species characteristic of undisturbed or recovered areas, but allows for the persistence of other species that may depend upon disturbed areas or ecotones.

In the simplest case, incorporation can be passive - a disturbance is incorporated simply by increasing the size of the managed unit (Urban et al. 1987). The management question is whether a particular region such as a park, a reserve, a Forest District, or a Management Area is of sufficient scale to incorporate a given disturbance. A rule of thumb relevant to habitats containing neotropical migrants has been developed from forest simulation modelling, which suggests that the focal area should be about 50 times the average size of the disturbance of interest (Shugart and West 1981). A managed landscape that is large enough to incorporate the factors that disturb its component patches will have a constant frequency distribution of patches of all types at all times; this is called an "equilibrating landscape" (Shugart and West 1981). A smaller "nonequilibrating landscape" is unable to incorporate a disturbance and has a transient frequency distribution of patch types, which changes in response to each disturbance event.

Perhaps the greatest effect of humans on landscapes has been to rescale patterns in time and space (Urban et al 1987). Most important, the size of managed landscapes has been reduced via habitat fragmentation, rendering them less able to incorporate natural disturbances of a given size and/or frequency. Less apparent has been the inadvertent increase in the size of otherwise "natural" disturbances, as in the control of fire (see above). By increasing the size of fires, humans may transform an equilibrial landscape into a nonequilibrating one, even with no alteration of the size of the managed ecosystem. Another example is the establishment of forest plantation monocultures, such as southern pines, which are not only more susceptible to pine beetle infestations (a species of relatively low palatability to birds), but also spread those impacts over a larger area.

In many cases, increasing the size of a management unit will not be feasible. Nonetheless options do exist to reduce the size of natural disturbances. As an example, a land manager could prescribe numerous small burns in a bounded area that has been reduced in size and has become thereby more susceptible to larger natural fires (Urban et al. 1987). In this case, block or patch burning may be better than one large burn (Givens 1962). Wright and Bailey (1982) thought that the most important concern for maximizing diversity was to have a wide variety of relatively small different-aged burns interspersed among areas that had not been burned for several hundred years. Wildfires deemed likely to cause excessive damage can be actively suppressed. Likewise, rather than attempting to eradicate a pest infestation throughout its entire extent, insect suppression activities could be concentrated at the periphery of the outbreak, limiting its spread. An integrated approach involving several pest management techniques should produce a landscape with a relatively small area of highly disturbed habitat. Although changing disturbance patch sizes may not restore a landscape to its original mosaic pattern (Baker 1992), it may nonetheless achieve a dynamic equilibrium. Clearly, the most pressing research need is to determine the scale of disturbances that are important and relevant to the species and habitats that we have an interest in preserving.

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LITERATURE CITED

- Askins, R.A., D.N. Ewert, and R.L. Norton. 1992. Abundance of wintering migrants in fragmented and continuous forests in the U.S. Virgin Islands. Pp. 197-206 in J.M. Hagen and D.W. Johnson (eds). Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C.
- Baker, W.L. 1992. Effects of settlement and fire suppression on landscape structure. *Ecology* 73:1879-1887.
- Bendell, J. F. 1974. Effects of fire on birds and mammals. Pp. 73-138 in T. T. Kozlowski and C. E. Ahlgeren (eds.). Fire and Ecosystems. Academic Press, New York.
- Crawford, H. S., and D. T. Jennings. 1989. Predation by birds on spruce budworm *Choristoneura fumiferana*: functional, numerical, and total responses. *Ecology* 70:152-163.
- DeSante, D. 1992. The Monitoring Avian Productivity and Survivorship (MAPS) program: overview and progress. This volume.
- Forman, R.T.T., and M. Godron. 1986. Landscape ecology. John Wiley and Sons, New York, NY.
- George, T.L., A.C. Fowler, R.L. Knight, and L.C. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. *Ecol. Appl.* 2:275-284.
- Givens, L. S. 1962. Use of fire on southeastern wildlife refuges. Tall Timbers Fire Ecol. Conf. 1:121-126.
- Hamel, P.B. 1986. Bachman's Warbler: a species in peril. Smithsonian Institution Press, Washington, D.C.
- Holmes, R. T., T. W. Sherry, and F. W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. *Ecol. Monogr.* 56:201-220.
- Kerpez, T. A. and D. F. Stauffer. 1989. Avian communities of pine-hardwood forests in the southeast: characteristics, management, and modeling. Pp. 156-168 in T.A. Waldrop (ed.). Proceedings of pine-hardwood mixtures: a symposium on management and ecology of the type. U.S.D.A. For. Serv. Gen. Tech. Rep. SE-58.
- Knight, D.H. 1987. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. Pp. 59-83 in M.G. Turner (ed.). Landscape heterogeneity and disturbance. Springer-Verlag, Berlin.
- Knight, D.H., and L.L. Wallace. 1989. The Yellowstone fires: issues in landscape ecology. *Bioscience* 39:700-706.

- Landers, J. L. 1987. Prescribed burning for managing wildlife in southeastern pine forests. Pp. 19-27 in J. G. Dickson and O. E. Maugh (eds.). Managing southern forests for wildlife and fish -- a proceedings. U.S.D.A. For. Serv. Gen. Tech. Rep. SO-65.
- Marr, T.G., and R.J. Raitt. 1983. Annual variations in patterns of reproduction of the Cactus Wren (*Campylorhynchus brunneicapillus*). Southwest. Natur. 28:149-156.
- Mattson, W.J., and R.A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. Bioscience 37:110-118.
- Maurer, B., F. Samson, and F. Knopf. 1992. Biological diversity, ecological integrity, and neotropical migrants: new perspectives for wildlife management. This volume.
- Mayfield, H.F. 1960. The Kirtland's Warbler. Bull. Cranbrook Inst. Sci. 40:1-242.
- McMahon, T. E. and D. S. de Calesta. 1990. Effects of fire on fish and wildlife. Pp. 233-250 in J. D. Walstad, S. R. Radosevich, and D. V. Sandberg (eds.). Natural and prescribed fire in Pacific Northwest forests. Oregon State Univ. Press, Corvallis.
- Michaels, P.J., and B.P. Hayden. 1987. Modeling the climate dynamics of tree death. Bioscience 37:603-610.
- Morris, R. F., W. F. Cheshire, C. A. Miller, and D. G. Mott. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. Ecology 39:487-494.
- Morse, D. H. 1978. Populations of bay-breasted and Cape May warblers during an outbreak of the spruce budworm. Wilson Bull. 90:404-413.
- Petersen, K.L., L.B. Best, and B.M. Winter. 1986. Growth of nestling Sage Sparrows and Brewer's Sparrows. Wilson Bull. 98:535-546.
- Raffaele, H.A. 1977. Comments on the extinction of *Loxigilla portoricensis grandis* in St. Kitts, Lesser Antilles. Condor 79:389-390.
- Remsen, J. V., Jr. 1986. Was Bachman's Warbler a bamboo specialist? Auk 103:216-219.
- Rotenberry, J.T., R.J. Cooper, J.M. Wunderle, and K.G. Smith. 1993. When and how are populations limited: the roles of insect outbreaks, fire, and other natural perturbations. In press in T.E. Martin and D. Finch (eds.). Ecology and management of neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press.
- Rotenberry, J.T., and J.A. Wiens. 1991. Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. Ecology 72:1325-1335.
- Scott, J.M., S. Mountspring, F.L. Ramsey, and C.B. Kepler. 1986. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. Stud. Avian Biol. 6:1-431.
- Sealy, S. G. 1979. Extralimital nesting of bay-breasted warblers: response to forest tent caterpillars? Auk 96:600-603.
- Sherry, R.T., and R.W. Holmes. 1992. Where and how are populations of neotropical landbirds limited: breeding, passage, or wintering habitats. This volume.
- Shugart, H.H., and D.C. West. 1981. Long-term dynamics of forest ecosystems. Amer. Sci. 69:647-652.
- Shukla, J., C. Nobre, and P. Sellers. 1990. Amazon deforestation and climate change. Science 247:1322-1325.
- Smith, H. R. 1985. Wildlife and the gypsy moth. Wildl. Soc. Bull. 13:166-174.
- Smith, K.G. 1982. Drought-induced changes in avian community structure along a montane sere. Ecology 63:952-961.
- Smith, K. G., and D. R. Petit. 1988. Breeding birds and forestry practices in the Ozarks: Past, present, and future relationships. Bird Conserv. 3:23-49.
- Sousa, W.P. 1984. The role of disturbance in natural communities. Ann. Rev. Ecol. Syst. 353-391.
- Stoddard, H. L., Sr. 1962. Use of fire in pine forests and game lands of the Deep Southeast. Tall Timbers Fire Ecol. Conf. 1:31-42.
- Taylor, C. M. and W. E. Taylor. 1979. Birds of upland openings. Pp. 189-197 in R. M. DeGraaf (tech. coord.). Proceedings of the workshop on management of northcentral and northeastern forests for nongame birds. U.S.D.A. For. Ser. Gen. Tech. Rep. NC-51.
- Terborgh, J.W., and J.R. Faaborg. 1980. Factors affecting the distribution and abundance of North American migrants in the eastern Caribbean region. Pp. 145-155 in A. Keast and E.S. Morton (eds.). Migrant birds in the neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C.
- Thurber, D. K. 1992. Impacts of a gypsy moth outbreak on bird habitats and populations. Ph.D. Dissertation, West Virginia University, Morgantown.
- Turner, M.G. (ed.). 1987. Landscape heterogeneity and disturbance. Springer-Verlag, Berlin.
- Urban, D.L., R.V. O'Neill, and H.H. Shugart. 1987. Landscape ecology. Bioscience 37:119-127.
- Van Lear, D. H., and T. A. Waldrop. 1989. History, uses and effects of fire in the Appalachians. U.S.D.A. For. Ser. Gen. Tech. Rep. SE-54.
- Wade, D. D., and J. Lundsford. 1990. Fire as a forest management tool: prescribed burning in the southern United States. Unasylva 41:28-38.
- Waide, R.B. 1991. The effect of Hurricane Hugo on bird populations in the Luquillo Experimental Forest, Puerto Rico. Biotropica 23(4a):475-480.
- Walkinshaw, L.H. 1983. Kirtland's Warbler. Bull. Cranbrook Inst. Sci. 58:1-207.
- Wauer, R.H., and J.M. Wunderle. 1992. The effects of Hurricane Hugo on bird populations on St. Croix, U.S. Virgin Islands. Wilson Bull., in press.
- West, N.E. 1979. Basic synecological relationships of sagebrush-dominated lands in the Great Basin and the Colorado Plateau. Pp. 33-41 in The sagebrush ecosystem: a symposium. Utah State University, College of Natural Resources, Logan, Utah.

- Wright, H. A., and A. W. Bailey. 1982. Fire Ecology. John Wiley & Sons. New York. 501pp.
- Wunderle, J.M. 1990. The effects of Hurricane hugo on bird populations in a Puerto Rican rainforest. Abstract, Wilson Ornithological Society meeting, Norton, Massachusetts.
- Wunderle, J.M., D.J. Lodge, and R.B. Waide. 1992. Short-term effects of Hurricane Gilbert on terrestrial bird populations on Jamaica. Auk 109:148-166.
- Wunderle, J.M., and R.B. Waide. 1992. Distribution of overwintering nearctic migrants in the Bahamas and Greater Antilles. Submitted to World Wildlife Fund-US.
- Zach, R., and J. B. Falls. 1975. Response of the ovenbird (Aves: Parulidae) to an outbreak of the spruce budworm. Can. J. Zool. 53:1669-1672.